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Ecology and life history predict avian nest success in the global tropics

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Nest predation rates critically influence avian biodiversity and evolution. In the north temperate zone, increased nest failure along edges of forest fragments is hypothesized to play a major role in the disappearance of bird species from disturbed landscapes. However, we lack comprehensive syntheses from tropical latitudes, where biodiversity is highest and increasingly threatened by habitat fragmentation and disturbance. We assembled data from five decades of field studies across the global tropics (1,112 populations of 661 species) and used phylogenetic models to evaluate proposed predictors of nest success. We found significant effects of several traits, including adult body mass and nest architecture. Contrary to results from many temperate locations, anthropogenic habitat disruption did not consistently reduce nest success; in fact, raw nest success rates were lower in large tracts of primary forest than in disturbed or fragmented landscapes. Follow-up analyses within species, using a subset of 76 species for which we had estimates of nest survival in habitats with different levels of disruption, confirmed that neither disturbance nor fragmentation significantly influenced nest success. These results suggest that nest predation alone cannot explain observed declines in avian biodiversity in tropical forest fragments, raising new questions about the demographic processes that drive extinction in the tropics.

forest fragmentation | tropical biology | reproductive success | nest survival | avian demography

Significance

Reproductive success is a crucial component of avian demography and life history. Elevated nest predation in forest fragments has been invoked to explain the disappearance of some bird populations from disturbed habitats worldwide, but previous analyses have been biased toward the north temperate zone. Here, we address that gap by synthesizing 50 y of data from the global tropics. We evaluated the importance of anthropogenic habitat disruption on nesting success of tropical land birds, controlling for phylogeny and nesting biology. Surprisingly, we found that neither disturbance nor forest fragmentation reduced nest survival. These results suggest that demographic processes other than nest predation—including limited dispersal into fragments—may be responsible for ongoing declines in avian biodiversity in fragmented tropical forest.

Reproductive success crucially affects the evolution of life histories and the ecology of plant and animal communities (1). In birds, nest predation is the primary cause of reproductive failure and is an important source of variation in fitness, influencing population demography as well as the evolution of reproductive traits (2–5). Nest survival rates are influenced by behavioral and life history traits (6–8), but also by biogeographic and ecological factors that structure predator assemblages, including anthropogenic habitat fragmentation and disturbance (9–11). Many studies in the temperate zone have suggested that rates of nest failure increase in disturbed and fragmented landscapes, possibly because habitat edges provide opportunities for nest predators and brood parasites to access remaining habitat (12, 13) (but see refs. 14 and 15). Elevated rates of nest predation have similarly been invoked to explain ongoing local extinctions of bird species from tropical forest fragments (16–18), despite indications that the temperate zone paradigm may not accurately represent prevailing dynamics in tropical forest (19–21). The effects of fragmentation on tropical nest survival are severely understudied, and the mechanisms driving observed population declines remain poorly understood (22). Understanding how fragmentation affects nest survival is of urgent conservation importance, as tropical landscapes harbor the majority of global avian biodiversity and are increasingly threatened by anthropogenic habitat disruption (23).

Although field ornithologists have studied the nesting biology of tropical birds for decades, most of this vast literature has never been systematically assembled. Foundational studies of avian biogeography relied on comparisons between single sites in the temperate zone and the tropics to make inferences about latitudinal trends in breeding biology (2, 24, 25). Although recent reviews of global nest survival rates have included some of the available literature from tropical latitudes (7, 8, 26), these datasets have been heavily biased toward the north temperate zone. Hundreds of studies by tropical authors, especially those published in languages other than English, have never been compiled and synthesized (27). As a result, we have lacked the comprehensive data and statistical power needed to understand how tropical nest survival is influenced by the combined effects of behavior, biogeography, and anthropogenic habitat disruption.

Here, we assemble the largest dataset to date on nest survival rate (and its inverse, nest predation rate) in tropical and subtropical land birds, including 1,112 populations of 661

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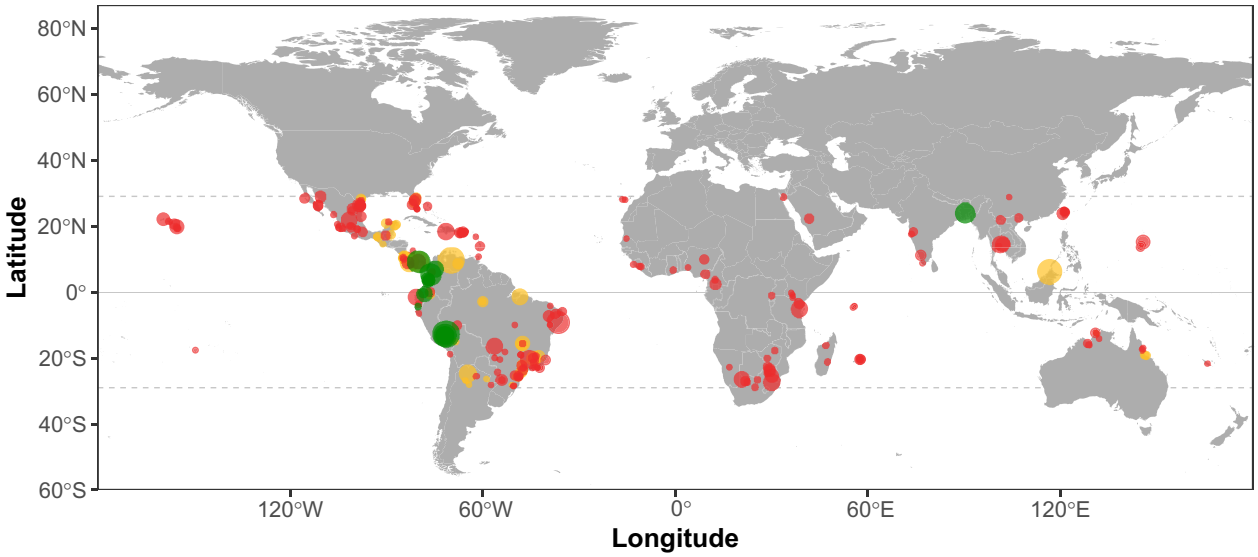

Fig. 1. Distribution of study sites (N = 253) across the global tropics and subtropics. Point size reflects the number of populations monitored at each site (range = 1 to 58). Sites are colored according to whether data were 1) included in a previous review of nest survival rates (yellow, N = 239 populations); 2) published but not included in previous reviews (red, N = 602 populations); or 3) new data from the authors' fieldwork (green, N = 271 populations). Dashed lines at 29°N and 29°S denote limits of review coverage.

species. This dataset is composed of published studies that were not included in past meta-analyses (N = 285 studies, 602 populations), a smaller number of published studies that were included in previous analyses (N = 83 studies, 239 populations), and new data from 271 populations from our own long-term field sites across the global tropics (Fig. 1).

We used phylogenetic mixed models to simultaneously evaluate several variables that have previously been proposed to influence nest survival rates, including behavioral and life-history traits (body mass, coloniality, nest architecture, nest placement, and parental care system); biogeographic factors (latitude, elevation, and island living); and ecological factors (habitat type and degree of anthropogenic disruption). Finally, we investigated the possibility that fragmentation and disturbance might have different effects on nest survival in forest and nonforest habitats since the microclimatic gradient between fragmented and unfragmented conditions is greater in tropical forest (28). Hypotheses and proposed mechanisms are summarized in Table 1.

Results

Nest Survival Varies with Location and Phylogeny. Our final dataset comprised 1,112 populations of 661 species distributed across 253 tropical and subtropical sites. Of these, 850 populations provided daily nest survival rate (DSR) estimates (from 540 species in 82 families, monitored at 215 sites) and 646 populations provided daily nest predation rate (DPR) estimates (from 464 species in 72 families, monitored at 151 sites; Fig. 2, *SI Appendix*, Table S1 and Fig. S1 and Dataset S1). As DSR (the rate at which nests survive all sources of mortality, including weather, desertion, and predation) and DPR (the rate at which nests fail due to predation alone) are inversely correlated but not synonymous, we conducted separate analyses using phylogenetic mixed models on the two datasets (*SI Appendix*, Tables S2–S4). Among populations for which both DSR and DPR estimates were available (N = 558), predation averaged 83% (±0.08%) of daily mortality. DPR analyses largely confirmed and recapitulated DSR results (Fig. 3 *A* and *B*). Instances of divergence are highlighted in the main text (full results are in *SI Appendix*, Table S2).

Daily nest survival estimates ranged from 0.708 (*Aplopelia larvata*) to 1.00 (hornbills, Bucerotidae), with an overall mean DSR of 0.948 (±SE = 0.001). Compounded over species' nesting periods, observed DSRs translate into cumulative nest survival rates ranging from <0.1% to nearly 100%, encompassing the full range observed in temperate populations. Of the families for which ≥10 DSR estimates were available, mean nest survival was highest in the parrots (Psittacidae; DSR range = 0.97 to 0.99, N = 30 populations of 22 species), and lowest in the bulbuls (Pycnonotidae; DSR range = 0.775 to 0.995, N = 16 populations of 12 species) (Fig. 2*B* and *SI Appendix*, Fig. S2).

Overall, phylogeny accounted for ~30% of the variance in DSR, indicating that closely related species have similar nest survival rates (Fig. 2*B*). This estimate comes from a model with no fixed effects (with phylogeny, site, and repeated measures as random effects), indicating that similarity between related species results from macroevolutionary constraints on life history (e.g., body size) and behavioral (e.g., nesting preferences) traits, as well as underlying genetic constraints. Within species, however, DSR was not consistently repeatable across different populations, with species-level repeatability accounting for only ~9% of the variance in DSR. Across seven populations of red-rumped caciques (*Cacicus haemorrhous*), for example, DSR ranged from 0.91 to 0.99 (50). Consistent with this pattern, study location accounted for a large proportion of the variance in DSR (~32%), indicating that local ecological factors influence rates of nest success across species. We recovered similar estimates of the variance explained by study location, phylogeny, and species identity when we estimated these terms from a subset of the data including only species with nest survival estimates from multiple study locations (N = 393 populations of 126 species at 118 sites; I^2 phylogeny = 21%, I^2 repeated = 15%, I^2 site = 29%).

Effects of Life History, Behavior, and Biogeography. We standardized and centered all predictors of nest success (Table 1) to estimate the effect of each variable as a slope. We report the slope of each predictor from a global model (β_{global}), which included all ten variables (Fig. 3), and we highlight cases where the slope of each predictor differed from the global model when modeled

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Table 1. Hypothesized predictors of nest survival rates for tropical birds

Predictor	Levels	Predicted relative effect on DSR	Hypothesized mechanism	Evidence for effect	Evidence against effect
Behavior and life history					
Nest architecture	Open, Enclosed, Cavity	Cavity > Enclosed > Open	More physically enclosed nests less accessible or detectable	(8, 18, 29)	(30–32)
Nest placement	Ground, Vegetation, Artificial	Artificial > Vegetation > Ground	Accessibility by predators (ground nests most accessible)	(2, 33)	(6, 34, 35)
Parental care	Female Only, Pair, Group	Group > Pair > Female Only	Increased nest defense with number of caregivers	(36)	(34)
Coloniality	Solitary, Colonial	Colonial > Solitary	Collaborative nest defense in colonies, or placement of colonies in inaccessible sites	(37, 38)	(39)
Body mass	Continuous	Large body mass > Small body mass	Increased nest defense with body mass, or fewer predators able to swallow large eggs	(7, 40)	
Biogeography and ecology					
Latitude	Continuous	Higher latitude > Lower latitude	Increased predator diversity or abundance at lower latitudes	(8, 24, 25, 41)	(26, 32)
Elevation	Continuous	Higher elevation > Lower elevation	Reduced predator diversity or abundance at higher elevations	(11, 24, 25)	
Island living	Mainland, Island	Island > Continental	Reduced predator diversity or abundance on islands	(42, 43)	(44, 45)
Habitat type	Forest, Nonforest	Nonforest > Forest	Greater predator diversity or abundance in more complex habitats	(24, 25, 46)	(6, 29)
Habitat disruption	Primary, Disturbed, Fragmented	Primary > Disturbed > Fragmented	Influx of predators into fragments from matrix, or decreased habitat quality with greater disruption	(17, 18, 47)	(20, 25, 31, 48)
Disruption × habitat type	Interaction	Effect of fragmentation is greater in forest than nonforest	Fragmentation alters microhabitat more in forest than in nonforest	(19, 28, 49)	

independently of the others ($\beta_{independent}$). Parameter estimates from both the global and independent models are reported in *SI Appendix*, Table S2.

Controlling for phylogeny and study location, nest architecture emerged as the strongest predictor of DSR (β_{global} = 0.011, P_{MCMC} = <0.001; Fig. 3 and *SI Appendix*, Table S2), with both cavity nests and enclosed nests (domed, roofed, or pouched nests) experiencing higher survival rates than open-cup nests (DSR for cavity nests = 0.972; enclosed nests = 0.953; open-cup nests = 0.943; *SI Appendix*, Fig. S3*A*). Among cavity nests, nests in human-provided nest boxes experienced higher survival rates than those in natural cavities (*SI Appendix*, Fig. S3*B*). Adult body mass was also significantly positively associated with nest survival (β_{global} = 0.003, P_{MCMC} = 0.024; Fig. 3 and *SI Appendix*, Fig. S4). Parental care system (ordered as female-only < pair < cooperative) did not affect DSR.

Colonial nesting species showed higher DSRs than noncolonial species, but the effect was significant only when modeled independently of other fixed predictors (β_{global} = 0.010, P_{MCMC} = 0.086; $\beta_{independent}$ = 0.016, P_{MCMC} = 0.002; Fig. 3). Post hoc investigation of these results revealed that the difference between the global and independent models was likely due to uneven sampling: Many of the 19 colonially nesting species in the dataset were from a small number of families (including Corvidae and Psittacidae), and the body masses of these species were, on average, three times heavier than the solitary nesting species in our sample (mean = 165 g and 52 g, respectively). Greater representation of small-bodied colonial species would be necessary to ascertain whether there is a protective effect of colonial nesting independent of body mass.

Nest placement was significantly associated with DSR only when modeled independently of other predictors, with higher survival associated with nesting on artificial or inaccessible substrates (β_{global} = 0.005, P_{MCMC} = 0.072; $\beta_{independent}$ = 0.007, P_{MCMC} = 0.014; Fig. 3*A* and *SI Appendix*, Fig. S5). In the DPR dataset, however, artificial or inaccessible nest placement was a significant predictor of predation rate even when other effects were included (Fig. 3 and *SI Appendix*, Table S2). There was no difference in survival or predation rates between nests built on the ground or in aboveground vegetation (*SI Appendix*, Fig. S5).

None of the biogeographic variables tested (latitude, elevation, island location, or habitat type) significantly predicted DSR or DPR (Fig. 3 and *SI Appendix*, Table S2). Although the apparent effect of island-living on DSR was positive and relatively strong (island mean ± SE = 0.959 ± 0.002, N = 113; mainland mean ± SE = 0.947 ± 0.001, N = 859; *SI Appendix*, Fig. S6), the CI around the slope estimate was wide (β_{global} = 0.005, P_{MCMC} = 0.144; Fig. 3). Island-living species had significantly higher DSR

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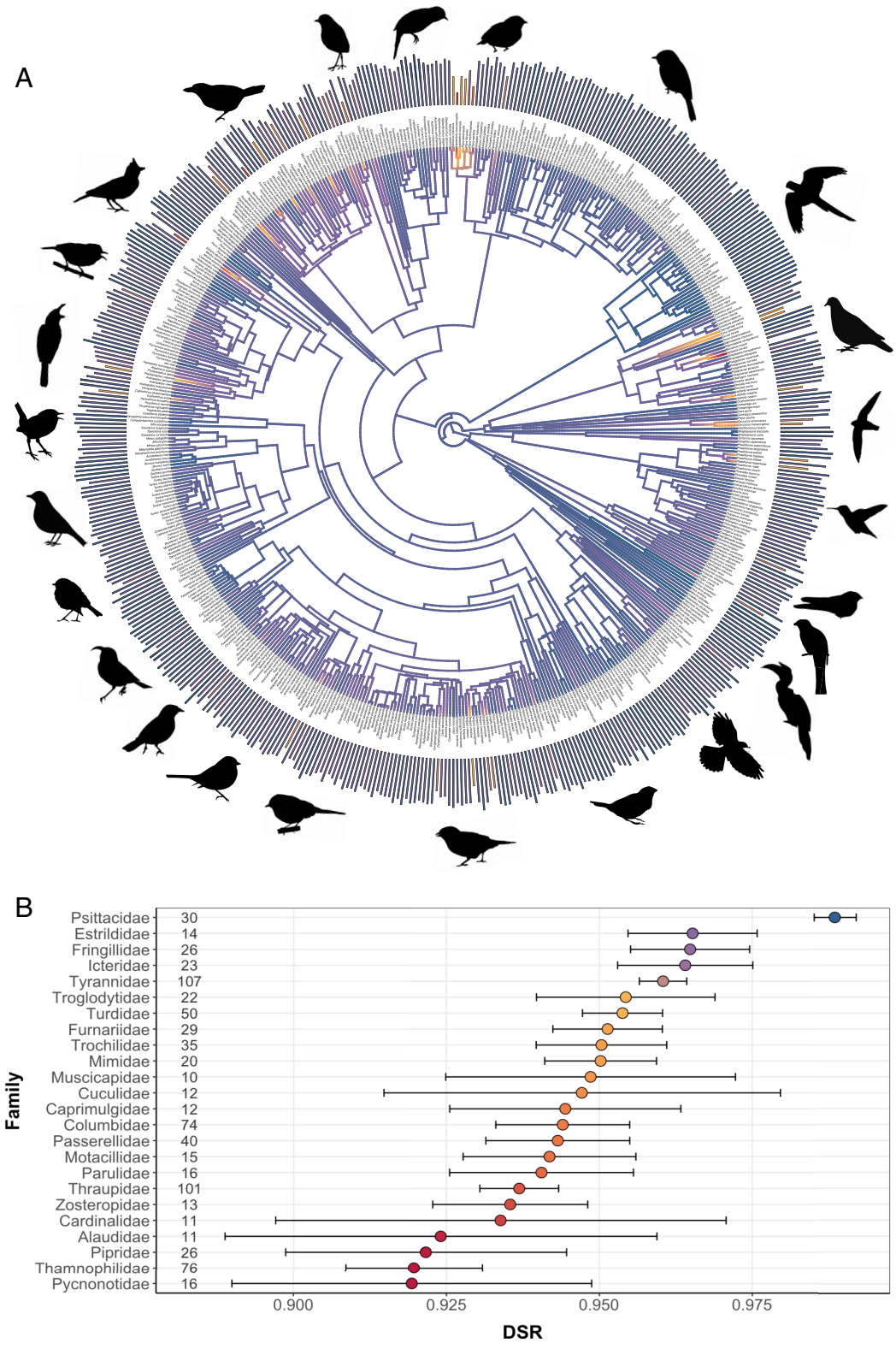

Fig. 2. (*A*) DSRs for nests of 540 species of tropical and subtropical birds arranged according to phylogeny. For each species, average DSR is represented by both color and line lengths at branch tips, ranging from 0.71 to 1.00. Red/yellow = low DSR, purple = intermediate, blue = high. Details and image sources in Dataset S2. (*B*) Mean DSR of nests by family for 24 avian families for which 10 or more DSR estimates were available from the tropics. Error bars represent 95% CI. Number of DSR estimates (independent samples) from each family is given along the *y* axis.

than mainland species only when modeled without the effects of site and phylogeny ($P_{MCMC} = 0.014$). Therefore, the difference between the phylogenetically controlled model and the raw data may reflect taxonomic sampling biases in our dataset (e.g., a third of island species sampled are from two families, Columbidae and Fringillidae), such that phylogeny and site account for a substantial amount of the observed differential nest success on islands.

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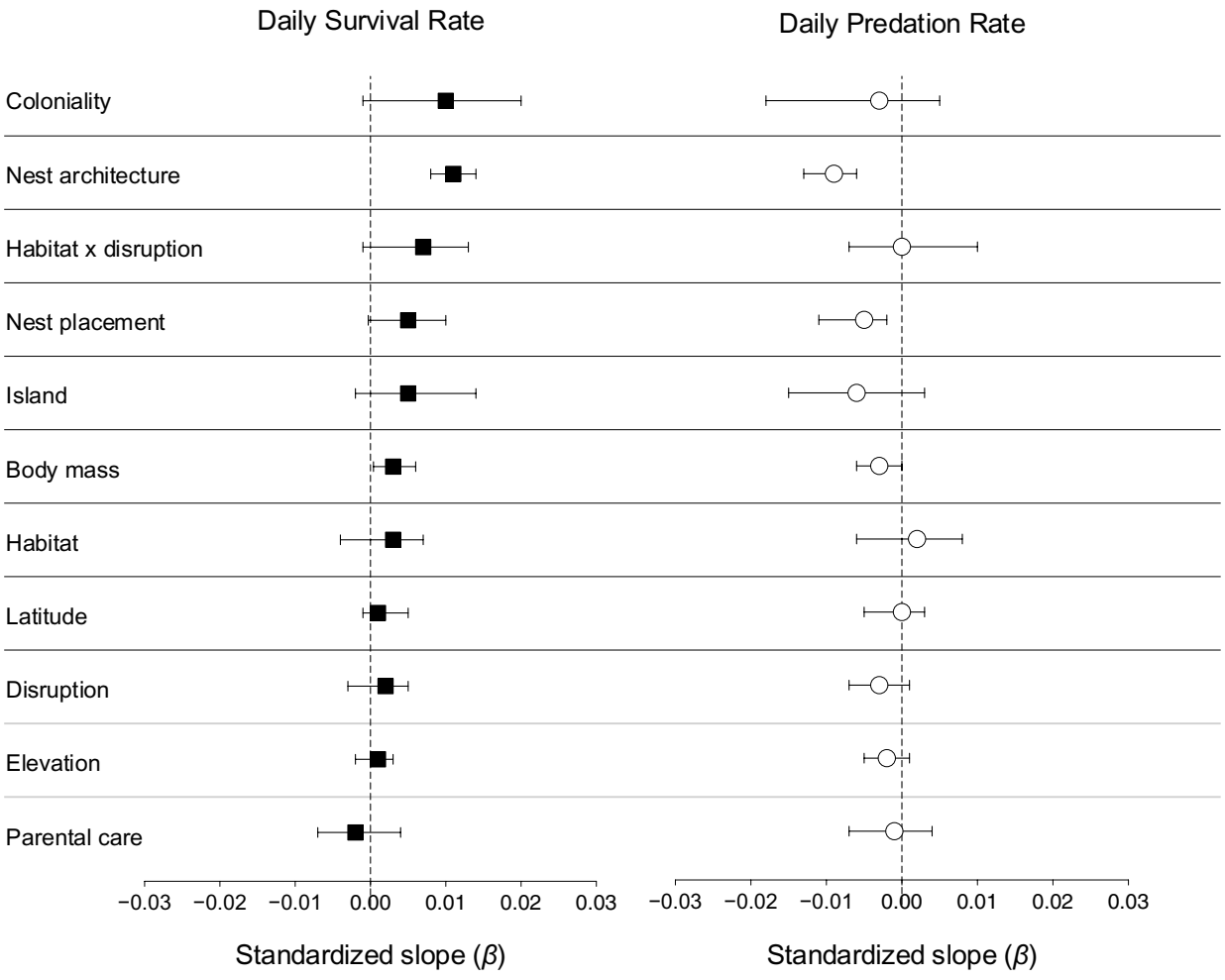

Fig. 3. Standardized slope estimates (ß) ±95% credible intervals for the effect of each predictor on DSR (*Left*) and DPR (*Right*). Black squares denote estimates from the DSR global model (including all fixed and random effects); white circles denote estimates from the DPR global model (including all fixed and random effects). Sample sizes: DSR global model N = 846 populations of 538 species; DPR global model N = 640 populations of 458 species.

Habitat Disturbance and Fragmentation Do Not Reduce Tropical Nest Survival. We examined the effects of anthropogenic habitat disruption on reproductive success in forest and nonforest habitats. We categorized disruption as an ordinal factor with three levels: 1) primary (≥10,000 ha with little selective logging or anthropogenic disruption), 2) disturbed (7,000 to 10,000 ha patches of secondary and/or disturbed habitat), or 3) fragmented (<7,000 ha patches that were isolated from similar habitat, subject to varying levels of disturbance; see *Methods*). Contrary to predictions, anthropogenic disruption did not significantly affect nest survival or nest predation rates in either type of habitat (DSR: $ß$ = 0.002, P_{MCMC} = 0.242; DPR: $ß$ = −0.003, P_{MCMC} = 0.478). In fact, in forested habitats, it had a positive effect, with nests in primary forests experiencing lower DSRs (and higher DPR) than those in disturbed or fragmented forests (Fig. 4 and *SI Appendix*, Table S5). In nonforested habitats, anthropogenic disruption did not affect DSR, though few data were available from primary nonforest habitats. The difference in response to disruption between forest and nonforest habitats was not statistically significant in a model with the interaction between habitat type and disruption as the only fixed predictors of DSR ($ß_{independent}$ = 0.006, P_{MCMC} = 0.076; Fig. 3*A* and *SI Appendix*, Table S2), nor when this interaction was included in the global model containing all predictors ($ß_{global}$ = 0.007, P_{MCMC} = 0.084; Fig. 3*A* and *SI Appendix*, Table S2).

For 76 species in our dataset, we were able to conduct within-species analyses of the effects of disruption on nest survival by comparing estimates from sites with different levels of disruption. Daily survival rate increased with disruption in half of these (N = 36 species) and decreased with disruption in the remainder (N = 40 species; *SI Appendix*, Fig. S7). Consequently, the average within-species response to disruption was close to zero (average slope across species = 0.003, PMCMC = 0.978; *SI Appendix*, Table S6). For daily predation rate, we had within-species data on the effects of disruption for 44 species. DPR increased with disruption in 12 of these species and decreased in 32 species (*SI Appendix*, Fig. S8). As with DSR, therefore, the average within-species response to disruption was not significant (average slope across species = −0.012, PMCMC = 0.386; *SI Appendix*, Table S6). These results concur with our cross-species analyses and are consistent with the conclusion that neither habitat disturbance nor fragmentation has a consistent effect on daily nest survival or predation rates.

One caveat to this result is that these species were, by definition, those that are able to persist and breed in both primary and disrupted forests, and therefore do not represent species which are found exclusively in large tracts of undisturbed habitat. We are not able to rule out the possibility that a set of species exists which are more vulnerable to nest predation in disrupted landscapes than in primary forests, and therefore do not persist in fragments long enough to be sampled. However, our phylogenetically controlled analyses do not suggest that nest predation would be likely to exert such a differential effect between species, instead indicating

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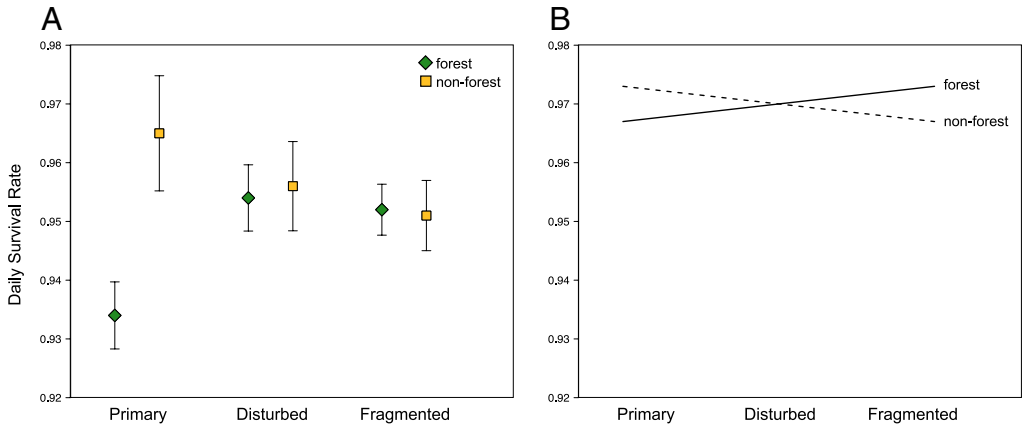

Fig. 4. (*A*) Raw DSR of nests by level of anthropogenic habitat disruption for birds nesting in tropical forest (green diamonds) and nonforest habitat (yellow squares). Error bars represent 95% CI. Sample sizes (number of populations) for forest nests: *N* = 208 (primary), 148 (disturbed), 295 (fragmented); nonforest nests: *N* = 16 (primary), 64 (disturbed), 117 (fragmented). (*B*) Model-predicted slopes for DSR across disruption categories for forest and nonforest species, derived from multivariate regression controlling for life-history and biogeographic variables (see text).

broadly similar DSR values both across closely related species and among species experiencing the same local ecological conditions (Fig. 2*A*). Moreover, this scenario would require one or more species-level variables to have a substantial effect on nest fates. This is not supported by our results, which instead suggest a limited predictive role for life-history traits beyond body size, nest architecture, and nest accessibility in determining survival rates in the tropics (Fig. 3).

Implications for Avian Demography and Diversity in Tropical Forests. Our results indicate that nest survival rates are not significantly higher in intact, primary tropical forest than in disturbed or fragmented sites; if anything, estimates tend to be lower. This is notable, given that our definition of primary forest was strict (≥10,000 ha with little to no logging, roads, or other human modifications) and included some of the largest remaining tracts of tropical forest in the world, including Manu National Park, Peru; Yasuní Biosphere Reserve, Ecuador; and Kinabalu National Park, Borneo. These sites are comparable in size to those included in several of the foundational studies conducted in temperate North America that originally proposed that nest survival decreases with habitat fragmentation [e.g., Great Smoky Mountains National Park, NC (51), northwest Wisconsin (12), and Chequamegan National Forest, WI (52)]. Although the differences in daily survival rate we find are small (1.9% lower in primary than fragmented forest), over the course of a typical 30-d nest cycle this difference translates into a 77% higher cumulative nest survival rate in fragmented than primary forest (12.9% in primary forest vs. 22.9% in fragmented sites).

Some earlier tropical naturalists, including Snow and Snow (48) and Skutch (24, 25) noted reduced abundance of nest predators in disrupted tropical forests and hypothesized that forest fragments might function as relatively predator-free refugia for nesting birds. However, this hypothesis has historically received relatively little attention, overshadowed by influential studies in the temperate zone that suggested decreased nest survival in forest fragments (12, 13). In the temperate zone, observed declines in nest success are typically attributed to generalist nest predators, particularly cowbirds (*Molothrus ater*) and small mammals, accessing forest fragments from the surrounding matrix (9, 15). This may not be the case in many tropical forests, in which dominant nest predator species, especially arboreal snakes, may be more abundant in intact habitats (11, 53–55). As increasing numbers of tropical studies identify predators at video-monitored nests, available evidence suggests that some key predator species, including some snakes, small mammals, and primates, are reluctant to approach habitat edges (20, 53) and exist at significantly lower densities in forest fragments (54) (but see ref. 56).

We emphasize that fragmentation of tropical forest is detrimental to avian biodiversity, associated with ongoing population declines, loss of species, and risk of eventual extinction (57–60). However, our results suggest that demographic processes other than nest predation may be primarily responsible for these declines. Although several plausible hypotheses exist (19, 21), one of the most promising is that many tropical insectivores, which tend to be sedentary and adapted to low light conditions in the forest understory, are less likely to disperse across areas of unfavorable habitat into forest remnants (16, 61, 62). Populations in fragments might therefore disappear due to small population sizes and stochastic events, leading to the extirpation of less vagile species that are not likely to recolonize fragments surrounded by deforested habitats (60, 63, 64). Alternatively, microclimatic differences between forest interiors and fragments, which are exposed to comparatively more light and are thought to be hotter and drier as a result, might exceed the physiological tolerance of understory species, potentially reducing foraging success or directly suppressing breeding activity (65–67) (but see ref. 68). However, these hypotheses are primarily relevant to understory forest birds, and the mechanisms by which fragmentation affects species in other habitat types and guilds deserve further study. Finally, it is important to note that many tropical species have multiple breeding attempts, smaller clutches, and prolonged periods of parental care relative to their temperate zone counterparts, so factors such as whether and how often individuals attempt breeding, as well as postfledging survival may be more important determinants of annual reproductive success and fitness than rates of nest loss (69). More data are needed on how fragmentation affects outcomes at stages of the reproductive cycle outside the nesting period.

Conclusions

We provide the largest synthesis to date of the literature on tropical avian nest survival, including over 200 studies that were not included in previous reviews (a Spanish translation of this paper is provided in *SI Appendix*). Our analysis finds a wide range of nest survival rates that overlaps with those documented in the temperate zone. Nest survival rates were affected by phylogeny, reproductive biology, and local ecology, indicating that nest success

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should not be treated solely as a characteristic of a species or of a site. We recovered several patterns that have been documented in smaller-scale meta-analyses, including positive effects of adult body mass and enclosed nest architecture (7, 8). Most surprisingly, we found nest survival rates to be similar in primary and disrupted tropical habitats, suggesting that—contrary to the temperate forest paradigm—bird nests in tropical forest fragments are not more vulnerable to nest predators (53, 54). This finding raises new questions about the processes that lead to population declines and local extinctions in fragmented tropical landscapes (58). Data on demographic factors beyond nest survival, including the number of breeding attempts, postfledging survival, dispersal success, and overall reproductive output (70), are critically needed to understand how habitat fragmentation and disturbance lead to biodiversity loss in tropical forests.

Methods

Data Collection from Published Literature. We used Google Scholar to systematically search the published literature on the reproductive biology of tropical and subtropical birds, using the terms "nest success OR breeding biology OR reproductive ecology OR Mayfield AND [name of geographic region]" or their Portuguese, Spanish, or French equivalents, which we repeated for 151 tropical and subtropical regions (*SI Appendix*, Table S1). We restricted the dataset to studies of altricial landbirds (excluding raptors) between latitude 29°N and 29°S. To ensure statistically valid comparisons, studies were required to include exposure-controlled DSRs or DPR (71). These two metrics of nest success tend to be inversely correlated since predation is typically the most important cause of nest failure. However, they can differ slightly since DPR is the daily rate at which nests are depredated, whereas DSR is the daily rate at which nests survive (accounting for other causes of nest failure, including weather, observer disturbance, or abandonment in addition to predation). We compiled data on both DSR and DPR; some studies included estimates of both, while other studies presented just one. In the main text, we focus on the DSR analyses (the larger dataset); here, we present results from both analyses.

Raw rates of nest success systematically underestimate failures (because some nests fail before they are ever found), so are statistically incompatible with exposure-controlled data (71). In our dataset, all studies included a statistical control for exposure such as the Mayfield method (71), MARK (72), or logistic exposure (73). Although methods have been proposed to enable post hoc extraction of comparable rates from raw success data (2, 24, 74), and have been used by some reviews (5, 7, 75), such manipulations are likely to introduce uncertainty (8, 76). We therefore included raw success data only when two conditions were met: 1) all nests were monitored from the beginning of the nesting cycle, and 2) 100% of the observed nests succeeded in producing fledglings, such that the daily survival rate was 1.0, and thus not susceptible to distortion introduced by proration ($N = 4$ studies).

We included all species-site combinations with a sample size of at least five known-fate nests, for which we could obtain either a DSR or DPR. We excluded all studies in which survival and predation rates were derived from fewer than five known fates, even if the total number of monitored nests was larger. For studies involving experimental manipulations or conservation management, we included only DSR or DPR estimates for control or unmanipulated nests. If separate estimates were given for the same species under multiple conditions of interest (e.g., levels of habitat disruption), we included them as separate samples as long as there was sufficient sample size in each.

Data Collection from New Field Data. Our dataset also included nest-monitoring data from the authors' long-term field sites (271 populations of 208 species). Fieldwork was carried out in Bangladesh (2008–2017) (77), Colombia (2014–2019) (78–81), Ecuador (2000–2014) (82), Panama (1996–2005) (5, 83), and Peru (2008–2014) (11). These data were not previously available for analysis because they were not the focal species of the original project; were collected from outside the original designed study area; were published in an aggregate form that precluded statistical analysis; or did not previously meet sample size requirements for a stand-alone publication on the species. Nest monitoring protocols broadly followed ref. 84. In all studies, field observers systematically searched study sites for active nests. Nests were encountered opportunistically and by following the movements of parent birds. Nests were monitored every 2 to 5 d until they were predated, abandoned, or succeeded in producing fledglings. Some nests were also continuously monitored using video camera traps and data loggers (11). DSRs and DPR were calculated following Mayfield (1961) (71), and SE following Johnson (1979) (85). Predation was inferred when nest contents disappeared more than 2 d before expected fledging age, when there were remains of eggs, nestlings, or parent birds present, or when directly confirmed via video monitoring.

Estimation of Daily Survival and Daily Predation Rate. DSRs and DPRs were derived from each paper in any of several ways, following Kubelka et al. (2018) (75): 1) calculated by the authors and stated in the paper as an exposure-controlled DSR or DPR; 2) calculated de novo from a given number of exposure days and the number of total failures (or for DPRs, the number of failures due to predation); 3) back-calculated by prorating a compounded survival rate by the given length (in days) of the nest period by which the DSR had been exponentiated; or 4) a combination of any of these methods. If the authors did not provide the nest period by which the DSR had originally been exponentiated, we used the average length of the species' nest period (without laying) from ref. 86 to prorate compounded survival rates. As typographical or arithmetical errors were common, we utilized multiple methods for each paper. We note that our method of back-calculating survival rates assumes that DSR are constant over the nesting cycle, which is also an assumption of the Mayfield method (71).

For studies that did not originally give DPRs, but provided Mayfield DSRs and enumerated causes of nest failure, we back-calculated exposure days from given DSRs and total failures and used that to calculate Mayfield DPRs and SE de novo. Nests that failed due to destruction by brood parasites or human activity were not considered predated for DPR calculations. We did not attempt to back-calculate exposure from DSRs that were estimated using MARK or logistic exposure methods, as both methods treat exposure time as a modifier for each individual nest, making it difficult to extract an aggregate value for the whole sample with comparable accuracy. For studies that provided non–Mayfield DSRs, we calculated de novo DPRs only if total exposure time (in days) was given in the original paper. The full dataset includes 972 DSR estimates and 698 DPR estimates from 1,112 independent populations (*SI Appendix*, Fig. S1), using the following methods to control for exposure time: traditional Mayfield methodology ($N = 857$) or a variation on the Mayfield method ($N = 27$); MARK ($N = 131$); logistic exposure ($N = 87$), Stanley (2004) (87) ($N = 4$), raw success ($N = 4$), or exposure-control method not described ($N = 2$).

To ensure independence of data, where multiple studies were based on the same data or samples were nested within those of other papers in the dataset, we used only the largest sample for statistical analysis. When a study presented DSRs or DPRs using multiple methods, we used the Mayfield value for statistical analysis, to minimize sources of variation across the dataset.

Assignment and Definition of Covariates. For each sample we assigned 10 covariates, corresponding to hypothesized predictors of nest predation (Table 1): five species-level behavioral and life-history characteristics that may affect nests' vulnerability to predation (nest architecture, nest placement, parental care, coloniality, and body size); and five site-level biogeographic and ecological characteristics that may affect predator communities (latitude, elevation, island living, habitat type, and level of anthropogenic disturbance). When possible, information on each covariate was extracted directly from the published study; if unclear or missing, this information was drawn from ref. 86 or other published literature. In some cases ($N = 176$), nests of a species were pooled across locations into a single sample. Where a majority of nests were found under one set of conditions, we assigned the pooled sample the covariates of the majority site. If there was no majority, variables that differed between sites were assigned "NA." Covariates were defined as follows:

Nest architecture (categorical, three categories). Nest architecture was classified as *open* (nests without a roof, including platforms, cup nests, and eggs laid directly on the ground); *enclosed* (nests with a constructed roof, including domes, pouches, and ovens); or *cavity* (nests built inside excavated or existing holes in trees, buildings, banks, and rock faces, including burrows, artificial nest boxes, and open stumps). Nests described as "semicavities" were included among cavity

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nests, as were instances of cups or enclosed nests constructed inside cavities. Differences in DSR between artificial nest boxes and natural cavity nests are shown in *SI Appendix*, Fig. S3*B*.

Nest placement (categorical, three categories). Nest placement was classified as *ground* (nests on the ground or eggs laid directly on the ground), *aboveground/vegetation* (nonground nests in natural vegetation, including those in nest boxes and built into sloped banks), and *artificial/exceptional* (nests in caves, on artificial structures, or in emergent vegetation). Although the "exceptional" label encompassed several placement types, each had a low sample size, and preliminary analyses indicated similar positive effects on DSR (*SI Appendix*, Fig. S5). When populations exhibited multiple placements (e.g., only some nests on artificial structures) and separate DSR and DPR estimates for each condition were not available, placement designation followed the plurality of nests.

Parental care system (categorical, three categories). Parental care system was classified as *female-only* (all nestling care provided by the female), *pair* (both male and female contribute to nestling care), and *cooperative* (auxiliary birds, including nonbreeding helpers or cobreeding adults, contribute to nestling care). Data derived from (in order of preference) 1) the source study, 2) ref. 86, and 3) ref. 88. When parental care information was not yet available in ref. 86, or when discrepancies existed between accounts, we contacted the authors of recent papers on the species for confirmation. Populations with variation in parental care were classified as cooperative if ≥10% of monitored nests were attended by three or more individuals (88).

Colonial nesting (binary, solitary/colonial). Populations were considered *colonial* if two or more nests were spatially clustered (in most cases <20 m apart), typically accompanied by collaborative nest defense (including vigilance and mobbing) and decreased territorial behavior toward nearby conspecifics. Most Columbidae were considered solitary rather than colonial, despite breeding in large aggregations, as most species defend exclusive territories within nesting groves.

Female body mass (continuous, g). Data were obtained from the CRC Handbook of Avian Body Masses (89) and from ref. 86 for species that were not included therein. Values used were (in order of preference) 1) mean female body mass (if sex-specific data were available) from the population geographically closest to the study site (if body mass data were available from multiple sites), or with the largest sample size (if populations were equidistant from the study site); 2) the midpoint of a range of body mass estimates given; and 3) the body mass of a closely related congener, if body mass data for a species were not available in either ref. 89 or ref. 86 (N = 23 of 661 species, 4%; in 20 of 23 cases, species were previously considered conspecific and absence of body mass data reflected recent taxonomic splits).

Latitude (continuous, decimal format). Study site latitude was obtained from (in order of preference) 1) the source study, 2) other publications from the same field site, or 3) attempting to reconcile published maps or descriptions of sites with Google Earth data. As source study coordinates were occasionally incorrect or contradicted those given in other papers, we used Google Earth to corroborate all study locations. If we could not satisfactorily locate a study site, or if DSRs and DPRs were aggregated from nests monitored at widely separated sites, we did not assign coordinates.

Elevation (continuous, m). Study site elevation was (in order of preference) 1) taken from the source study, 2) the average of elevation ranges or multiple elevations given in the source study, 3) obtained from another publication from the same site, 4) estimated using Google Earth, if site coordinates were known, or 5) left unassigned if the location could not be determined or sites differed widely in elevation.

Island living (binary, island/continental). Sites were considered *islands* if they were >10 km from the nearest mainland point. Nearshore estuarial islands and mangrove cays, often separated from mainland or adjacent islands by channels only a few m wide, were considered *continental*. Distances to mainland were measured using Google Earth. Extremely large islands (over 200,000 km^2) such as Madagascar and Borneo were considered continental for the purpose of this analysis.

Habitat (binary, forest/nonforest). Habitat definitions followed site descriptions in source studies whenever possible. *Forest* habitats encompassed both dry and humid forest, mangroves, restinga vegetation, remnant trees or recovering vegetation in previously forested areas cleared for pasture, as well as gardens and plantations with ornamental or exotic trees. *Nonforest* sites encompassed all those originally without a closed canopy of trees, including sites described in source studies as "marsh," "grassland," "prairie," "savannah," "savannah woodland," "brushland," "steppe," "desert," or "scrub." Two samples from highly urbanized areas with no remaining natural vegetation were also included among nonforest sites.

Habitat disruption (categorical, three categories). Sites were classified as *primary*, *disturbed*, or *fragmented*, according to habitat conditions. Disruption information was gathered from site descriptions and maps in source studies, other published descriptions of habitat composition and land-use histories, and, for recent studies, visual inspection of study sites using Google Earth. *Primary* sites were contiguous blocks of at least 10,000 ha, with minimal anthropogenic disruption and relatively intact apex predator communities. Some sites designated primary encompassed some secondary forest (e.g., Soberanía National Park, Panama, and Khao Yai National Park, Thailand), but were >75% intact, and have been considered reflective of unperturbed conditions in previous literature. Some were accessible by a single lightly trafficked road. Within otherwise primary habitat, samples were nonetheless designated "disturbed" under either of two conditions: 1) if sites were located within 1 km of a major habitat edge (increased tree mortality has been observed up to 1 km from newly cleared edges in tropical forest (90); or 2) if species nested exclusively in disturbed areas and secondary growth within the study site, including natural clearings, roadsides, and eroded streambanks (verified by contacting authors of source studies). *Disturbed* sites were smaller blocks of contiguous habitat (connected area 7,000 to 10,000 ha) which met any of the following conditions: 1) comprising mostly secondary vegetation, 2) impacted by livestock grazing, selective logging, or fires within the last 10 y, 3) supporting intensive human presence for hunting or recreation, 4) located within 1 km of major edges, 5) connected to other habitat only by narrow corridors, or 6) located near structures and roads within larger habitat blocks. *Fragmented* sites were patches smaller than 7,000 ha, fully isolated from similar habitat by cleared, developed, or agricultural areas or roads. Remnant and roadside vegetation, cropland, campuses, parks, gardens, villages, and plantations were all considered fragmented habitat. Sites designated "fragmented" were often also subject to disruption (such as livestock grazing, hunting, logging, or firewood collection). Islands <7,000 ha, regardless of habitat condition, were also considered fragments (91). This approach binned sites into categories rather than treating habitat area as a continuous numerical predictor, which was necessary because precise estimates of remaining contiguous habitat area were not available from every study site. Our criteria allowed us to easily categorize most sites as primary, disturbed, or fragmented, including those from older studies; however, obtaining more precise values for areas of contiguous habitat would likely require use of GIS technology or accessing historical satellite data, which were beyond the scope of the current study.

Statistical Analyses.

Ordering of variables. We ordered categorical variables according to the direction predicted by prior research (Table 1). We treated predictors with three levels (nest architecture, nest placement, parental care system, disruption) as ordered numeric variables with the first level scored as −1, the second scored as 0, and the third level scored as +1. For predictors with two levels (coloniality, island living, habitat), the first level was scored as 0 and the second level was scored as 1. All continuous predictors (log body mass, absolute latitude, log elevation) were standardized (mean = 0, SD = 1). This approach allowed us to estimate the effect of each variable on DSR or DPR as a slope, rather than estimating differences between each level of the categorical variable and the reference level. This facilitated the interpretation of the parameter estimates from our statistical models (92). For example, in our global model of DSR or DPR (see below), the intercept represents the mean DSR or DPR when all effects are zero. The slope estimates are the effect of each parameter on DSR or DPR from this mean.

Nonindependence. Three sources of nonindependence in our data are i) multiple observations from the same site, ii) multiple observations from the same species (species ID), and iii) and phylogenetic effects. We included three random terms in our statistical models to account for these sources of nonindependence. Note that random effects are not nested since different species occur on the same site and different sites host the same species.

Multicollinearity among predictors. To investigate whether our predictors are correlated with one another, which can affect the precision with which model parameters are estimated, we calculated variance inflation factors (VIFs) using the metafor R package. For both DSR and DPR, all VIFs were <1.3 (*SI Appendix*, Table S7). Given that most of the studies in our dataset used Mayfield estimates,

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we did not expect estimation methodology to affect our results. Consistent with that expectation, mean values and SE of DSR and DPR were similar between methodologies, and inclusion of estimation method as an additional random effect in our global statistical models (described below) accounted for 0% of the variance.

Measurement error. Most DSR/DPR estimates in our sample (850 DSR/646 DPR) were reported with measurement error, typically the SE. We incorporated this uncertainty into our statistical models by including the inverse sampling variance (calculated from the SE associated with each DSR/DPR) as an additional term in each of our statistical models. Several DSR/DPR estimates were missing SE, which reduced our sample sizes (*SI Appendix*, Fig. S1). The decision to account for measurement uncertainty in our models meant that we had to treat DSR and DPR as Gaussian variables (i.e., not transformed), although they are left and right skewed, respectively. To assess the sensitivity of our results to modeling skewed data, we reran our models on transformed response variables.

Model fitting. We used the MCMCglmm R package (93, 94) to fit our statistical models. MCMCglmm estimates parameters in a Bayesian framework by iterating through parameter space. This iterative process allowed us to account for phylogenetic uncertainty by sequentially updating the tree used to estimate phylogenetic effects in each model every 1,000 iterations. In total, we used 1,300 phylogenies downloaded from birdtree.org (95), each iterated 1,000 times, to account for nonindependence between species due to shared evolutionary history in our statistical models. We saved the last iteration from each phylogeny and discarded the first 300 iterations as a burn-in period, giving a posterior distribution of 1,000 iterations (each from a different phylogeny). We used inverse Wishart priors (variance = 1 and belief parameter = 0.002) for random effects. Model convergence was assessed by examining autocorrelation between iterations, by evaluating chain mixing through traces of posterior distributions, and by comparing within- and between-chain variance. Parameter estimates are the posterior modes and the 95% CI of posterior distributions. Significance is assessed by whether the 95% CI includes zero and we report P_{MCMC} values from the MCMCglmm models in the main text.

We assessed the sensitivity of our results to Bayesian methods by fitting the same models in the metafor R package (96) using restricted maximum likelihood for parameter estimation. It was not possible to account for phylogenetic uncertainty in these models, so we chose a random phylogeny from our sample of 1,300 phylogenies. The same phylogeny was used in all models. All parameter estimates from the two approaches are presented in *SI Appendix*, Table S2 to allow comparison.

We created two identical R scripts to analyze the DSR and DPR datasets (supplementary information: *DSR_code.R* and *DPR_code.R*). Our statistical analyses are organized into four parts in each R script (overview provided in *SI Appendix*, Table S3, including the names of each model in the R code). Sample sizes for each model are reported in *SI Appendix*, Table S4.

PART 1: Intercept-only models.

A. We calculated the percentage of variance in DSR/DPR explained by phylogeny (I^2 phylogeny), multiple observations per species (I^2 repeated) and site (I^2 site) by dividing each of these variance components by total heterogeneity (I^2 total, which includes sampling variance), following Nakagawa & Santos (2012) (97). Variance components were estimated by fitting an intercept-only model with DSR/DPR as the response variable and phylogeny, species ID, and site included as random effects. To visualize DPR/DSR across the phylogeny (Fig. 2*A*), we estimated ancestral states using maximum likelihood in the phytools R package (98).
B. For 158 of 661 species, there were multiple DSR observations per species, and for 126 of these species, there were multiple observations per site (DPR values: 101 species with multiple DPR observations and 87 species with multiple observations per site). To ensure that our I^2 estimates were not biased by most species and sites having a single DSR/DPR observation, we reran the model described above but limited to species with multiple observations from multiple sites.

PART 2: Predictors of DSR/DPR.

A. To test the effect of different predictors on DSR/DPR, we began by constructing a global model with DSR/DPR as the response variable and all 10 transformed/ordered predictors as fixed effects. We chose not to use a model selection approach because the list of candidate models, given 10 variables, was computationally unfeasible and could have resulted in incorrect identification of apparently significant predictors (Type II error). In addition, a model selection approach was not appropriate for the questions being asked since we were interested in the effect of all the predictors included in our model regardless of significance. We also chose not to include interactions between predictors other than habitat type and disruption (see below), as we did not have any a priori reasons for doing so. We chose not to include quadratic terms for elevation and latitude, although this approach has been adopted in some previous studies (7, 26). We detected no evidence of a quadratic effect (DSR: elevation^2 = 0.052, 95% CI = −0.032 to 0.125; DPR: elevation^2 = −0.001, 95% CI = −0.098 to 0.044; *Mod3.Elev2.SiPhRM* in the R code). Quadratic effects of latitude were not applicable because we examined absolute latitude. These models included random terms for phylogeny, multiple observations per species and site.
B. To assess the sensitivity of our results to modeling DSR and DPR as skewed response variables, we reran our global models after transforming these. We used the arcsine square root transform for DSR and the log transform for DPR, which both produced normally distributed data. This increased our sample size for each model (now unweighted) since we previously excluded DSR/DPR estimates without SE (*SI Appendix*, Table S4). The parameter estimates from this model are reported in *SI Appendix*, Table S2 to facilitate contrasts with the parameter estimates from the untransformed models. We also tested for an interaction between transformed habitat and transformed disruption by including this interaction in the global model with arcsine square root transform DSR and log transform DPR as response variables.
C. To examine the effect of each predictor variable in isolation, we tested each on DSR/DPR separately by constructing 10 further models. In each model, DSR/DPR was the response variable with each transformed predictor as the only fixed effect. This allowed us to evaluate whether parameter estimates (including error estimates) from our global model were affected by the inclusion of other fixed effects. The results for each parameter from the global model and separate models are reported together in *SI Appendix*, Table S2 to facilitate this comparison. These models included random terms for phylogeny, multiple observations per species and site.

PART 3: The interaction between habitat and disturbance.

A. To test whether the relationship between DSR/DPR and disturbance differed between forest and nonforest habitats, we extended our global model described above to include the interaction between transformed habitat and transformed disruption.
B. We also modeled the interaction between transformed habitat, transformed disruption, independently of other fixed effects, due to potential correlations between predictors.

PART 4: Within-species analyses. We used random intercept and slope models to estimate the average within-species response to disruption. This approach allows each species to have a different intercept and slope for the relationship between DSR/DPR and disturbance, which controls for nonindependence arising due to multiple observations from the same species. Our response variable was DSR/DPR and disruption was the fixed effect. Two unstructured covariance matrices were specified as random effects: one for the interaction between species identity and disruption, which allows intercepts and slopes to vary between species, and one for the interaction between phylogeny and disruption to account for similarity between species in intercepts and slopes that arises from shared evolutionary history. We had within-species data on DSR for 76 species and within-species data on DPR for 44 species.

Data, Materials, and Software Availability. The data set and R code reported in these analyses are available as supplementary data files (Data Set S01, Data Set S02, DSR_Code_R, DPR_Code_R). A Spanish translation of this paper is available in the *SI Appendix*. All other data are included in the article and/or supporting information.

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