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Forest losses predict bird extinctions in eastern North America

(endemism/deforestation/historical ecology/species–area relationships)

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ABSTRACT **Claims that there will be a massive loss of species as tropical forests are cleared are based on the relationship between habitat area and the number of species. Few studies calibrate extinction with habitat reduction. Critics raise doubts about this calibration, noting that there has been extensive clearing of the eastern North American forest, yet only 4 of its ≈200 bird species have gone extinct. We analyze the distribution of bird species and the timing and extent of forest loss. The forest losses were not concurrent across the region. Based on the maximum extent of forest losses, our calculations predict *fewer* extinctions than the number observed. At most, there are 28 species of birds restricted to the region. Only these species would be at risk even if all the forests were cleared. Far from providing comfort to those who argue that the current rapid rate of tropical deforestation might cause fewer extinctions than often claimed, our results suggest that the losses may be worse. In contrast to eastern North America, small regions of tropical forest often hold hundreds of endemic bird species.**

As forests or other habitats are destroyed, the remaining habitat may be too small to hold viable populations of all the species that require it (1). Consequently, extinction follows habitat reduction. The often unmistakable destruction of habitat is vital to arguments about the global loss of species (2). With important exceptions, the species losses themselves are hard to document. We can estimate only imprecisely the total number of species an area holds. Indeed, we have names for only a tiny fraction of the planet's species (3). Our confidence in predicting species loss from habitat reduction stems from the relationship between the number of well-known species an area holds and its size. Those who point to the extensive reductions in the forests of eastern North America during the nineteenth century (4, 5) challenge this confidence. Historically, few of the region's ≈200 terrestrial bird species have gone extinct. Birds are well-known and we cannot plead ignorance of their extinctions. Do these observations refute the predictions of the species–area calculations (6) and so call into question fears about massive loss of species on a global scale?

We review the history of deciduous and coastal plain coniferous forests in the eastern United States from European settlement to the present. Forest losses have been extensive, but they were not concurrent. In New England, for example, forests began to recover as deforestation—and many of the people who caused it—moved into the Ohio Valley. At the period of lowest forest cover, about half of the forest was gone. We also list the species of birds that became extinct and those that remain. Of the species found only in eastern North America, the species losses have been *higher* than we predict from forest losses. This region has surprisingly few range-restricted bird species, however, and most species could survive elsewhere as the forests were cleared. Many tropical forests are rich in such species and thus are likely to lose many of them following deforestation.

Pattern of Forest Clearing

Although agricultural fields and human-created grasslands occupied hundreds of square kilometers in some areas of the eastern forest biome before European settlement (7, 8), clearing probably was not extensive enough to cause the extinction of forest bird species. More extensive deforestation followed European settlement in the early 1600s. To assess the complex patterns of forest destruction after 1600, we divide the eastern forest into four regions (Fig. 1) and examine each on three spatial scales.

At the smallest spatial scale, we report forest cover for individual counties or townships. These may not be typical of the region as a whole, but they provide the temporal detail missing from regional summaries. At an intermediate scale, we report on individual states that are geographically typical of the region. At the largest scale, we compile summaries for each of the four regions. Estimates of forest cover at this largest scale can only be approximate, especially for the nineteenth century. Yet, if the estimates of forest cover generally do show similar patterns across all three scales—and if we understand the reasons when they do not—then we will have confidence in our final estimates of forest cover for the entire eastern forest.

During the eighteenth and nineteenth centuries, regions near the Atlantic Coast were almost completely cleared for agriculture, leaving only small patches of forest in the form of farm woodlots (18, 19). Foster (19) provides detailed data for Petersham County, Massachusetts, that are similar to estimates for the entire state in showing how quickly the forest was cleared. The pattern of forest loss was similar for Concord, Massachusetts (20), and Onondaga County, New York (21). In the early nineteenth century, much of the Ohio Valley was deforested (9, 10). Again, the process was rapid and estimates for Wayne County, Ohio, closely match those for the entire state.

Destruction of the eastern deciduous forest was neither simultaneous nor necessarily permanent. An accelerating wave of deforestation spread from the Atlantic Coast to the edge of the western prairie, followed by a wave of forest regeneration caused by farm abandonment (Fig. 1). By the time >50% of the original forest had disappeared from Ohio, forests in New England had already shown substantial recovery. Later, when hardwood forests of Minnesota and Wisconsin had been reduced to a small proportion of their original area, forests in Ohio had begun to grow back (Fig. 1). For example, Cadiz County (on the local scale) and the hardwood forests of Minnesota (on the state-wide scale) did not lose much forest until the end of the nineteenth century (11, 12). The regional scale shows a different pattern, probably because of the growth

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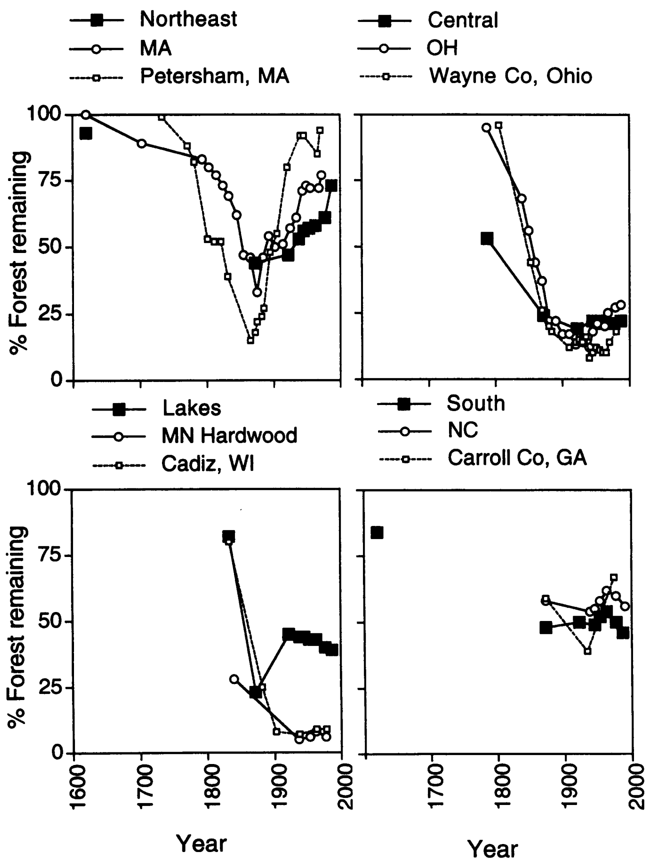

FIG. 1. Changes in the percentage of land covered with forest at the local (township or county), state, and regional scale in four regions of the eastern United States. The following states are included in each region: Northeast. CT, DE, ME, MD, MA, NH, NJ, NY, PA, RI, VT; Central. IL, IN, IA, MO, OH; Lake States. MI, MN, WI; and South. AL, AR, FL, GA, KY, LA, MS, TN, NC, SC, VA. The original percent cover for the Lake States and Central States is indicated for the time of initial European settlement in these regions. We derive data for states and regions from the same sources used to create Fig. 2. We used the following additional references for information on the local and state scales: 9–17.

of aspen and oak following extensive logging of coniferous forests in the northern parts of the three Lake States (8).

In summary, forest clearing reached a peak in the late nineteenth century, when logging and agricultural clearing were particularly intense in the Lake States and the South (7, 8, 22). Between 1850 and 1909, 22% of the eastern deciduous forest was destroyed. (We derive this estimate from ref. 7.) Yet even during the peak period of deforestation in the late nineteenth and early twentieth centuries, there were large forest refugia that provided habitat for forest birds. After 1920, the amount of deciduous forest showed a steady increase in the Northeast (19, 23) and the South (7, 24), resulting from the conversion of primarily agricultural landscapes into landscapes dominated by forest.

According to our best estimates of changes in forest cover for the four regions (Fig. 2), we estimate that 48%—or roughly half—of the area covered by the eastern forest at the time of European settlement (1620) was still wooded at the low point in 1872.

Predicting Species Losses from Forest Losses

The species–area function, $S = cA^z$, relates the number of species counted (S) to the area surveyed (A); c and z are constants. The function is reasonably consistent across different well-known animal and plant groups in different areas (33).

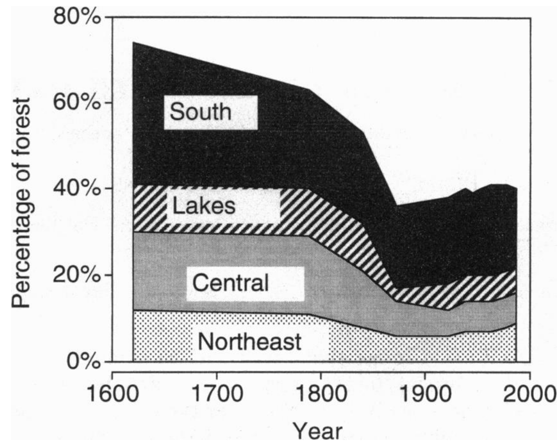

FIG. 2. Summary of the changes in the percentage of land covered with forest between 1620 and 1987 for four regions of the eastern United States. (The legend to Fig. 1 defines these regions.) We derive the data from the following sources: amount of forest before European settlement, U.S. Department of Commerce (25, 26); forest cover in 1872, Commissioner of Agriculture (27); forest cover in years after 1872, U.S. Bureau of the Census (28–32); and total area of regions, U.S. Bureau of the Census (32). Regional rates of forest loss between 1620 and 1872 for the Northeast, Central States, and Lake States are extrapolated from trends for Massachusetts, Ohio, and Minnesota, respectively (12, 18, 19). Comparable data are not available for the South, so we assume a steady rate of forest loss for this region from 1620 to 1872.

It suggests a simple recipe: if the original habitat area, A_o, is reduced to A_n, the original number of species, S_o, should decline to S_n, where $S_n/S_o = cA_n^z/cA_o^z$ or $(A_n/A_o)^z$. This expression is independent of c; z is often taken to be $\approx 1/4$. We estimate forest reduction, A_{1872}/A_{1620} to be $\approx 1/2$; thus $\approx 16\%$ of the region's species should have become extinct.

This simple recipe makes a critical assumption: we suppose that the same function applies equally to cases where habitats are actively being destroyed as to the counts of species in areas of different sizes. The recipe also begs our asking how good is the approximation of $z \approx 1/4$. We can estimate z using data on the current bird distributions. In doing so, we recognize that the estimate will reflect the extinctions and range reductions already caused by deforestation. We can also contrast our estimate of z to values derived from other studies. To estimate the number of species lost (rather than just the percentage), we also require an estimate, S_o—the number of species before deforestation. This would seem to be almost trivial for a fauna as well-known as eastern forest birds. Interestingly, it is the interpretation of S_o that has created the confusion.

Value of *z*. Using Peterson's range maps (34), we counted the number of native terrestrial species per state and for 31 eastern states combined. Contrasting any one state with the total area gives a z value. The highest of the 31 values ($z = 0.28$) compares Florida's species list (95) and area ($\approx 1.4 \times 10^5$ km^2) to the total list (215) and area ($\approx 2.9 \times 10^6$ km^2). The lowest value (0.09) comes from comparing a small, central state (Maryland; 140 species, 2.5×10^4 km^2) with the total list and area. Maryland, being central, has many species from both north and south, while geographically isolated Florida is relatively species poor. The 31 values are not statistically independent of each other, but statistical inference is not the issue. Each value suggests the consequence of a scenario of forest reduction. Hypothetically, were Maryland the sole habitat reserve left after the total destruction of all other eastern forests, we might expect it to shelter more surviving bird species than if Florida were the sole reserve. Neither scenario is even approximately correct. Forests have been lost throughout the eastern region, so some intermediate value of z would seem to be sensible.

These estimates of z are flawed. We include the species lost from the region in the total count, but we do not know how many species are now missing from each state's modern total. Interestingly, there is an increasing arithmetic contradiction in adding many extinct species to these totals. The more we add, the smaller will be the z value we will calculate. A small z value then predicts that the state should have lost few species following deforestation.

Eliminating the contradiction is easy using an iterative procedure, for which we present only the last step. Suppose that Maryland had lost 8 species. We add those 8 to the state's total and recalculate z as 0.08. Given this value, Maryland should have lost 8 species following a 50% deforestation. The values ($z = 0.08$, 8 species) are not contradictory, but other pairs are. Suppose Maryland had lost 75 species and so once would have held all the eastern species. One recalculates z as 0.0. Consequently, no species should have become extinct following a 50% loss of its forests, yet we supposed that 75 were.

Across all 31 states, comparable calculations show that z values are not changed perceptibly by this process. This is not the circular argument it might appear. If each state now held few species and if those species were unique to the state, then the z values we calculate would be large and the predictions of each state's losses would also be large. We do not observe this pattern. This alone constrains the value of z, even in our ignorance of the original species ranges.

What value of z should we expect? Rosenzweig (33) suggests at least three broad categories of values. Archipelagos where rises in the sea level have isolated once-continuous blocks of habitat provide a model close to the habitat fragmentation process. They typically yield estimates of $z \approx 1/4$. The largest values ($z \approx 0.6$–1.0) are for very small easily counted woodlots or similar habitat patches. The smallest patches may contain very few individuals and obviously few species. Which species survive often will be a matter of chance, so different species will remain in different fragments. Progressively aggregating areas will quickly increase the species list. Similarly, progressively aggregating species lists across widely separated, oceanic islands also yield high values of z, because the species have evolved independently on different islands. Conversely, the smallest estimates of z (often $<1/4$) are from nested areas within continuous habitat—such as the states within the eastern United States (above). Here, the continuous habitat means that immigration from the surrounding area constantly rescues populations in small areas. Extinctions are infrequent even in small areas and z is lower as a consequence.

Selecting $z = 1/4$ seems to be a reasonable approximation for the large, isolated, but biologically related, forest remnants of the late nineteenth century. Moreover, even within a range of z values, extinctions should be numerous. With a 50% loss of habitat, a value of $z = 0.15$ predicts a 10% loss of species, while a value of $z = 0.35$ predicts a 22% loss.

Birds of Eastern North America. The 31 states running from Louisiana north to Minnesota and east to the Atlantic, plus Kansas and southern Ontario, are home to 215 native species of terrestrial birds (34). Of these, we consider that only 160 belong to the eastern forests. Our choice is subjective and others would produce slightly different lists. These differences will not alter our key arguments. We exclude all introduced species: 16 species that occur in open, typically grassland habitats on the western fringes of the area; 7 species that occur only in nonforested, subtropical habitats in Florida; and 3 species of the marine fringe that are rarely found away from salt marshes. We have included Minnesota, Michigan, and the northern New England states because they have some deciduous forest, but we exclude 25 species from the boreal forests in the northern part of these states. One of these, Kirtland's warbler (*Dendroica kirtlandii*), is a critically endangered species found only in Michigan. The remaining species are eastern forest species to varying degrees. We return to the meaning of "varying degrees" presently. On request, we will provide a complete list of the species we included and excluded.

There are four well-known extinctions in eastern North America: passenger pigeon (*Ectopistes migratorius*), Carolina parakeet (*Conuropsis carolinensis*), ivory-billed woodpecker (*Campehilus principalis*), and Bachman's warbler (*Vermivora bachmanii*). [The isolated Cuban subspecies of the ivory-billed woodpecker is also now extinct (35).] Bachman's warbler has not been reported since 1984 despite exhaustive, intensive field surveys in its former breeding range (36). One species is critically endangered: red-cockaded woodpecker (*Picoides borealis*).

Ornithological exploration began well before the peak period of deforestation, suggesting that few, if any, extinctions were overlooked. Certainly, 5 "species" Audubon portrays in *The Birds of America* (1827–1838) are not members of the current fauna (37). They are small-headed flycatcher (*Musicapa minuta*), Cuvier's wren (*Regulus cuvieri*), Blue-mountain warbler (*Sylvia montana*), carbonated warbler (*Sylvia carbonata*), and Townsend's bunting (*Emberiza townsendi*). These birds have puzzled ornithologists and many doubt whether they are true species. Parkes (37) concludes that they are probably hybrids, birds in juvenile plumage, or, in one case, an individual lacking the normal carotenoid pigments. We do not count them in our totals.

With 160 species and a 50% loss of forest, the species–area function (with $z = 1/4$) predicts $\approx$26 extinctions. It is this prediction, some six times greater than the well-documented extinctions, that has caused so much controversy. Does this discrepancy cast doubt on the predictions of species losses from habitat reduction? It does not for two reasons.

The first reason is that not all the 160 species require deciduous or coastal pine forest. In excluding species on the borders of these habitats, we have tried to be conservative. Others might exclude even more species. And while we have excluded species of the grasslands to the west, we still include species of the open areas within these forests. Sixteen species occur only in open habitats, including marshes and farmland, within the region: northern harrier (*Circus cyaneus*), short-eared owl (*Asio flammeus*), horned lark (*Eremophila alpestris*), marsh wren (*Cistophorus palustris*), sedge wren (*Cistophorus platensis*), loggerhead shrike (*Lanius ludovicianus*), red-winged blackbird (*Agelaius phoeniceus*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), eastern meadowlark (*Sturnella magna*), bobolink (*Dolichonyx oryzivorus*), lark sparrow (*Chondestes grammacus*), vesper sparrow (*Pooecetes gramineus*), savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus savannarum*), and Henslow's sparrow (*Ammodramus henslowii*). The brown-headed cowbird (*Moluthrus ater*) has thrived on agriculture. Chimney swifts (*Chaetura pelagica*) and 6 species of swallows feed with equanimity above forests, fields, and even urban areas. Others may wish to exclude these 23 species, and perhaps several other species, such as northern bobwhite (*Colinus virginianus*), that thrive in early successional forests. There is no undisputed definition of an obligate eastern forest dweller.

Reducing the list to those species found only in mature forests may seem to be special pleading. Certainly, most of the 160 *are* dependent on forests of some kind. Even if we excluded another 23 species from our forest total, we would still predict 22 extinctions (= 16% of 137). This is still five times more than the observed number.

The second, more significant reason is the difference between global and local extinction. Those who point to the small number of observed extinctions in the eastern forests mean *global* extinctions—species that are lost everywhere (4–6). The predicted number of extinctions is based on the total number of species. However, most of these would not become globally extinct even if *all* the eastern forests were cleared. Their distribution across, say, the relatively intact boreal forests of Canada makes them invulnerable to forest losses in the United States.

We have not counted the local extinctions in the eastern forests. Typically, no one else has either. We may not feel local extinctions as keenly as global extinctions and thus they are less familiar. There are also three technical reasons why local extinctions are hard to count.

(*i*) While global extinctions are obvious, local extinctions are not: we do not have range maps for 1620. Certainly, we can document some local extinctions. For example, the peregrine falcon (*Falco peregrinus*) does not appear in the list of 160 species. Peterson classifies it as extinct in the area we consider, though it has been reintroduced since the publication of his book. An eastern race of the greater prairie chicken (*Tympanuchus cupido*)—the heath hen—is extinct. In general, our inadequate historical knowledge limits such examples and we will likely underestimate their true number.

(*ii*) Local extinctions are reversible. Some species will have returned as the forests recovered.

(*iii*) Even if we had historical range maps, their interpretation would be difficult. Species may persist locally at very low numbers because the flow of individuals from outside the locality can rescue a population otherwise headed for local extinction. With such immigration, a population might last for many decades at a level far below that needed for independent persistence. It is very difficult to answer the question, "What if that flow of immigrants were discontinued?" Equally difficult is to ask, "What would have happened to the 160 species if they were restricted only to the eastern forests—and could not be rescued from outside?" Under such a scenario, quite likely the bald eagle (*Haliaeetus leucocephalus*), peregrine falcon, northern goshawk (*Accipiter gentilis*), wild turkey (*Meleagris gallopavo*), ruffed grouse (*Bonasa umbellus*), and other large and thus typically uncommon species would have now declined to extinction. (Or else in small and fragmented ranges, their survival would depend on our active intervention.)

There are problems enough in predicting the fate of currently endangered species with fragmented ranges (§, ref. 38), without pondering their hypothetical nineteenth century analogs. Rather, we pose a question that we can answer. How many species *could* become globally extinct if all the eastern forests were felled? This question asks which species are found *only* in these forests. We have posed this question to many of our colleagues; without exception, the answer has surprised them.

Only 9 species are found almost exclusively in the states that comprise the eastern forests: chuck-will's-widow (*Caprimulgus carolinensis*), red-cockaded woodpecker, fish crow (*Corvus ossifragus*), Carolina chickadee (*Parus carolinensis*), brown-headed nuthatch (*Sitta pusilla*), yellow-throated warbler (*Dendroica dominica*), worm-eating warbler (*Helmitheros vermivous*), Swainson's warbler (*Limnothlypis swainsonii*), and Bachman's sparrow (*Aimophila aestivalis*). We estimate that an additional 12 species have >75% of their ranges in the eastern forests: red-bellied woodpecker (*Melanerpes carolinus*), Acadian flycatcher (*Empidonax virescens*), wood thrush (*Hylocichla mustelina*), blue-winged warbler (*Vermivora pinus*), golden-winged warbler (*Vermivora chrysoptera*), pine warbler (*Dendroica pinus*), prairie warbler (*Dendroica discolor*), cerulean warbler (*Dendroica cerulea*), prothonotary warbler (*Protonotaria citrea*), Louisiana waterthrush (*Seiurus motacilla*), Kentucky warbler (*Oporonis formosus*), and hooded warbler (*Wilsonia citrina*). Three more species are mostly eastern in distribution but they penetrate the prairie states in interspersed woodlands: white-eyed vireo (*Vireo griseus*), yellow-throated vireo (*Vireo flavifrons*), and scarlet tanager (*Piranga olivacea*).

Of the extinct species, the warbler and parakeet were strictly eastern forest species, the pigeon ranged to the west, and the woodpecker was once found in Cuba. Depending on whether one adopts a strict or a loose definition of eastern forest species, there were between 11 and 28 species restricted to the region. It is only these species that were at risk of extinction from forest clearing. The possible extinction rates range from 2/11 = 18%, if one defines eastern forest birds strictly, to 4/28 = 14% otherwise. Adding red-cockaded woodpecker to the list (on the grounds that it would go extinct without our intervention) and the numbers become 27% and 18%, respectively.

These data are not the counter example they are claimed to be. Rather, they are in remarkable accord with the predictions of the simple "habitat reduction predicts species loss" theory we have outlined. Indeed, three of the four rates just calculated exceed the prediction of species loss from deforestation (16%). The addition of any one of Aububon's missing birds to the total of extinct species would obviously increase the observed extinction rate. So would the addition of Kirtland's warbler—another species that would surely be extinct without active conservation efforts.

We have one caveat. There are too few species restricted to the eastern forests to calculate an empirical estimate of z based on them alone. There is no reason to expect a dramatically different value of z for this subset of species, however, (33).

Conclusions and Some Implications for Tropical Deforestation

These analyses of forest clearing strongly support simple predictions of consequent species losses based on species–area relationships. When there are discrepancies, the observed extinctions *exceed* the predicted ones.

Was habitat destruction the sole cause of these extinctions? Some consider that hunting or introduced diseases, not habitat destruction, exterminated the passenger pigeon and Carolina parakeet (39–41). More plausibly, hunting was so effective because the habitat fragmentation concentrated the birds. The pigeon was last collected in 1899, the parakeet in 1901, years when forest cover was near its minimum extent. Moreover, Bucher (42) argues that the extinction of passenger pigeons was a direct result of large-scale habitat destruction. Loss of breeding habitat is almost certainly the reason for the loss of the ivory-billed woodpecker. Its last stronghold in the United States was cleared in 1948 and there have been only sporadic sightings since (39). The loss of habitat is the reason for the endangerment of the red-cockaded woodpecker. The loss of winter habitat may have contributed to the extinction of the Bachman's warbler (36). However, its major decline was in the 1920s and could plausibly follow from the major forest clearings decades earlier.

Arguments about the causes of particular extinctions miss the point. There is nothing unique about the danger of hunting rare species in fragmented habitats or of the loss of seasonally important habitats. These factors, plus the consequences of introduced competitors, predators, and pathogens, are typical explanations for extinctions in habitat fragments worldwide (43). Habitat loss is but one of many causes of extinction, causes that typically exacerbate its effects. Eastern forest extinctions are thus appropriate models of extinctions elsewhere.

The failure of others, particularly Budiansky (5, 6), to draw the same conclusion is not just a matter of documenting the forest losses and listing the appropriate species. Of course, careful scholarship is essential, but the principal error is in

§Thomas, J. W., *A Conservation Strategy for the Northern Spotted Owl*, Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl, 1990, Portland, OR.

choosing incompatible sets of rules. One can count all the species and all the extinctions for a region. The majority of the extinctions will be local ones and hard to document. Alternatively, one can count only the species restricted to a region—that is, its endemics. The extinctions from this subset will be global by definition. To divide global extinctions by the total species list is obviously nonsense.

Calculations of extinctions following tropical deforestation usually consider the total number of species in an area, not its smaller number of endemics. Does this reliance on the total number of species inflate the concerns expressed about high extinction rates? It does not because many tropical areas are not only rich in species, they are also unusually rich in endemic species (44).

For example, the Hawaiian islands once held ≈135 species of terrestrial birds; *all* were endemic (45). The islands in the Old World tropics (Philippines, Indonesia) comprise an area half the size of eastern North America yet hold almost 20 times the number of endemic species of birds. Some islands have lost most of their forests and ≈30% of the endemic species are at risk of global extinction. The region allows the calibration of species loss from habitat loss using many species and we consider it elsewhere (44, 46). Tropical mainland regions are also rich in endemics. In Central and South America, regions smaller than the eastern forests house substantially more endemic bird species (47). For example, in the Atlantic coastal forest of Brazil and Argentina where >80% of the forest has been destroyed, some 70 of 199 endemics are at risk of extinction. The conclusion is that eastern North America lost few bird species because it had so few endemics to start with. This conclusion, combined with our knowledge of high tropical endemism in birds (and other taxa), supports the concerns about worldwide deforestation and species loss.

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