

of committing a moral act later (Fig. 4). In addition, a moral self-licensing pattern emerged (18), such that committing a moral act earlier in the day was associated with an above-average likelihood of a subsequent immoral act and a decreased likelihood of a subsequent moral act (Fig. 4). Together, the analysis of everyday moral dynamics revealed evidence both for moral contagion through other people's good deeds and moral self-licensing through one's own good deeds outside of the laboratory. Given these different mechanisms, it seems important to find out more about how the principles of moral contagion can be used in public policy interventions, and how moral slacking may be prevented.

By tracking people's everyday moral experiences, we corroborated well-controlled but artificial laboratory research, refined prior predictions, and made illuminating discoveries about how people experience and structure morality, as well as about how morality affects people's happiness and sense of purpose. A closer, ecologically valid look at how morality unfolds in people's natural environments may inspire new models and theories about what it means to lead the "good" or "bad" life.

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#### SUPPLEMENTARY MATERIALS

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Materials and Methods  
Figs. S1 to S3  
Tables S1 to S6  
References (21–27)

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## BIODIVERSITY LOSS

# Loss of avian phylogenetic diversity in neotropical agricultural systems

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Habitat conversion is the primary driver of biodiversity loss, yet little is known about how it is restructuring the tree of life by favoring some lineages over others. We combined a complete avian phylogeny with 12 years of Costa Rican bird surveys (118,127 detections across 487 species) sampled in three land uses: forest reserves, diversified agricultural systems, and intensive monocultures. Diversified agricultural systems supported 600 million more years of evolutionary history than intensive monocultures but 300 million fewer years than forests. Compared with species with many extant relatives, evolutionarily distinct species were extirpated at higher rates in both diversified and intensive agricultural systems. Forests are therefore essential for maintaining diversity across the tree of life, but diversified agricultural systems may help buffer against extreme loss of phylogenetic diversity.

**A**s human-converted habitats expand over Earth's surface, the fate of global biodiversity will depend increasingly on the quality and characteristics of farming landscapes (1, 2). Agricultural systems vary widely in their ability to support biodiversity, with many species extirpated from some but sustained in others (1, 3). Additionally, characteristics of the species themselves, evolved over millions of years, may predispose some lineages to benefit (or suffer) from human environmental impacts (4–6).

Phylogenetic diversity, the total evolutionary history or phylogenetic branch lengths of all species in a community (7), is recognized as having intrinsic conservation value (8, 9). Also, ecological experiments in small plots indicate that communities with more phylogenetic diversity are more stable (10), possess higher productivity (11), and support more species at other trophic levels (12). Despite the known impact of agriculture on species loss, how habitat conversion affects phylogenetic diversity remains unknown. Studies of plants and invertebrates have established that local environmental disturbances (e.g., lake acidification and species invasion) favor subsets of closely related clades and often result in phylogenetic diversity loss (13–15). Further, some studies that examine the global extinction risk of birds and mammals suggest that particular branches of the

tree of life are at greater risk than others (5, 6, 16), although whether evolutionarily distinct species are more at risk than species with many living relatives remains contested (6, 16, 17).

We quantified changes in phylogenetic diversity across multiple landscapes in Costa Rica, combining a recent complete avian phylogeny (18) with temporally and spatially extensive tropical bird censuses to assess how habitat conversion is restructuring the avian phylogeny (19). The data set comprised 44 transects, surveyed in wet and dry seasons over 12 years (2001 to 2012) across four regions in two biomes (fig. S1). Transects were located in three land-use types: forest reserves, diversified agricultural systems, and intensive monocultures. Compared with intensive monocultures, diversified agricultural systems had more crop types, complex configurations of vegetation, and substantial surrounding tree cover (1) (table S1). Our analysis focused on three unresolved questions. First, do certain bird clades thrive in agriculture, or is this capacity broadly distributed across the tree of life? Second, how much phylogenetic diversity is lost when native forest is replaced with agriculture? Last, are evolutionarily distinct species capable of persisting in agriculture?

We found that clades from across the bird phylogeny thrived in agriculture (Fig. 1). Affinity for different habitats showed phylogenetic signal, meaning that closely related species were more likely to share habitat preferences than species that were distantly related (table S2) (20). The phylogenetic signal was best described by using Pagel's lambda transformation of the phylogeny (21), which reduces the degree of correlation of traits between species below the Brownian motion expectation (across habitat types and seasons,  $\lambda = 0.25$  to 0.48; table S3). Although most taxonomic families had species associated with all habitat types, some families tended to affiliate with particular habitats. For example, pigeons, seedeaters, swallows, and blackbirds were

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agriculture-affiliated, whereas trogons, antbirds, ovenbirds, and manakins were forest-affiliated (Fig. 1 and table S4).

Despite the variety of lineages that were found in agriculture, average within transect phylogenetic diversity was 40% lower in intensive monocultures than in forest reserves and 15% lower in diversified agricultural systems than in forest reserves (Fig. 2A and table S5). Across all transects and years, forest reserves, diversified agricultural systems, and intensive monocultures housed 4.10, 3.85, and 3.26 billion years of evolutionary history. Two processes were responsible for changes in phylogenetic diversity: species loss and increasing species relatedness. We found roughly the same number of bird species in diversified agricultural systems ( $N = 59$  species) as in forest reserves [ $N = 62$  species; likelihood ratio test (LRT)  $P = 0.75$ ] but half as many species in intensive monocultures ( $N = 29$  species; LRT  $P < 0.001$ ; Fig. 2B and table S5).

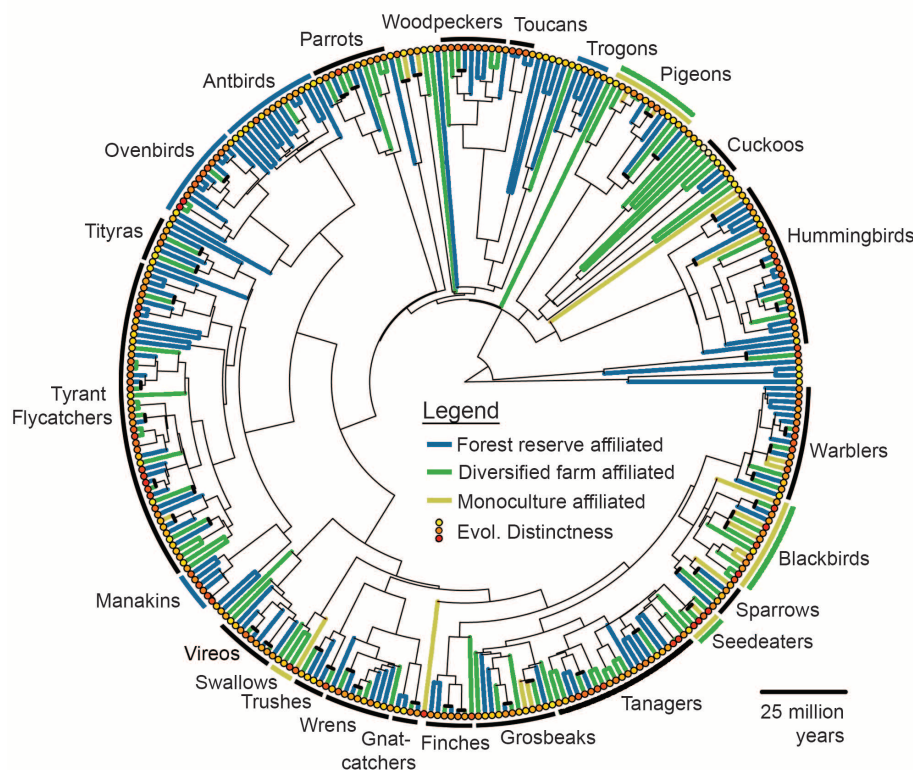
However, species loss alone did not account for declining phylogenetic diversity in agriculture (fig. S2). Species in forest reserves were less related to one another than expected by chance, whereas species in diversified agricultural systems and intensive monocultures were more closely related (Fig. 2C, fig. S3, and table S5). These patterns indicate that phylogenetic diversity loss in agriculture occurs in two steps. First,

habitat conversion from forest to diversified agricultural systems causes a shift in community composition while maintaining species richness: Agricultural species are not nested subsets of forest species (fig. S4). Because species in diversified agricultural communities are closely related, this shift results in a moderate decline in phylogenetic diversity within a transect. Then, as agricultural practices intensify, species loss from this agricultural bird community causes another more-substantial decline in phylogenetic diversity.

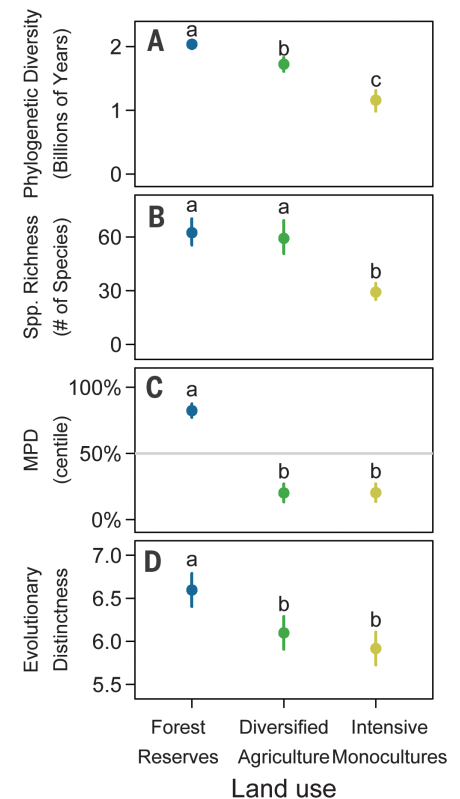
Whether phylogenetic diversity loss will substantially reshape the global tree of life depends on the capability of species from evolutionarily distinct lineages to persist in agricultural lands. We quantified each species' evolutionary distinctness (fair proportion metric) as its contribution to the phylogenetic diversity of the world's 9993 bird species (17). Species in forest reserves had slightly greater average evolutionary distinctness than those in diversified agricultural systems (LRT  $P < 0.001$ ) or intensive monocultures (LRT  $P < 0.001$ ; Fig. 2D, fig. S5, and table S5). This pattern did not result from a small number of highly distinct, forest affiliated species—repeating the analysis after removing the top 10% most distinct species did not alter results (table S5). Conversely, communities in intensive monocultures hosted younger species with more-rapid diversification rates (DRs) (18) (LRT  $P < 0.001$ ; fig. S6 and table S5). At the

species level after accounting for phylogenetic covariance, DR was negatively correlated with forest affiliation and positively correlated with affinity for diversified agricultural systems (table S6).

To explore how habitat conversion affects the temporal population dynamics and local extirpation risks of evolutionarily distinct species, we developed a temporal, multispecies, hierarchical occupancy model that accounted for detection bias (fig. S7). The model provided a dynamic assessment of which species were extirpated from and/or recolonized sites at the greatest rates from year to year (22). Extirpation was estimated as the probability that a species did not persist from one year to the next, whereas colonization was the probability that a species was absent one year but present the next. We modeled occupancy dynamics



**Fig. 1. Agricultural affiliation is distributed across the avian phylogeny.** Tips represent the 308 species detected more than 25 times. Terminal branches are colored by primary habitat affiliation. Families with more than four species present are labeled, grouped by arcs, and colored if more affiliated with a particular habitat type than expected by chance (randomization test  $P < 0.05$ ). A species' evolutionary distinctness is indicated by a colored dot at the branch tip (yellow, high evolutionary distinctness; red, low evolutionary distinctness).



**Fig. 2. Habitat conversion causes phylogenetic diversity declines.** (A) Diversified agriculture maintains intermediate phylogenetic diversity, measured as the total evolutionary history present at a site. Loss of phylogenetic diversity in agriculture was caused by two processes: (B) loss of species richness and (C) increasing relatedness among species in agricultural communities. In (C), larger values indicate greater mean phylogenetic distance (MPD; i.e., overdispersion and low relatedness), whereas smaller values indicate communities contain more close relatives (i.e., phylogenetic clustering). (D) The median evolutionary distinctness of the community was higher in forests than in agricultural habitats. Points depict estimated mean  $\pm$  SEM from generalized linear mixed models (table S5). Different letters denote significant differences between groups (LRT  $P < 0.05$ ).  $N_{\text{total}} = 528$  ( $N_{\text{transects}} = 44$ ,  $N_{\text{years}} = 12$ ).

over 12 years, validating our model through examining dry and wet season surveys separately.

We found that extirpation probability was highest in intensive monocultures and lowest in forest reserves (Fig. 3). More evolutionarily distinct species experienced higher extirpation rates than less-distinct species in both diversified agricultural systems and intensive monocultures. Evolutionarily distinct species fared worst in intensive monocultures, where the top 10% most-distinct species experienced extirpation rates ~two times greater than in diversified agricultural systems. Between-year colonization probabilities were low in all land-use types, but evolutionarily distinct species colonized both diversified agricultural systems and intensive monocultures less frequently than less-distinct species (fig. S8). Repeating analyses at the genus level confirmed that the results were not driven by a few clades. These findings suggest that, over time, evolutionarily distinct species will face challenges in maintaining populations in agricultural systems, especially in intensive monocultures.

We offer two possible explanations for why evolutionarily distinct species and phylogenetic diversity should decline in agriculture. First, species that today inhabit tropical agriculture may have evolved primarily in open habitats, such as grasslands. During geologically recent periods of glaciation when open grassland habitats in the Neotropics proliferated (23), several clades may have undergone increased speciation (or experienced less extinction), leading to the enrichment

of younger species in agriculture (24, 25). Indeed, we found that species that use natural open habitats (e.g., shrub-brush, savannas, or along waterways) were more likely to thrive in agriculture (table S6). However, whereas species associated with savannas had slightly higher diversification rates than other species ( $N_{\text{spp}} = 308$ ,  $LRT P < 0.05$ ), there were no consistent differences in diversification rates between species that use natural open habitats and those that do not (table S6).

Another explanation is that birds in agriculture represent a novel community. In comparison to forest, agricultural habitats are less stable (26) and more regularly disturbed (e.g., pruned, harvested, and replanted). These attributes could preclude sustained competition (27) and favor related species with traits that allow them to persist in agriculture's novel and variable conditions (Fig. 2C) (14, 15). Previous work with the same data set demonstrated that bird functional diversity is lower in intensive monocultures than in forest reserves or diversified agricultural systems, suggesting that agriculture can act as an ecological filter (1). We further explored this idea by analyzing whether land use affects the distribution of several functional traits thought to regulate bird responses to environmental disturbances (28). Indeed, granivores and birds with wider diet breadths and larger clutch sizes had higher colonization rates in agriculture (figs. S9 and S10). Additionally, compared with smaller species, larger birds experienced higher extirpation rates in intensive monocultures but lower ex-

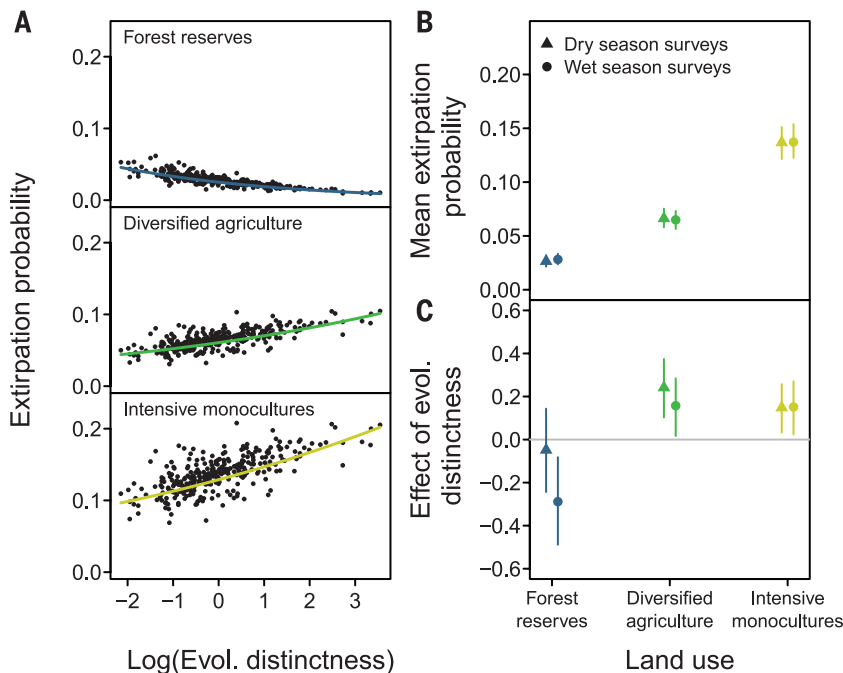
ting rates in diversified agricultural systems (fig. S9).

Our results suggest that both agricultural expansion and intensification threaten evolutionarily distinct species, aligning with earlier findings of heightened global endangerment among birds from basal lineages (6). In contrast, species from recently diversifying clades appear best able to exploit agricultural habitats and may thus benefit from ongoing agricultural expansion. The persistence of some species from younger lineages cannot prevent the species losses, and concomitant declines in phylogenetic diversity, that accompany agricultural intensification.

Ultimately, protected areas are essential for preserving evolutionary history. Yet in the absence of a much-expanded global reserve system, prioritizing diversified agricultural systems over intensive monocultures, especially surrounding reserves, provides a strategy for enhancing the conservation value of human-modified landscapes. About the same number of species persisted in diversified agricultural systems as in forest reserves, and, as a result, diversified agricultural systems maintained 1.5 times the phylogenetic diversity of intensive monocultures. Shepherding biodiversity through the human pressures of the 21st century will require a shared vision for conservation and agriculture, one that simultaneously preserves species and ecosystem functions while also enhancing food production and human well-being.

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**Fig. 3. Evolutionarily distinct species have higher extirpation probability in agriculture but not in forest.** (A) Species-specific extirpation probabilities as a function of evolutionary distinctness (standardized and on a log scale) from wet season surveys in each of the three land uses. (B) Average extirpation probabilities across species (means from the left panels) for both wet and dry seasons. (C) How evolutionary distinctness modifies the effect of habitat type on the extirpation probability of a species [slopes from (A)]. For (B) and (C), points indicate mean  $\pm$  95% Bayesian credible interval.  $N_{\text{spp}} = 308$ ,  $N_{\text{transects}} = 44$ ,  $N_{\text{years}} = 12$ ,  $N_{\text{visits/season}} = 3$ .

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## SUPPLEMENTARY MATERIALS

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Materials and Methods  
Tables S1 to S6  
Figs. S1 to S10  
References (29–31)

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## MICROBIAL ECOLOGY

# Biogeographic patterns in ocean microbes emerge in a neutral agent-based model

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A key question in ecology and evolution is the relative role of natural selection and neutral evolution in producing biogeographic patterns. We quantify the role of neutral processes by simulating division, mutation, and death of 100,000 individual marine bacteria cells with full 1 million-base-pair genomes in a global surface ocean circulation model. The model is run for up to 100,000 years and output is analyzed using BLAST (Basic Local Alignment Search Tool) alignment and metagenomics fragment recruitment. Simulations show the production and maintenance of biogeographic patterns, characterized by distinct provinces subject to mixing and periodic takeovers by neighbors (coalescence), after which neutral evolution reestablishes the province and the patterns reorganize. The emergent patterns are substantial (e.g., down to 99.5% DNA identity between North and Central Pacific provinces) and suggest that microbes evolve faster than ocean currents can disperse them. This approach can also be used to explore environmental selection.

An important ongoing endeavor in ecology and evolution is to understand the mechanisms underlying the geographic distribution patterns of organisms. One mechanism that can create such patterns is natural

selection by contemporary environmental factors acting on adaptive mutations or a persistent seed bank of species. Neutral evolution (selectively neutral mutations and genetic drift) coupled with dispersal limitation or isolation is another

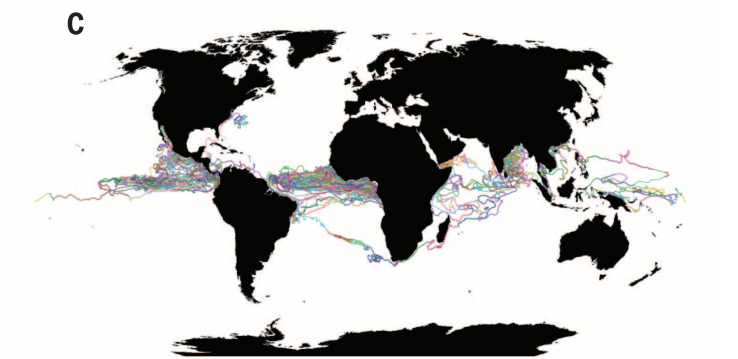
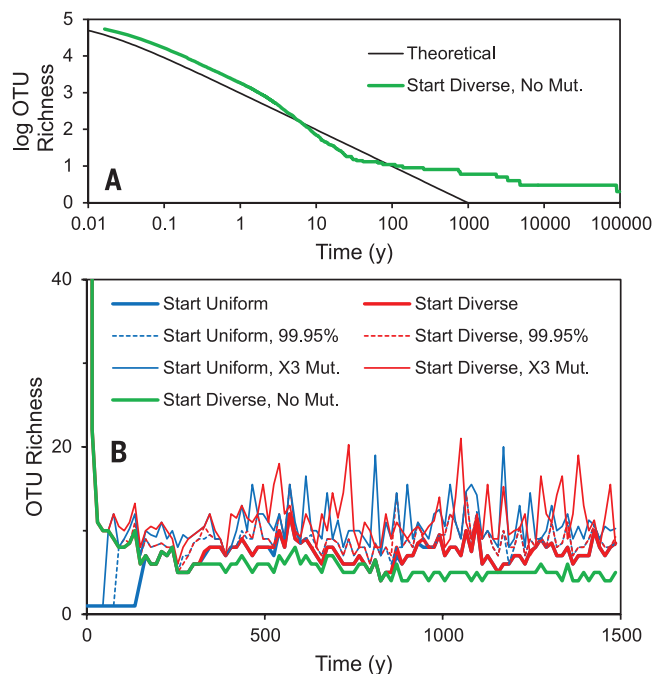
mechanism (1–6). These processes are not mutually exclusive, and for microbes in the global surface ocean, molecular observations [e.g., shotgun sequencing (7)] provide support for the role of both mechanisms (8–11).

How does neutral evolution influence the biogeographic distribution of surface ocean microbes? To what extent does dispersion allow for different operational taxonomic units (OTUs) to develop and persist? Are there emerging spatial patterns [e.g., provinces (12)], and how do these change in time?

Several approaches are available to quantify the contribution of the various processes in generating and maintaining biogeographic patterns among ocean microbes (2). A common empirical approach involves correlating observations (e.g., microbial composition) with environmental variables, subtracting out this environment effect, and then correlating with geographic distance. In the ocean, hydrodynamic models coupled with tracers (either Eulerian concentration or Lagrangian particles) can be used as a measure

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**Fig. 1. Diversity (OTU richness) in global surface ocean microbes predicted by a neutral agent-based model.** Results from several simulations are presented: “Start Diverse” indicates that all initial cells have an individual, completely random genome, whereas “Start Uniform” denotes that all initial cells have the same, completely random genome. “No Mut.” and “X3 Mut.” represent zero and three times higher mutation rates, respectively. “99.95%” is representative of a 99.95% cutoff (versus 99.9% used in other analyses). “Theoretical” denotes a model based on neutral theory, not considering dispersal limitation (31). (A and B) OTU richness over time. Note the x- and y-axis scales. Start diverse (red) and start uniform (blue) lines overlap after 200 years. (C) Life history of an individual cell isolated near Bermuda at 1000 years. Color changes demarcate mutation events. This cell was initialized with the *P. ubiquus* HTCC1062 genome (34).