

Predicting biodiversity change and averting collapse in agricultural landscapes

Chase D. Mendenhall^{1,2}, Daniel S. Karp^{1,2,3,4}, Christoph F. J. Meyer^{5,6}, Elizabeth A. Hadly² & Gretchen C. Daily^{1,2,7,8,9}

The equilibrium theory of island biogeography¹ is the basis for estimating extinction rates² and a pillar of conservation science^{3,4}. The default strategy for conserving biodiversity is the designation of nature reserves, treated as islands in an inhospitable sea of human activity⁵. Despite the profound influence of islands on conservation theory and practice^{3,4}, their mainland analogues, forest fragments in human-dominated landscapes, consistently defy expected biodiversity patterns based on island biogeography theory^{6–13}. Countryside biogeography is an alternative framework, which recognizes that the fate of the world's wildlife will be decided largely by the hospitality of agricultural or countryside ecosystems^{12,14–17}. Here we directly test these biogeographic theories by comparing a Neotropical countryside ecosystem with a nearby island ecosystem, and show that each supports similar bat biodiversity in fundamentally different ways. The island ecosystem conforms to island biogeographic predictions of bat species loss, in which the water matrix is not habitat. In contrast, the countryside ecosystem has high species richness and evenness across forest reserves and smaller forest fragments. Relative to forest reserves and fragments, deforested countryside habitat supports a less species-rich, yet equally even, bat assemblage. Moreover, the bat assemblage associated with deforested habitat is compositionally novel because of predictable changes in abundances by many species using human-made habitat. Finally, we perform a global meta-analysis of bat biogeographic studies, spanning more than 700 species. It generalizes our findings, showing that separate biogeographic theories for countryside and island ecosystems are necessary. A theory of countryside biogeography is essential to conservation strategy in the agricultural ecosystems that comprise roughly half of the global land surface and are likely to increase even further¹⁴.

The mark of humanity on the biosphere is now so widespread and profound that many consider Earth to have entered a new geological epoch, the Anthropocene. This new epoch has brought an explosion of countryside ecosystems—arenas where villages, farmland and minimally altered habitats weave together to form intricate, human-dominated ecosystems—where the fate of much of the planet's wildlife is being determined^{14,15}. Driven by the unrelenting pace of biodiversity loss and the erosion of benefits that nature provides to society¹⁸, conservation science has entered a new phase of prolific innovation¹⁹. Despite the broadly defined and rapidly adapting framework of conservation science²⁰, many of the biological theories at its centre persist, relatively unchanged. For example, theories from simple island ecosystems are still used in ways that incorrectly estimate rates of species extinction²¹ and distort projections of ecological risk in human-dominated ecosystems^{2,22}, further exhausting an environmental, apocalyptic narrative²³. Confusion and controversy surrounding the biodiversity crisis are substantially related to the overextension of the theory of island biogeography to human-dominated ecosystems, exacerbating a rift between conservation theory and real-world practices^{20,24}.

More than 30 years after the establishment of experiments⁶ designed to test the efficacy of island biogeographic theory in countryside ecosystems, we now know that wildlife often defies patterns predicted by island biogeography theory—emphasizing the critical role of human-made habitats in ecosystems^{11,14–16,21,24}. Despite its known shortcomings^{10,11}, this theory persists as the basis for estimating extinction rates and making policy recommendations^{2,21,22}. In response, a new, holistic view of biogeography is emerging for countryside ecosystems—one that incorporates human-made habitats and their associated biodiversity^{14–17,24,25}.

Here we predict that human-made habitats typical of many countryside ecosystems will provide resources for many species to increase their abundances and mitigate the extirpation of populations and species. We propose three hypotheses to contrast countryside and island biogeographic theories empirically: first, that forest fragments in agricultural landscapes, in comparison with true islands, support more species and have lower rates of local extinction; second, that forest fragments surrounded by deforested habitat host more evenly distributed abundances of species than do true islands surrounded by water because human-made habitats support individuals to differing degrees, through part or all of their life cycles; and third, that the expansion by many forest species into human-made habitats in the countryside ecosystem is generating novel assemblages of biodiversity, whose members and their abundances reflect species-specific responses to habitat change (Fig. 1).

We test these hypotheses by using data on Neotropical bat biodiversity, a group acutely sensitive to tropical deforestation⁹. First, we contrast bat biodiversity within a mosaic of forest fragments embedded in farmland with that on true islands within a large, human-made lake. Second, we perform a meta-analysis of 29 studies of bat species richness across countryside and island ecosystems worldwide, to assess the generality of our findings.

Specifically, we contrast bat biodiversity in a Costa Rican countryside dominated by coffee plantations and pastures with a Panamanian island ecosystem dominated by water (Fig. 2). The two ecosystems are ideal for testing biogeographic theories because of their approximately similar ages, their close geographic proximity, their evolutionarily homologous bat diversity and their similarly sized historical biogeographic species pools.

Bats were captured over a 2–4-year period in sites located in forest reserves, forest fragments and coffee plantations in the countryside ecosystem and in mainland forests, mainland forest edges and true islands in the island ecosystem²⁶ (Fig. 2; see Methods). We captured 9,283 individual bats (4,282 and 5,001 individuals in the countryside and island ecosystem, respectively) and 62 bat species (43 and 33 species in the countryside and island ecosystem, respectively; 14 species were shared between the ecosystems). We found striking differences between ecosystems in three dimensions of biodiversity corresponding to our three hypotheses: species richness, species evenness and abundance-based assemblage composition (Fig. 3 and Extended Data Tables 1–3; see Methods).

¹Center for Conservation Biology, Stanford University, Stanford, California 94305, USA. ²Department of Biology, Stanford University, Stanford, California 94305, USA. ³Department of Environmental Science, Policy & Management, University of California, Berkeley, California 94720, USA. ⁴The Nature Conservancy, Berkeley, California 94705, USA. ⁵Institute of Experimental Ecology, University of Ulm, 89069 Ulm, Germany. ⁶Centre for Environmental Biology, University of Lisbon, 1749-016 Lisbon, Portugal. ⁷Woods Institute for the Environment, Stanford University, Stanford, California 94305, USA. ⁸Global Economic Dynamics and the Biosphere, Royal Swedish Academy of Sciences, Stockholm SE-104 05, Sweden. ⁹Stockholm Resilience Centre, University of Stockholm, Stockholm SE-106 91, Sweden.

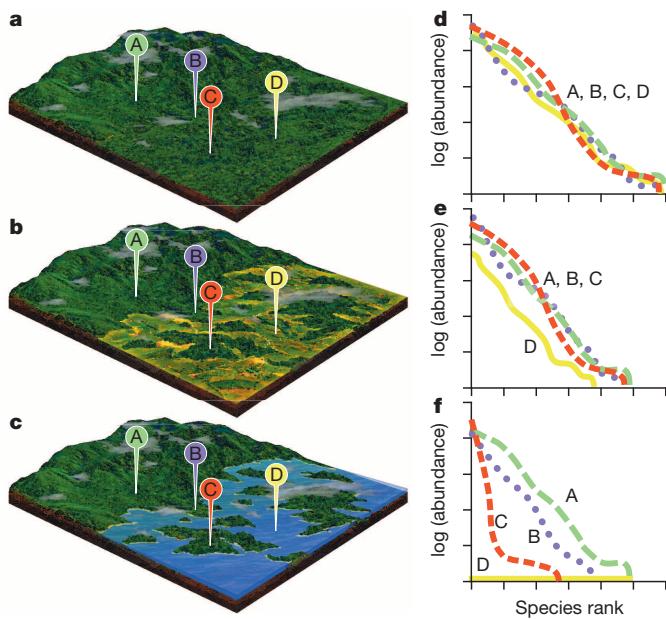


Figure 1 | Hypothetical biodiversity changes in countryside and island ecosystems. **a–c,** Conceptual diagrams showing hypothesized patterns of biodiversity in a minimally altered ecosystem (**a**) and corresponding countryside (**b**) and island (**c**) ecosystems derived from hypothetical land conversion either to agriculture or a lake, respectively. **d–f,** Proposed patterns of biodiversity for minimally altered (**d**), countryside (**e**) and island (**f**) ecosystems, depicted by rank–abundance plots. In each rank–abundance plot, the most abundant species at each site is given a species rank of 1, the second most abundant is 2, and so on. Pin labels mark sites and habitats with letters in each ecosystem and are referenced in the rank–abundance plot. In the countryside and island ecosystems, letters represent sites located in the mainland or reserve interior (**A**), mainland or reserve edge (**B**), forest fragment or true island (**C**) and deforested habitat or water matrix (**D**). We speculate that species loss generally occurs after landscape alteration, but there is wide variation between countryside and island ecosystems in how biodiversity changes in terms of species loss, changes in abundances and the formation of novel assemblages of biodiversity among habitats, because of the resources afforded in human-made habitats in countryside ecosystems.

To test our first hypothesis, we compared estimated species richness in forest fragments with that in true islands (Fig. 3b). In agreement with the species–area relationships that include human-made habitats^{12,13}, the best-fit statistical models that explained bat species richness in forest reserves and fragments in the countryside ecosystem suggested either no change in species richness between habitats (mean species estimated

per site = 25 (s.d. = 4); Extended Data Table 4) or little change (competing model with a difference in the corrected Akaike information criterion (ΔAIC_c) = 0.220 yielded a mean species estimated per reserve site of 28 (s.d. = 5) and a mean species estimated per forest fragment site of 23 (s.d. = 3)). Fragment size and isolation distance were poor predictors of species richness among countryside forest reserves and fragments (Extended Data Table 3).

Aligning with our first hypothesis and predictions of island biogeographic theory, the estimated number of bat species in the island ecosystem declined with isolation distance but increased with island size (Extended Data Table 4). The area of remaining tropical forest within 1 km, a more ecologically relevant measure of habitat amount¹¹, was the

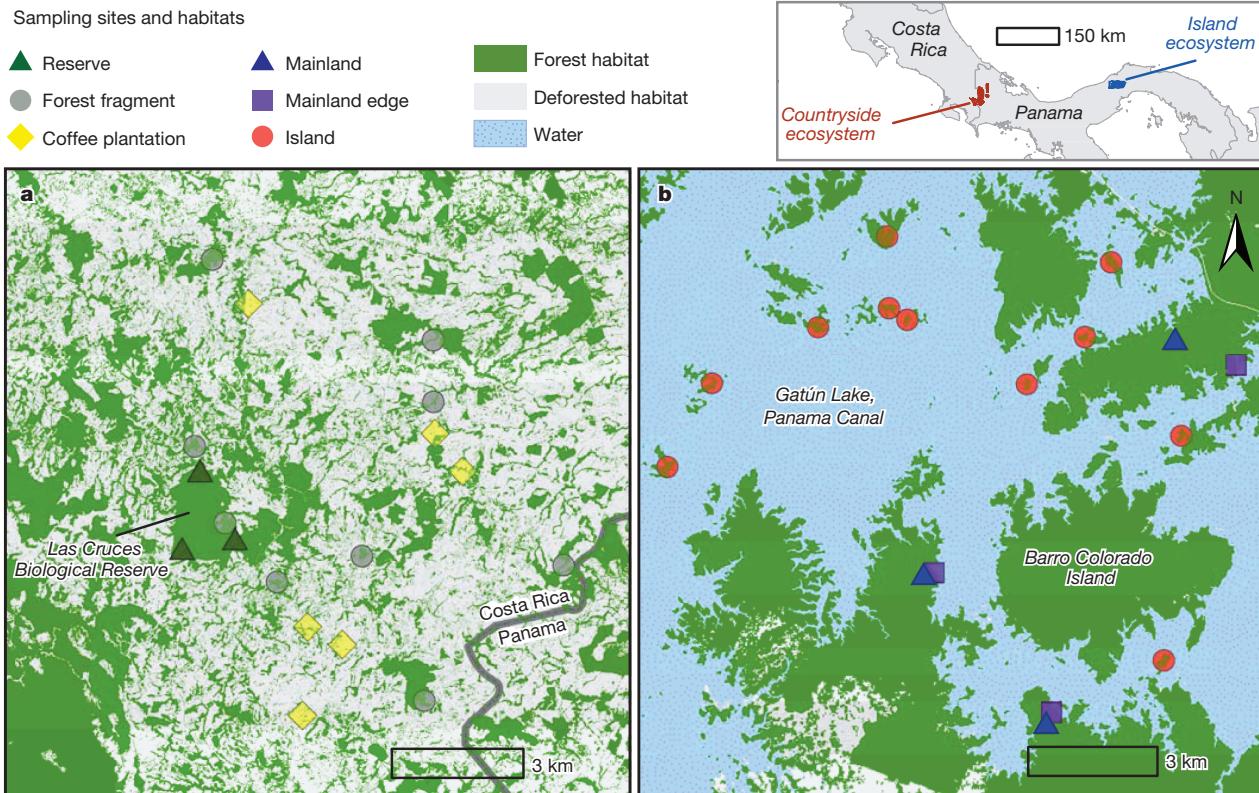


Figure 2 | Bat sampling locations. A total of 36 locations were sampled for bat biodiversity: 19 across the countryside ecosystem located in southern Costa Rica (**a**) and 17 in the human-made island ecosystem of Gatún Lake, constituting a major part of the Panama Canal (**b**). The two ecosystems are separated by about 350 km and occupy the neighbouring tropical life zones of premontane wet and lowland moist forests. Both ecosystems were extensively sampled for bats by using ground-level mist nets over multiple years. In the countryside ecosystem, sampling was conducted in two different forest

reserves, a variety of forest fragments, and coffee plantations. In the island ecosystem, sampling was conducted in the interior mainland, mainland edges and on a variety of islands. The island ecosystem was sampled from 2003 to 2005 and the countryside ecosystem from 2009 to 2012 with similar sampling techniques and effort (see Methods). In the countryside ecosystem figure the sampling location inside La Amistad International Park is not shown but is located about 25 km northeast of the Las Cruces Biological Reserve of the Organization for Tropical Studies.

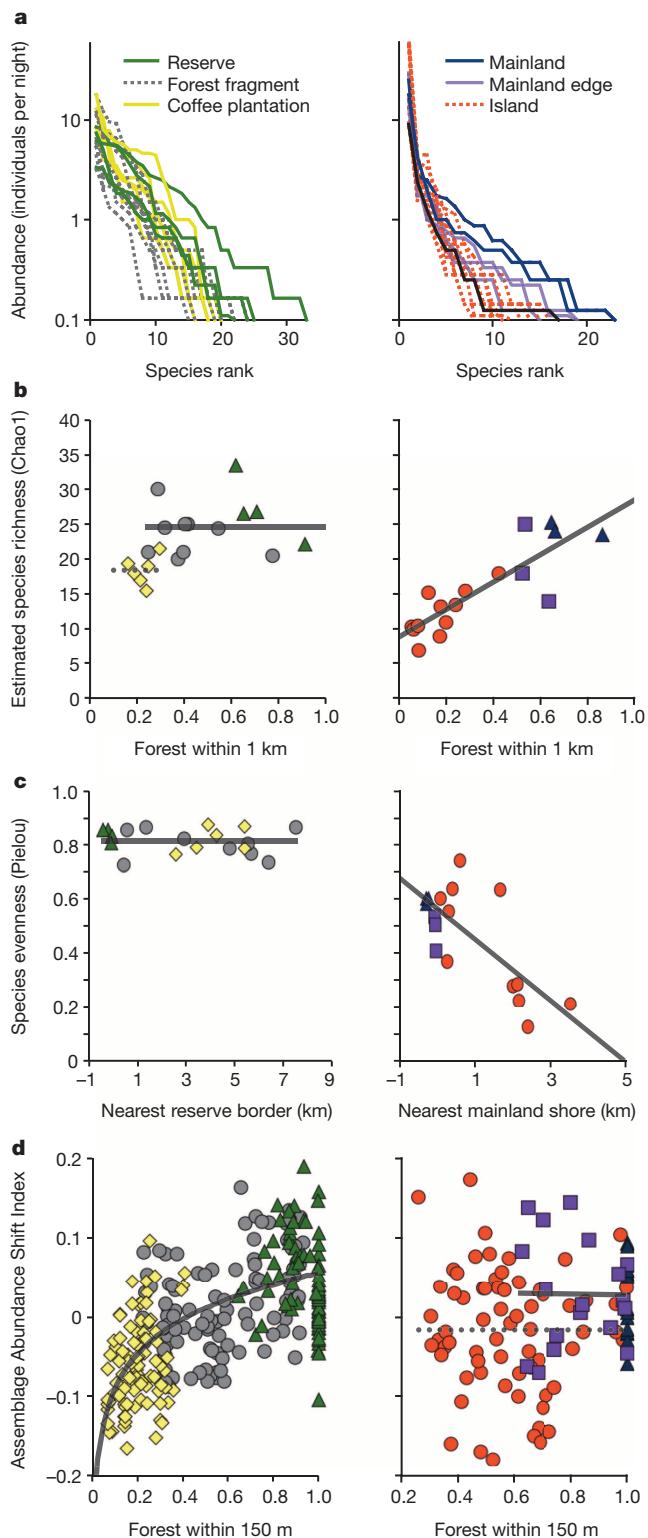


Figure 3 | Countryside and island bat biodiversity patterns. Countryside and island ecosystems support bat biodiversity in fundamentally different ways. A total of 62 bat species were recorded: 43 were captured in the countryside ecosystem (left column) and 33 in the island ecosystem (right column); of these, 14 bat species were shared. Shown are the countryside and island ecosystem rank-abundance distributions for each site (**a**) and patterns of bat species richness (**b**), species evenness (**c**) and the Assemblage Abundance Shift Index (**d**), which accounts for changes in species richness. Symbol shapes and colours correspond to those shown in Fig. 2. Lines depict best-fit relationships after model selection and optimization. Dotted lines correspond to coffee plantations in **b** and islands in **d**, where broad habitat type was the best predictor. Analyses in **b** and **c** were conducted at a site level (36 sites). Species richness was estimated to account for rare species using the Chao1 method and species evenness is standardized between 0 and 1 using the Pielou method. Analysis in **d** was conducted at a net level (383 nets), because assemblage differences were observed within sites relative to fine-scale changes in forest cover at 150 m. See Methods for further details, and Extended Data Tables 1–4 for model comparisons and regression coefficients.

however, species abundances were increasingly uneven on more isolated islands (Fig. 3c and Extended Data Table 5). Uneven abundance distributions of bats in the island ecosystem are probably explained by island biogeography's faunal density compensation theory²⁷.

To test our third hypothesis, we examined bat biodiversity patterns in a variety of coffee plantations in the countryside ecosystem (Fig. 3). In coffee plantations we captured 1,508 individuals representing 26 of the 43 bat species (mean species estimated per coffee plantation site = 18 (s.d. = 2); Fig. 3b and Extended Data Table 4), nine of which were observed roosting and/or breeding on farmland but not in pastures²⁸ (Extended Data Table 6). Moreover, bat species in coffee plantations were evenly distributed in their abundances (Fig. 3c). Species varied considerably in their abundance responses to deforestation, but 14 of the 30 bat species with at least seven captures in the countryside ecosystem were more abundant outside the forest reserves. Further, no species showed complete dependence on a single habitat type (Extended Data Fig. 1).

Finally, to evaluate whether a novel bat assemblage is forming in coffee plantations because of predictable, species-specific changes in abundances, we developed and compared an index that measured assemblage-level changes in bat abundances across habitats in both ecosystems. The Assemblage Abundance Shift Index is based on ordination analyses of bat abundances and how they shift collectively, relative to bat assemblages in forest reserves in the countryside ecosystem and to mainland sites in the island ecosystem. The Assemblage Abundance Shift Index accounts for changes in species richness and detection bias (see Methods and Extended Data Fig. 2). Patterns of the Assemblage Abundance Shift Index revealed that the abundances of many bat species in the countryside ecosystem underwent predictable transitions in tandem with declining forest cover, particularly at small spatial scales¹¹ (150 m) and especially in coffee plantations. In the island ecosystem, bat abundances differed significantly between assemblages on the mainland interior and edge sites in comparison with islands, probably because of density compensation²⁷ (Fig. 3d).

Our meta-analysis found strong evidence that bat biodiversity patterns follow predictions of island biogeographic theory on true islands—both natural and human-made—but countryside ecosystems are more complex. A review of 206 peer-reviewed papers on bat biodiversity in island and countryside ecosystems yielded several key findings from the 29 studies that met meta-analysis search criteria (Fig. 4a; see Methods). First, we confirmed that the equilibrium theory of island biogeography accurately forecasted the change in bat species richness with island size on true islands (Fig. 4b), and bats on islands followed typical species-area relationships (Fig. 4c). Second, we found that declines in bat species richness expected from island biogeography were almost never realized in countryside forest fragments (Fig. 4b). Third, we found a variety of bat species richness responses in open habitats of countryside ecosystems, including relatively high richness in some agricultural systems^{15,24} (Fig. 4d). Finally, we found that 10 of the 12 studies that compared bat assemblages between minimally altered forest, forest

strongest predictor of species richness on islands ($R^2 = 0.746, P < 0.001, n = 17$; Fig. 3a and Extended Data Table 4). In support of our first hypothesis, the rate of species loss as forest area declined was substantially and significantly higher in the island ecosystem than in the countryside ecosystem (Extended Data Table 2).

To test our second hypothesis, we analysed Pielou's evenness index (Fig. 3c). Forest reserves and fragments in the countryside ecosystem did not vary in evenness—probably because bat populations are supported beyond forest edges in the deforested habitat. In the island ecosystem,

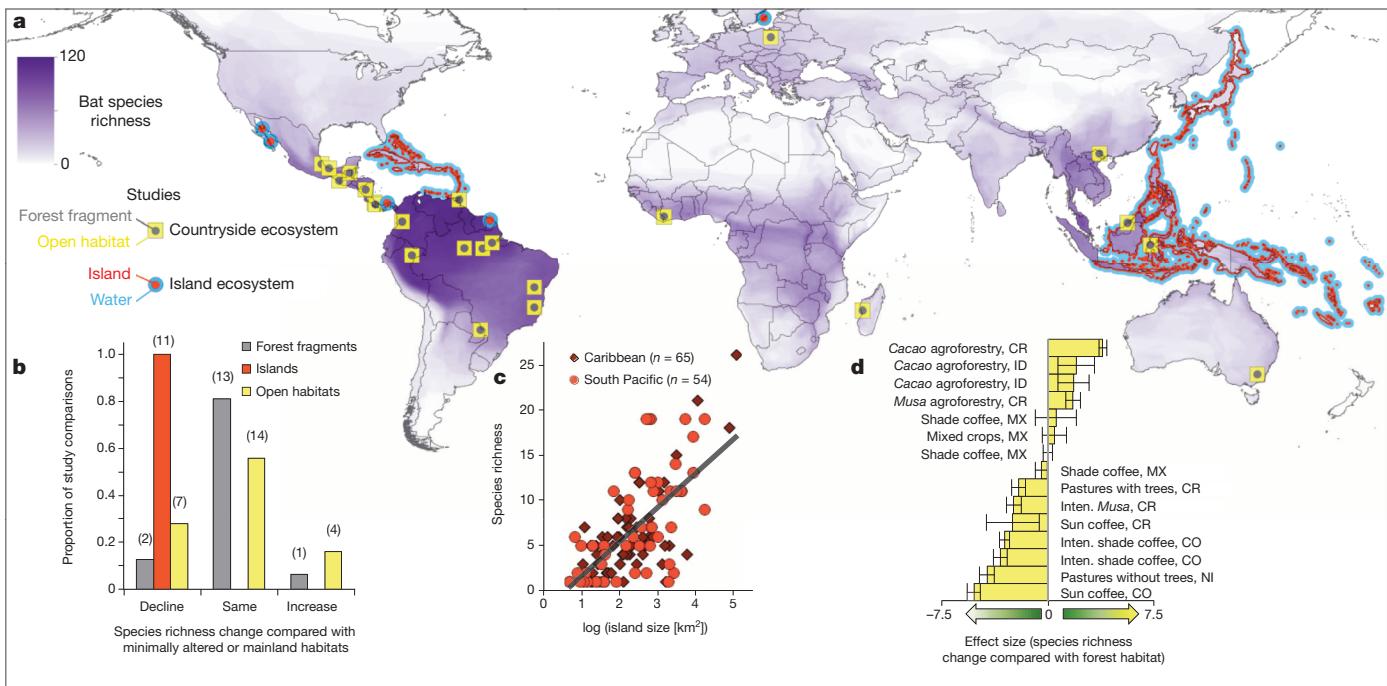


Figure 4 | Bat species richness responses in countryside and island ecosystems worldwide. Globally, countryside ecosystems and island ecosystems support biodiversity in fundamentally different ways, necessitating separate biogeographic theories for prediction and management. **a**, Map identifying the locations of 52 bat species richness comparisons in different countryside and island habitats gathered from 29 studies. In all, the studies surveyed more than 700 bat species, representing more than 60% of all bat and 10% of all mammal species globally. **b–d**, Island bat species richness always declined relative to the mainland or to larger islands in island ecosystems (**b**). For example, bat species richness on islands in the Caribbean and South Pacific yielded a typical species-area relationship (**c**; $S = cA^z$, $c = 0.043$, $z = 0.269$, where S is the number of species, A is the habitat area, c is the

fragments and/or human-made habitats reported a significant assemblage shift in bat biodiversity (see Supplementary Data).

In view of humanity's incomplete knowledge of nature, the designation of protected areas is, and will continue to be, an essential strategy for conserving biodiversity⁹. The widespread application of island biogeographic theory to countryside—less so in Europe, but especially in the Tropics—is, however, distorting our understanding and conservation strategies in agriculture, the enterprise on which the future of biodiversity hinges most critically. The hospitality of the world's agricultural lands is threatened by an increasing use of chemical inputs and practices that sterilize, structurally level, and standardize plots^{14,15,17,24}—homogenizing and decimating biodiversity²⁹. Here we provide evidence that a countryside biogeographic framework that is inclusive of human-made habitats and the opportunities it can afford to many species—given appropriate management of those habitats^{15,24}—better represents how, at least, bat biodiversity is responding in the Anthropocene. Approaches for estimating biodiversity that explicitly account for human-made habitats^{4,11–13,21,30} are critical for predicting biodiversity change and avoiding its collapse in the agricultural landscapes that will increasingly dominate the Earth.

METHODS SUMMARY

Bats were sampled by using constant-effort mist netting. In the Costa Rican countryside ecosystem, mist-netting protocols consisted of 20 ground-level mist nets (12 m × 2.5 m, 32-mm mesh) in a 3–5-ha plot haphazardly placed at each site, except the ‘supersite’ located in La Amistad International Park, which consisted of 60 haphazardly placed mist nets within a 10-ha plot. Constant-effort mist netting for bats in the countryside ecosystem took place between 24 January and 28 March for four years (2009–2012). Sampling began at sunset and lasted 4 h each night. Countryside ecosystem sites were sampled on three nights each year from 2009 to 2011

constant associated with the area measurement, and z is the slope of the species-area relationship in log-log space). In contrast, bat species richness in countryside forest fragments generally had the same number of species as minimally altered forest habitat (**b**). Bat species richness in open habitats compared to forest habitat varied (**b**). Studies with enough information to calculate effect sizes demonstrated how some agricultural practices, such as agroforestry, support more bat biodiversity than more intensive agricultural practices (**d**; effect size direction indicates species richness decline or increase compared to forest habitat, error bars represent 95% confidence intervals). Inten., intensive. Country code abbreviations: CR, Costa Rica; CO, Colombia; ID, Indonesia; MX, Mexico.

and on only one night in 2012, except the ‘supersite’ located in La Amistad International Park, which was sampled for three nights in 2009 and three nights in 2010. In the Panamanian island ecosystem, mist-netting protocols consisted of six ground-level mist nets (6 m × 2.5 m, 16-mm mesh) placed around the perimeter of a 0.5-ha plot at each site. Constant-effort mist netting for bats in the island ecosystem took place between October 2003 and October 2005. Each site in the island ecosystem was sampled for seven or eight complete nights (that is, from sunset to sunrise) over a 2-year period. All captured bats in both ecosystems were identified and standard measurements were collected. Adult bats from larger species (more than 5–10 g) were marked individually.

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 20 December 2013; accepted 10 February 2014.

Published online 16 April; corrected online 7 May 2014 (see full-text HTML version for details).

1. MacArthur, R. & Wilson, E. *The Theory of Island Biogeography* 203 (Princeton Univ. Press, 1967).
2. Millennium Ecosystem Assessment. *Ecosystems and Human Well-being* (Island Press and World Resources Institute, 2005).
3. Simberloff, D. & Abele, L. Island biogeography theory and conservation practice. *Science* **191**, 285–286 (1976).
4. Hanski, I. & Gilpin, M. Metapopulation dynamics. *Biol. J. Linn. Soc.* **42**, 3–16 (1991).
5. Wilson, E. & Willis, E. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 522–534 (Belknap, 1975).
6. Laurance, W. F. et al. Ecosystem decay of Amazonian forest fragments. *Conserv. Biol.* **16**, 605–618 (2002).
7. Debinski, D. & Holt, R. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* **14**, 342–355 (2000).
8. Laurance, W. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biol. Conserv.* **141**, 1731–1744 (2008).
9. Laurance, W. et al. Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**, 290–294 (2012).

10. Lomolino, M. A call for a new paradigm of island biogeography. *Glob. Ecol. Biogeogr.* **9**, 1–6 (2000).
11. Fahrig, L. Rethinking patch size and isolation effects. *J. Biogeogr.* **40**, 1649–1663 (2013).
12. Pereira, H. & Daily, G. Modeling biodiversity dynamics in countryside landscapes. *Ecology* **87**, 1877–1885 (2006).
13. Guilherme, J. & Pereira, H. Adaptation of bird communities to farmland abandonment in a mountain landscape. *PLoS ONE* **8**, e73619 (2013).
14. Mendenhall, C., Kappel, C. & Ehrlich, P. in *Encyclopedia of Biodiversity* (ed. Levin, S.) 347–360 (Elsevier, 2013).
15. Perfecto, I., Vandermeer, J. & Wright, A. *Nature's Matrix: Linking Agriculture, Conservation and Food Sovereignty* 242 (Earthscan, 2009).
16. Daily, G. Ecological forecasts. *Nature* **411**, 245 (2001).
17. Daily, G., Ceballos, G., Pacheco, J., Suzán, G. & Sánchez-Azofeifa, A. Countryside biogeography of Neotropical mammals. *Conserv. Biol.* **17**, 1814–1826 (2003).
18. Cardinale, B. et al. Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
19. Kueffer, C. & Kaiser-Bunbury, C. Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. *Front. Ecol. Environ.* **10**, 1890/120201 (2013).
20. Kareiva, P. & Marvier, M. What is conservation science? *Bioscience* **62**, 962–969 (2012).
21. He, F. & Hubbell, S. Species-area relationships always overestimate extinction rates from habitat loss. *Nature* **473**, 368–371 (2011).
22. Gibson, L. et al. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* **341**, 1508–1510 (2013).
23. Heise, U. *Sense of Place and Sense of Planet: The Environmental Imagination of the Global* 250 (Oxford Univ. Press, 2008).
24. Tscharntke, T. et al. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* **151**, 53–59 (2012).
25. Rosenzweig, M. *Win-Win Ecology: How the Earth's Species Can Survive in the Midst of Human Enterprise* 211 (Oxford Univ. Press, 2003).
26. Meyer, C. & Kalko, E. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation. *J. Biogeogr.* **35**, 1711–1726 (2008).
27. MacArthur, R., Diamond, J. & Karr, J. Density compensation in island faunas. *Ecology* **53**, 330–342 (1972).
28. Reid, J., Holste, E. & Zahawi, R. Artificial bat roosts did not accelerate forest regeneration in abandoned pastures in southern Costa Rica. *Biol. Conserv.* **167**, 9–16 (2013).
29. Karp, D. et al. Intensive agriculture erodes β -diversity at large scales. *Ecol. Lett.* **15**, 963–970 (2012).
30. Rybicki, J. & Hanski, I. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecol. Lett.* **16**, 27–38 (2013).

Supplementary Information is available in the online version of the paper.

Acknowledgements We thank P. Ehrlich, E. Kalko, F. Oviedo Brenes, R. Zahawi, L. Frishkoff, K. Holl, H. Kim Frank, M. Knope, J. L. Reid, A. Wrona, H. York and dozens of field assistants and Costa Rican landowners, and the communities and staffs of the Organization for Tropical Studies, Las Cruces Biological Station, the Smithsonian Tropical Research Institute and the Center for Conservation Biology at Stanford University. Research was funded by the Winslow Foundation, the Moore Family Foundation, the German Academic Exchange Service, the German Science Foundation, Peter and Helen Bing, Ralph and Louise Haberfeld, and a Restoration Workshop Research Grant through the Las Cruces Biological Station. C.D.M. and D.S.K. were supported by National Science Foundation Graduate Research Fellowships.

Author Contributions C.D.M. and G.C.D. conceived the study. C.D.M. collected data from Costa Rica, performed analyses, and wrote the manuscript. C.F.J.M. collected data from Panama. D.S.K. assisted with key elements of analysis. All authors contributed ideas to the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to C.D.M. (cdm@stanford.edu).

METHODS

Costa Rican countryside ecosystem bat sampling. The countryside investigation was centred on the Las Cruces Biological Station and Wilson Botanical Garden located in the Coto Brus Valley in southwestern Costa Rica. The Las Cruces Biological Reserve ($8^{\circ} 47' N$, $82^{\circ} 57' W$, 1,100 m above sea level), which serves as a regional biological baseline, protects about 280 ha of primary and mature secondary forest (Fig. 2). The climate is characterized by a long rainy season (9–10 months) followed by a brief dry season, with an average annual rainfall of 3.4 m (ref. 31). Forests in the area are classified as premontane tropical wet forest³². More than 60% of the Coto Brus Valley, once forested, has been converted into cropland and pasture since the 1950s (refs 33, 34). Despite relatively recent deforestation, sediment core analyses reveal a robust, 3,000-year history of agriculture, forest clearing and fire in the region up to the sixteenth century^{35,36}.

Bats were sampled in seven general habitat types at 19 locations within 25 km of Las Cruces Biological Reserve (Fig. 2). All except one habitat type were represented by three sites located in (1) the Las Cruces Biological Reserve (three sites, located 1.3, 1.8 and 1.8 km apart from their nearest neighbouring site in the reserve), (2) small forest fragments (1–20 ha, three sites), (3) 10–20-year-old secondary forest located in large forest fragments (50–75 ha, three sites), (4) thin strips of riparian remnant forests (10–100 m wide, three sites), (5) coffee plantations with about 25% local tree cover on farms (three sites) and (6) coffee plantations with about 5% local tree cover (three sites). Moreover, one ‘supersite’, or a site equivalent in sampling effort to three sites (that is, 60 mist nets were deployed, instead of the normal 20 mist nets at the other 18 sites), operated in La Amistad International Park located about 25 km northeast of the Las Cruces Biological Reserve of the Organization for Tropical Studies. Bat sampling was conducted using constant-effort mist netting. Mist-netting protocols consisted of 20 ground-level mist nets (12 m × 2.5 m, 32-mm mesh) in a 3–5-ha plot haphazardly placed at each site, except the ‘supersite’ located in La Amistad International Park, which consisted of 60 haphazardly placed mist nets within a 10-ha plot. Constant-effort mist netting for bats took place between 24 January and 28 March for four years (2009–2012). Sampling began at sunset and lasted for 4 h each night. Sites were sampled on three nights each year from 2009 to 2011 and only one night in 2012, except the ‘supersite’ located in La Amistad International Park, which was sampled for three nights in 2009 and three nights in 2010.

Captured bats were identified and standard measurements were collected by the method of ref. 37. In 2009, bats were individually, but temporarily, marked by using wing punches³⁹. From 2010–2012 most bats (species weighing more than 5 g, excluding juveniles) were marked with collars fashioned from self-locking cable ties and individually numbered aluminium bands³⁷. All bats were released on site shortly after identification, marking and measurement. All animals were handled and treated ethically within the guidelines of the Institutional Animal Care and Use Committee.

Panamanian island ecosystem bat sampling. The island investigation was conducted on the human-made Gatún Lake ($9^{\circ} 11' N$, $79^{\circ} 53' W$, 26 m above sea level) located in Central Panama. The 1914 damming of the Chagres River during construction of the Panama Canal created the lake and more than 200 islands ranging in size from less than 1 ha to the well-studied 1,560-ha Barro Colorado Island (BCI). Together with five adjacent mainland peninsulas, BCI forms the 5,400-ha Barro Colorado Nature Monument and is contiguous with 22,000-ha Soberanía National Park. The climate is strongly seasonal, with a long rainy season followed by a 4-month dry season. Average annual rainfall is 2.1 m (ref. 38). Dry-season winds have affected exposed islands, resulting in lower forest stature and tree species diversity⁴⁰. Forests in the area are classified as lowland tropical moist forest³².

Bats were sampled at six sites on the mainland peninsulas and at eleven sites on islands of various sizes and distances from the mainland. Bat sampling was conducted with constant-effort mist netting. Mist-netting protocols consisted of six ground-level mist nets (6 m × 2.5 m, 16-mm mesh) placed around the perimeter of a 0.5-ha plot at each site. Constant-effort mist netting for bats took place between October 2003 and October 2005. Each site was sampled for seven or eight complete nights (that is, sunset to sunrise) over a 2-year period. Bats were also captured with a single, large wall net. Bats captured in the wall net were excluded from this study because comparable sampling of the forest canopy was not conducted in the Costa Rican countryside ecosystem.

Captured bats were identified, and standard measurements and demographic data were collected as described in ref. 41. Most bats (species weighing more than 10 g, excluding juveniles) were marked with individually numbered ball-chain necklaces, or, in the case of larger species, with passive, subcutaneous transponders (EURO-ID). All bats were released on site shortly after marking and measurement.

Detailed site descriptions and additional methods and results in the Panamanian island ecosystem can be found in ref. 26. All animals were handled and treated ethically within the guidelines of the Institutional Animal Care and Use Committee.

Landscape habitat classifications. To characterize landscape context in Costa Rica we conducted a manual habitat classification by digitizing aerial photographs. Manual habitat classification was favoured over automated approaches to facilitate the accurate identification of fine-scale landscape features in a complex countryside ecosystem³². Orthorectified aerial photographs used in the habitat classification were from Costa Rica Airborne Research and Technology Applications taken in 2003 and 2005 at 2 m spatial resolution. The habitat map covered 23,600 ha and included all sampling locations. The area was delineated to encompass all study locations sampled by Stanford University’s Center for Conservation Biology (see, for example, refs 33, 42–48). The four ecosystem elements digitized at 2 m resolution over this extent included forest elements (primary and secondary forest of all sizes, single trees, *charral* (early secondary forest), large shrubs, live fences, hedgerows, non-native timber and fruit tree plantations, and non-native garden ornamentals; Fig. 1); agricultural plots (the majority being sun coffee plantations, but also including banana, plantain, tomato, and chili plantations); pasture; and houses, roads and other rural infrastructure. The final map was verified in the field from multiple vantage points, compared with previous studies in the landscape and checked with 150 random samples across the landscape. Forest elements from the manual habitat classification were used in analyses, whereas agricultural plots, pasture, houses, roads and other rural infrastructure were broadly treated as deforested habitat.

To characterize landscape context in Panama we used the ‘BCI Basemap’ data set⁴⁹ to delineate shorelines and islands of Lake Gatún with the ‘BCI Landcover Map 2003’ data set⁵⁰ to confirm forest, water and agriculture cover. Both data sets were accessed in early 2013 online through the Smithsonian Tropical Research Institute GIS Data Portal (<http://mapserver.stri.si.edu/geonetwork/>). All islands were completely forested except for 1 ha on a 16-ha island.

Landscape explanatory variable calculations. Several relevant landscape metrics were calculated for the Costa Rican countryside ecosystem and the Panamanian island ecosystem. The landscape metrics included measures that captured the related variables of habitat area and habitat isolation. We also examined the importance of spatial scale when measuring some of the landscape characteristics in this study. The specific landscape variables calculated and used in statistical modelling included fragment/island size, isolation from contiguous tropical forest, general habitat type, and total forest area within a range of spatial scales. We do not report effects of forest or island fragmentation in this study because measures of fragmentation are often confounded with area and merit a separate, in-depth analysis for clarity⁵¹.

First, we calculated forest fragment or island size in each ecosystem. In the Panamanian island ecosystem each island was clearly distinct and the contiguous forest habitat on each island was easily measured as the total size of the island. The forest fragments in the countryside ecosystem of Costa Rica, however, were slightly more difficult to measure: forest fragments are not easily distinguished because of many fine-scale forest connections across the farming landscape³³ (Fig. 2). In the countryside ecosystem nearly every forest fragment is connected to other forest remnants by live fences, riparian strips and fine-scale ribbons and clusters of trees that weave across ridges, valleys and property boundaries. In most cases these fine-scale forest connections are less than 20 m in width. We therefore arbitrarily omitted forest element connections that were less than 20 m in width to calculate forest fragment size in the countryside ecosystem.

Second, habitat isolation for the countryside and island ecosystems was measured as the Euclidean distance from the centre of a site or mist net to the nearest edge of the Las Cruces Biological Reserve, La Amistad International Park or the nearest Panamanian mainland shore. Sites located inside reserves or mainland peninsulas received negative values that measured their distances from reserve edges and mainland shores.

Third, we included general and broad habitat types as discrete explanatory variables in our models. In the countryside ecosystem each site and net was labelled as reserve, forest fragment or coffee plantation. In the island ecosystem we assigned sites and nets into three categories: mainland interior, mainland edge or island, following ref. 26. Moreover, some categories were lumped during analysis to check for broader differences between islands and all mainland sites in the Panamanian island ecosystem or between forest and non-forest sites in the Costa Rican countryside ecosystem.

Finally, we calculated the total forest area—contiguous or not—for each site and each mist net at multiple spatial scales. For example, the total amount of forest area at each site and mist net, including nearby forest fragments and neighbouring islands, was measured at radii ranging from 50 m to 1 km (measurements were calculated at 50-m increments).

Selecting spatial scales for measuring forest area. Countryside ecosystems and island ecosystems differ substantially because of landscape context. Countryside ecosystems often contain high proportions of human-made habitat that, generally, includes considerable vegetative structure and, depending on the spatial scales used to view habitat characteristics, many smaller ‘patches’ of habitat—often embodied in the form of single trees or fallowed agricultural fields. The surrounding landscape

context in island ecosystems is strictly homogeneous, except for neighbouring islands and the mainland shore. In view of the substantial differences in landscape context and recently proposed ideas, specifically the habitat amount hypothesis¹¹, we champion total habitat area within an appropriately selected spatial scale as a more ecologically relevant measure of habitat.

We used an established approach described in detail in ref. 33 to compare and select appropriate spatial scales during analysis. All results were robust to forest area measured at different spatial scales. For clarity, two spatial scales were selected to measure forest area after *a priori* and *post hoc* analyses, and statistical modelling revealed that few differences in results were observed when forest area was measured among a broad range of spatial scales. We chose spatial scales that emerged as strong predictors after we verified that forest area measured at all spatial scales generally agreed. Site-level analyses used forest area measured within a 1-km spatial scale, and net-level analyses used forest area measured within a 150-m spatial scale. We do not report the nuances observed between different spatial scales in this study, which merit a separate, in-depth analysis to determine their ecological relevance¹¹.

Dimensions of bat biodiversity: species richness estimates. Bat captures in the countryside and island ecosystems were used to inform three dimensions of biodiversity metrics at the resolution of a site or a mist net. The first dimension of bat biodiversity was an estimate of bat species richness at each site (that is, the estimated number of unique species at each site). Chao species richness estimates of bats were used because they perform well with small sample sizes and uneven sampling effort⁵². Chao species richness estimates were used in analyses except when the standard error surrounding the species richness estimate was undefined when calculated in R v.2.15.2 with the vegan package. In cases in which species richness estimates were obtuse, the observed species richness (that is, the observed number of unique species captured at a given site) was used in analysis. In all, four sites used observed species richness values (two Costa Rican coffee plantation sites, one Costa Rican forest fragment site and one Panamanian island site). Results were consistent when observed species richness was used, but the inclusion of Chao species richness estimates dealt with differences in sampling effort between studies in Costa Rica and Panama.

Dimensions of bat biodiversity: species evenness estimates. The second dimension of bat biodiversity is Pielou's species evenness index; this was calculated for each site. Species evenness refers to how equal the assemblage of bat species is numerically, or how close in abundance species at a site are. Pielou's species evenness index is based on the Shannon–Weaver diversity index (denoted by H'):

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (1)$$

In the Shannon–Weaver diversity index, p_i is the proportion of species i at a site, and S is the number of species at a site. Pielou's species evenness index, J , was then calculated for each site; it is defined as

$$J = \frac{H'}{\ln S} \quad (2)$$

Dimensions of bat biodiversity: Assemblage Abundance Shift Index. The third dimension of bat biodiversity in this study centred on changes in abundance-based assemblages of bats relative to bat assemblages found in the baseline habitats for each ecosystem. Bat assemblage abundance shifting was calculated for each mist net because field observations and preliminary analyses of bat assemblages in the countryside ecosystem suggested that differences in the bat assemblage existed between nets within the same site relative to a net's proximity to nearby trees, coffee plantations and pastures. For example, patterns of assemblage differences emerged nightly at a given site when field assistants compared species and abundances of bats extracted from groups of nets closer to habitat transitions with those of bats captured in nets located uniformly in forested habitat or coffee plantations.

The degree of assemblage abundance shift was based on an index we developed that compared a net's abundance-based assemblage similarity to that of the set of nets located in the Las Cruces Biological Reserve and La Amistad International Park, in the countryside ecosystem, or the Panamanian mainland, in the island ecosystem. We used Chao abundance-based similarity coefficients to calculate the similarity of a net's abundance-based assemblage to that of all the nets in each ecosystem baseline. The Chao abundance-based similarity coefficient measures similarity between two samples, and implements a Jaccard-type index that accounts for unseen, shared species; it is defined as

$$\hat{J}abd(U, W) = \frac{\hat{U}\hat{W}}{\hat{U} + \hat{W} - \hat{U}\hat{W}} \quad (3)$$

In equation (3), \hat{U} and \hat{W} represent estimates of each site in such a way that they are adjusted for unseen shared species. To account for the effect of unseen shared

species, the index uses frequencies of observed, rare, shared species to estimate an appropriate adjustment term that accounts for the unseen, shared species. The adjustment is achieved by using the following equations for each estimate:

$$\hat{U} = \sum_{i=1}^{D_{12}} \frac{X_i}{n} + \frac{(m-1)}{m} \frac{f_{+1}}{2f_{+2}} \sum_{i=1}^{D_{12}} \frac{X_i}{n} I(Y_i = 1) \quad (4)$$

$$\hat{W} = \sum_{i=1}^{D_{12}} \frac{Y_i}{m} + \frac{(n-1)}{n} \frac{f_{+1}}{2f_{+2}} \sum_{i=1}^{D_{12}} \frac{Y_i}{m} I(X_i = 1) \quad (5)$$

In equations (4) and (5) each function accounts for unseen, shared species between two sites by using the following logic: if a random sample of n individuals (sample 1) is taken from site 1 and a random sample of m individuals (sample 2) from site 2, and species frequencies in each sample are denoted as $(X_1, X_2, \dots, X_{S1})$ and $(Y_1, Y_2, \dots, Y_{S2})$, respectively, with zero used where species were missing from the sample. Then the pairs of frequencies for the S_{12} species truly shared by the two assemblages are $(X_1, Y_1)(X_2, Y_2) \dots (X_{S12}, Y_{S12})$. Assume that D_{12} of the S_{12} shared species available are actually observed in both samples and that their frequencies are the first D_{12} pairs. Thus, an additional $S_{12} - D_{12}$ species are shared by the two assemblages but absent from one or both samples.

In equations (4) and (5) the indicator function $I(\text{expression})$ is defined such that $I = 1$ if the expression is true, and $I = 0$ if false. Let $f_{1+} = \sum_{i=1}^{D_{12}} I[X_i = 1, Y_i \geq 1]$ be the observed number of shared species that are singletons ($X_i = 1$) in sample 1 (these species must be present in sample 2, but may have any abundance). Now, let f_{2+} represent the observed number of shared species that are doubletons ($X_i = 2$) in sample 1. Similarly, f_{+1} and f_{+2} are the observed number of shared species that are, respectively, singletons ($Y_i = 1$) and doubletons ($Y_i = 2$) in sample 2. If $f_{+2} = 0$ or $f_{2+} = 0$, replace f_{+2} and f_{2+} in the denominators by $f_{+2} + 1$ or $f_{2+} + 1$, respectively. If \hat{U} or \hat{W} is greater than 1, then it is replaced by 1. See ref. 53 for more details, explanations and derivation of equations.

The Chao abundance-based similarity coefficients were calculated for each net (denoted as k) with all nets in the Las Cruces Biological Reserve and La Amistad International Park in the countryside ecosystem, or the mainland in the Panamanian island ecosystem (denoted as b_i), using variations of equations (3) and (4) in R v.2.15.2 with the vegan package. The arithmetic means of all Chao abundance-based similarity coefficients for each net with each baseline sample were calculated (denoted as M):

$$M_b = \frac{1}{n} \cdot \sum_{i=1}^n \hat{J}abd(k, b_i) \quad (6)$$

The mean Chao abundance-based similarity coefficients for each baseline were also calculated relative to all baseline nets for each ecosystem. Finally, we standardized all values by dividing each M_b value by the maximum M_b value in each ecosystem ($M_b\max$):

$$M = \frac{M_b}{M_b\max} \quad (7)$$

The resulting values for each net (that is, M) are between 0 and 1, and represent the abundance-based assemblage similarity of a single net to all the nets located in the corresponding ecosystem baseline, while accounting for detection biases of unseen, shared species. Therefore, the closer a net's value is to 1 in the countryside ecosystem, the more similar that net is in bat species composition and abundances to those of all the nets located inside the Las Cruces Biological Reserve and La Amistad International Park. Similarly, the closer a net's value is to 0 in the island ecosystem, the less similar that net is in bat species composition and abundances to those of all the nets located on the Panamanian mainland.

As calculated in equations (3)–(7), the Abundance-Based Assemblage Similarity Index (that is, M) is dependent on changes in species richness and abundances. The Abundance-Based Assemblage Similarity Index was therefore modified to account for species richness. To account for the effect of species richness in the Abundance-Based Assemblage Similarity Index we performed a regression between that index and the observed species richness values for each net and calculated the residuals from the best-fit model (Extended Data Fig. 2). Nets with five or fewer total captures were excluded from the Assemblage Shift Index (21 nets from the countryside ecosystem and zero nets from the island ecosystem). Positive residuals indicate a greater similarity than expected in assemblage abundances of a net to those of all nets in the corresponding baseline. Negative residuals indicate greater differences in the assemblage abundances than expected.

In its final form, the Assemblage Abundance Shift Index was independent of observed species richness, estimated species richness, species evenness, and total bat abundance. The Assemblage Abundance Shift Index is a holistic measure of how the bat assemblage changes in abundances across space, independently of changes in species richness.

Statistical analyses. All statistical analyses were conducted in a GLMM (generalized linear mixed effects models) framework⁵⁴. Analyses were conducted in R v.2.15.2 (R Development Core Team 2012) and relied extensively on vegan, lme4, nlme and AICcmodavg packages. All variables were tested for normality to meet assumptions of statistical tests.

In our first study contrasting a Costa Rican countryside ecosystem and an island ecosystem, we conducted three suites of analyses for each dimension of bat biodiversity (that is, species richness estimates, species evenness estimates, and the Assemblage Abundance Shift Index). Each set of analyses was designed to identify the effects of ecosystem change on bat biodiversity—specifically concentrating on fragment/island size, isolation from contiguous tropical forest, general habitat type, and total forest area within a wide range of spatial scales (see the section above on selecting spatial scales for measuring forest area). All models avoided collinearity of explanatory variables by disqualifying any linear models that used multiple dependent variables (for example, fragment or island size and total forest area are collinear and were therefore not used in the same statistical model to explain any of the bat biodiversity response variables).

At the onset of each suite of analyses we explicitly tested for interaction terms between landscape variables and the ecosystem type (that is, countryside ecosystem versus island ecosystem). The logic behind testing for interaction terms stems from the fact that the countryside ecosystem and the island ecosystem are separated by about 350 km; they have slightly different species pools and therefore different intercepts within a linear modelling framework. We therefore tested statistically for differences between ecosystems through differences in slopes of functions by using interaction terms in our modelling, rather than only looking for differences in the intercept value.

In each suite of analyses we first tested for differences between the countryside ecosystem and the island ecosystem and restricted our analysis to forested habitats by excluding data from coffee plantations (Extended Data Tables 1 and 2). After differences were confirmed between the two ecosystem types, the second suite of analyses included data from coffee plantations and focused on fitting the best model and selecting the best landscape variable or variables for predicting the bat biodiversity response variable of interest (for example estimated species richness, estimated species evenness or the Assemblage Abundance Shift Index).

After differences between ecosystems were tested, each ecosystem was modelled independently (that is, analyses were performed with data from only a single ecosystem, rather than including a factor within each model that denoted ecosystem type as countryside ecosystem or island ecosystem). Nonlinear functions were included in ecosystem-specific analyses, and the most relevant models are presented in Extended Data Tables 3 and 4.

In all analyses, models were compared by using the corrected Akaike information criterion (AIC_c) and maximum likelihood. Because landscape forest areas measured at multiple spatial scales were autocorrelated and collinear, we identified a single appropriate spatial scale by comparing models using AIC_c and maximum likelihood. Little differences in AIC_c values were observed between landscape variables measured at different spatial scales.

In the GLMM framework we made use of spatial correlation structures to avoid issues of spatial autocorrelation³¹. The UTM (Universal Transverse Mercator) coordinates of each site or net, measured as the centre of each site or net, were used to account for spatial autocorrelation between sites and nets. Models were compared that used a variety of correlation structures, including ‘corSpher’, ‘corLin’, ‘corRatio’, ‘corGaus’ and ‘corExp’ (see pp. 161–170 of ref. 54 for more information). The ‘corRatio’ correlation structure, or the ratio correlation structure, consistently performed best in all models and in all analyses. All analyses make use of the ratio correlation structure with a ‘nugget’. Moreover, site identity was included as a fixed, random effect in analyses conducted at the net level.

The three suites of analyses focused on identifying how the response variables of, respectively, bat species richness estimates, bat species evenness estimates, and the bat Assemblage Abundance Shift Index respond to fragment or island size, isolation from contiguous tropical forest, general habitat type, and total forest area within a range of spatial scales. The model comparisons for each suite of analyses are presented in Extended Data Tables 1–4. Results from models that included forest area measured at multiple spatial scales are not presented for clarity, but few differences between models were observed (see the section above on selecting spatial scales for measuring forest area).

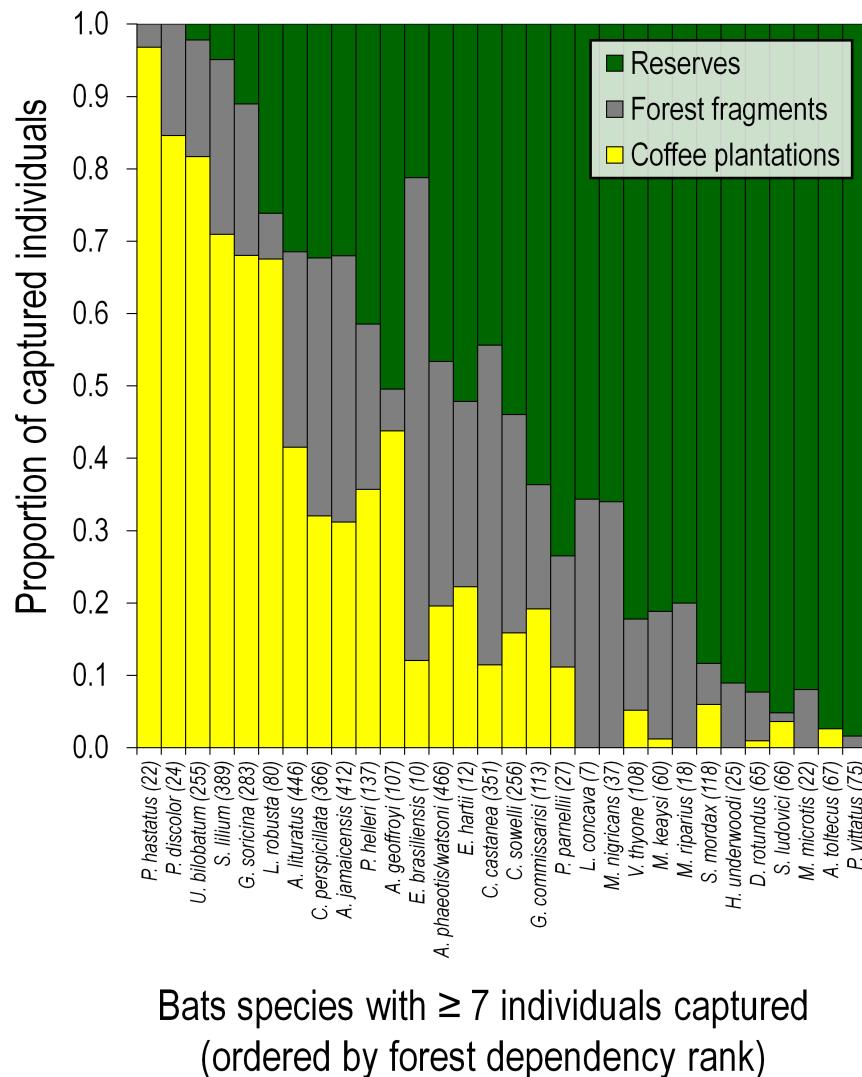
Meta-analysis of studies of bat biodiversity across countryside and island ecosystems worldwide. We searched for all relevant research articles from any time period by using the following Web of Science search query: Title = (bat) AND

Topic = (conservation and fragment*), Timespan = All years, Search language = English. Moreover, we asked authors of many of the research articles we reviewed to ensure that our list was representative—especially authors whose studies were conducted outside the Neotropics (Fig. 4a). From this list we reviewed articles and retained studies that included comparisons between habitats, studies that sampled a minimum of ten different bat species, and studies with replicate sampling sites and similar sampling effort in each habitat type.

For studies that met our criteria, we compared species richness between habitat types in each study. Habitat types in each study fell into the following three broad categories: minimally altered reference habitats (for example forest reserves or contiguous mainland forest); fragmented or isolated reference habitat (for example forest fragments and natural or human-made, true islands); or human-made or naturally open habitat (for example cropland, pasture and, in one study, African savanna). When sufficient data were available, the bias-corrected Hedge’s g^* was calculated and used to determine whether bat species richness differed between habitat types. Reported statistical differences in species richness were used in studies if there were insufficient data to calculate Hedge’s g^* .

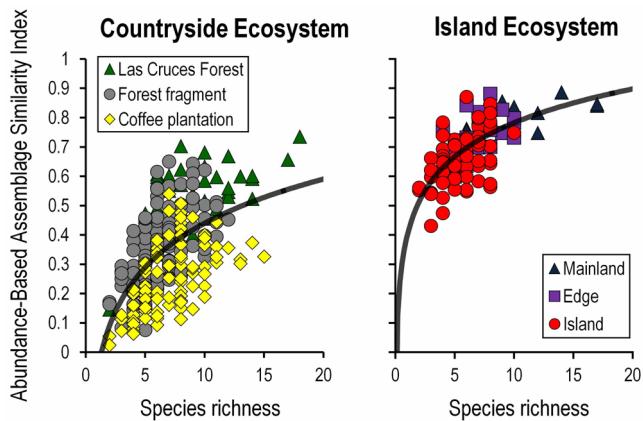
Wide arrays of metrics were used across studies to report bat assemblage shifts between habitat types. Because it is difficult to compare multiple measures of bat assemblage shift between studies, we chose to report assemblage shifts in each study as observed or unobserved. The detailed list of studies used is presented in Supplementary Data.

31. Stiles, F. & Skutch, A. *A Guide to the Birds of Costa Rica* 632 (Instituto Nacional de Biodiversidad, 1989).
32. Holdridge, L. R. *Life Zone Ecology* 146 (Tropical Science Center, 1979).
33. Mendenhall, C., Sekercioğlu, C., Oviedo Brenes, F., Ehrlich, P. & Daily, G. Predictive model for sustaining biodiversity in tropical countryside. *Proc. Natl Acad. Sci. USA* **108**, 16313–16316 (2011).
34. Sansonetti, V. *Quemé Mis Naves en estas Montañas: La Colonización de la Altiplanicie de Coto Brus y la Fundación de San Vito de Java* 99 (Jiménez & Tanzi, 1995).
35. Clement, R. & Horn, S. Pre-Columbian land-use history in Costa Rica. *Holocene* **11**, 419–426 (2001).
36. Mann, C. 1491: *New Revelations of the Americas before Columbus* 541 (Knopf, 2005).
37. Kunz, T. & Parsons, P. *Ecological and Behavioral Methods for the Study of Bats* 920 (Johns Hopkins Univ. Press, 2011).
38. Leigh, E. Jr, Rand, S. & Windsor, D. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term changes* 480 (Smithsonian Institution Press, 1982).
39. Bonacorso, F., Smythe, N. & Humphrey, S. Improved techniques for marking bats. *J. Mamm.* **57**, 181–182 (1976).
40. Leigh, E. Jr, Wright, S., Herre, E. & Putz, F. The decline of tree diversity on newly isolated tropical islands. *Evol. Ecol.* **7**, 76–102 (1993).
41. Handley, C. Jr, Wilson, D. & Gardner, A. *Demography and Natural History of the Common Fruit Bat, Artibeus jamaicensis, on Barro Colorado Island, Panama* 173 (Smithsonian Institution Press, 1991).
42. Mendenhall, C., Daily, G. & Ehrlich, P. Improving estimates of biodiversity loss. *Biol. Conserv.* **151**, 32–34 (2012).
43. Daily, G. C., Ehrlich, P. R. & Sánchez-Azofeifa, G. A. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol. Appl.* **11**, 1–13 (2001).
44. Ricketts, T., Daily, G., Ehrlich, P. & Fay, J. Countryside biogeography of moths in a fragmented landscape. *Conserv. Biol.* **15**, 378–388 (2001).
45. Horner-Devine, M., Daily, G., Ehrlich, P. & Boggs, C. Countryside biogeography of tropical butterflies. *Conserv. Biol.* **17**, 168–177 (2003).
46. Mayfield, M. & Daily, G. Countryside biogeography of Neotropical herbaceous and shrubby plants. *Ecol. Appl.* **15**, 423–439 (2005).
47. Brosi, B., Daily, G., Shih, T., Oviedo Brenes, F. & Duran, G. The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* **45**, 773–783 (2008).
48. Karp, D. et al. Forest bolsters bird abundance, pest control and coffee yield. *Ecol. Lett.* **16**, 1339–1347 (2013).
49. Smithsonian Tropical Research Institute GIS Section. BCI Basemap. Scale 1:50 000 (Smithsonian, 2012).
50. Panama Canal Authority Remote Sensing Unit. BCI Landcover Map 2003 (Cobertura Boscosa 2003—Area de BCI). (Panama Canal Authority, 2003).
51. Fahrig, L. Rethinking patch size and isolation effects. *J. Biogeogr.* **40**, 1649–1663 (2013).
52. Chao, A. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43**, 783–791 (1987).
53. Chao, A., Chazdon, R., Colwell, R. & Shen, T. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* **8**, 148–159 (2005).
54. Zuur, A., Ieno, N., Walker, N., Saveliev, A. & Smith, G. *Mixed Effects Models and Extensions in Ecology with R* 574 (Springer, 2009).



Extended Data Figure 1 | Bats use a variety of habitats in the countryside ecosystem. Shown are the proportions of captured individuals from 30 species in different countryside habitats. Forest dependence rank ranges from forest avoidance (left side of x axis) to reserve dependent (right side of x axis) and was determined by comparing relative abundance in reserves (green) with that in

coffee plantations (yellow). The proportions of individuals captured in smaller forest fragments of various sizes are also shown. Total numbers of individuals per species are listed parenthetically after abbreviated species names. A total of 4,424 individuals are represented.



Extended Data Figure 2 | Assemblage Abundance Shift Index based on ordination analyses of bat abundances and how they collectively shift relative to bat abundances in minimally altered habitat. The plots demonstrate how the Assemblage Abundance Shift Index accounted for changes in species richness to focus on predicting changes in assemblage-level shifts in abundances between habitats. In both ecosystems regression analyses favoured logarithmic relationships between the abundance-based assemblage similarity of the bats captured in a net relative to the reserve or mainland nets and the observed species richness of the bats captured in the net (see Methods). Logarithmic models (solid lines) outperformed linear models in model comparisons (countryside ecosystem $\Delta AIC_c = 22.75$; island ecosystem $\Delta AIC_c = 5.92$). For each ecosystem, logarithmic models were used to calculate the residual assemblage shift for each net that was not explained by changes in species richness but by changes in the abundances of species. The residuals are therefore an index of assemblage abundance shifting after accounting for changes in species richness. Regression coefficients and statistics are described in Extended Data Table 3.

Extended Data Table 1 | Summary of model performances of forest habitat comparisons in an island ecosystem and a countryside ecosystem

Model structure for predicting: Estimated species richness (Chao 1)	K	AICc	ΔAICc	AICcW	CumW	LL
total forest area within 1 km [%] * ecosystem type [factor]	7	176.58	0.00	0.59	0.59	-78.75
general habitat type [factors: island, mainland edge, mainland interior, forest fragment, reserve]	8	178.78	2.20	0.20	0.79	-77.96
log(fragment/island size [ha]) + isolation distance [km] * ecosystem type [factor]	8	180.56	3.98	0.08	0.87	-78.85
total forest area within 1 km [%] + ecosystem type [factor]	6	181.33	4.75	0.06	0.93	-82.84
log(fragment/island size [ha]) * ecosystem type [factor]	7	181.84	5.26	0.04	0.97	-81.38
total forest area within 1 km [%]	5	184.80	8.22	0.01	0.98	-86.15
log(fragment/island size [ha]) + ecosystem type [factor]	6	185.14	8.55	0.01	0.99	-84.74
log(fragment/island size [ha]) + isolation distance [km] + ecosystem type [factor]	7	186.65	10.07	0.00	0.99	-83.78
isolation distance [km] * ecosystem type [factor]	7	187.11	10.53	0.00	1.00	-84.01
isolation distance [km] + ecosystem type [factor]	6	187.48	10.90	0.00	1.00	-85.92
log(fragment/island size [ha])	5	188.58	12.00	0.00	1.00	-88.04
log(fragment/island size [ha]) + isolation distance [km]	6	191.03	14.45	0.00	1.00	-87.69
Null [intercept]	4	195.35	18.77	0.00	1.00	-92.88
isolation distance [km]	5	195.73	19.14	0.00	1.00	-91.61
Model structure for predicting: Estimated species evenness (Pielou)	K	AICc	ΔAICc	AICcW	CumW	LL
isolation distance [km] * ecosystem type [factor]	7	-36.47	0.00	0.97	0.97	27.78
isolation distance [km] + ecosystem type [factor]	6	-28.21	8.26	0.02	0.99	21.93
total forest area within 1 km [%] + ecosystem type [factor]	6	-26.04	10.43	0.01	0.99	20.85
log(fragment/island size [ha]) + isolation distance [km] + ecosystem type [factor]	7	-24.91	11.56	0.00	1.00	22.00
Null [intercept]	4	-22.19	14.27	0.00	1.00	15.90
general habitat type [factors: island, mainland edge, mainland interior, forest fragment, reserve]	8	-22.09	14.37	0.00	1.00	22.48
log(fragment/island size [ha]) + ecosystem type [factor]	6	-19.61	16.85	0.00	1.00	17.63
total forest area within 1 km [%] * ecosystem type [factor]	7	-19.51	16.96	0.00	1.00	19.30
log(fragment/island size [ha])	5	-19.43	17.04	0.00	1.00	15.97
total forest area within 1 km [%]	5	-19.36	17.11	0.00	1.00	15.93
log(fragment/island size [ha]) + isolation distance [km]	6	-18.31	18.15	0.00	1.00	16.98
log(fragment/island size [ha]) + isolation distance [km] * ecosystem type [factor]	8	-16.96	19.50	0.00	1.00	19.91
log(fragment/island size [ha]) * ecosystem type [factor]	7	-16.74	19.73	0.00	1.00	17.91
isolation distance [km]	5	6.67	43.13	0.00	1.00	2.92
Model structure for predicting: Assemblage Abundance Shift Index	K	AICc	ΔAICc	AICcW	CumW	LL
total forest area within 150 m [%] + ecosystem type [factor]	7	-822.21	0.00	0.61	0.61	418.30
log(fragment/island size [ha]) * ecosystem type [factor]	8	-819.93	2.28	0.20	0.81	418.22
total forest area within 150 m [%]	6	-819.25	2.96	0.14	0.95	415.77
log(fragment/island size [ha]) + ecosystem type [factor]	7	-814.46	7.75	0.01	0.96	414.43
total forest area within 150 m [%] * ecosystem type [factor]	8	-814.44	7.77	0.01	0.98	415.47
log(fragment/island size [ha]) + isolation distance [km] + ecosystem type [factor]	8	-814.03	8.18	0.01	0.99	415.27
log(fragment/island size [ha]) + isolation distance [km] * ecosystem type [factor]	9	-812.19	10.02	0.00	0.99	415.41
log(fragment/island size [ha])	6	-811.89	10.32	0.00	0.99	412.09
general habitat type [factors: island, mainland edge, mainland interior, forest fragment, reserve]	9	-810.56	11.65	0.00	1.00	414.60
isolation distance [km] + ecosystem type [factor]	7	-810.36	11.85	0.00	1.00	412.38
log(fragment/island size [ha]) + isolation distance [km]	7	-809.93	12.28	0.00	1.00	412.16
isolation distance [km] * ecosystem type [factor]	8	-808.51	13.70	0.00	1.00	412.51
Null [intercept]	5	-805.75	16.46	0.00	1.00	407.98
isolation distance [km]	6	-805.35	16.86	0.00	1.00	408.82

The summary shows comparisons of forest fragments embedded in a human-dominated landscape and true forest islands surrounded by water; see Extended Data Table 3 for analyses with deforested habitat matrix sampling included. Listed are relevant outputs summarizing the performances of generalized linear mixed effects models predicting estimated bat species richness (green heading), bat species evenness (orange heading) and the Species Assemblage Abundance Shift Index (purple heading; see Methods), using a variety of landscape metrics as explanatory variables. Bat biodiversity and landscape data were gathered from a Costa Rican countryside ecosystem and a Panamanian island ecosystem (that is, ecosystem type). All models are generalized linear mixed-effects models with Gaussian error structures and identity links. In addition, all models include a 'corRatio' correlation structure based on site or net coordinates (UTM). Net-level analyses included site identity as a random effect in all models.

Extended Data Table 2 | Regression coefficients and relevant statistics generated from best-fit models from Extended Data Table 1

Estimated species richness (Chao1)	Estimate	SE	DF	t-value	p-value
(intercept)	8.923	1.476	30	6.048	0.000
total forest area within 1 km [%]	18.818	3.602	30	5.225	0.000
ecosystem type [factor]	15.411	3.141	30	4.906	0.000
total forest area within 1 km * ecosystem type	-18.236	6.222	30	-2.931	0.007

Estimated species evenness (Pielou)	Estimate	SE	DF	t-value	p-value
(intercept)	0.575	0.036	30	15.948	0.000
isolation distance [km]	-0.114	0.024	30	-4.672	0.000
ecosystem type [factor]	0.265	0.060	30	4.395	0.000
isolation distance * ecosystem type	0.107	0.027	30	3.960	0.001

Assemblage Abundance Shift Index	Estimate	SE	DF	t-value	p-value
(Intercept)	-0.052	0.020	262	-2.641	0.009
total forest area within 150 m [%]	0.074	0.025	262	2.979	0.003
ecosystem type [factor]	0.029	0.013	28	2.279	0.031

The models explain relationships between three dimensions of bat biodiversity and the remaining landscape variables after model optimization for forest habitats in an island ecosystem and a countryside ecosystem. Model performances and comparisons are listed in Extended Data Table 1. Summarized models are in bold in Extended Data Table 1. After model selection, best-fit models were rerun and are presented here using restricted maximum likelihood⁵⁴. Data from the deforested habitat in the countryside ecosystem (that is, sun coffee plantations) are not included in these analyses. In-depth ecosystem-specific analyses that include the deforested habitat in the countryside ecosystem are presented in Extended Data Tables 4 and 5.

Extended Data Table 3 | Summary of model performances of ecosystem-specific models

Model structure for predicting: Estimated species richness (Chao 1)	K	AICc	ΔAICc	AICcW	CumW	LL
Countryside ecosystem						
broad habitat type [factors: coffee plantation, forest]	5	113.93	0.00	0.49	0.49	-49.66
general habitat type [factors: coffee plantation, forest fragment, reserve]	6	114.15	0.22	0.44	0.94	-47.58
total forest area within 1 km [%]	5	120.76	6.83	0.02	0.95	-53.07
isolation distance [km]	5	120.86	6.92	0.02	0.97	-53.12
Null [intercept]	4	121.03	7.09	0.01	0.98	-55.08
log(fragment size [ha])	5	121.10	7.16	0.01	1.00	-53.24
log(fragment size [ha]) + isolation distance [km]	6	123.92	9.99	0.00	1.00	-52.46
Island ecosystem						
total forest area within 1 km [%]	5	100.61	0.00	0.87	0.87	-42.58
broad habitat type [factors: coffee plantation, forest]	5	106.32	5.71	0.05	0.92	-45.43
log(island size [ha])	5	106.70	6.09	0.04	0.97	-45.62
general habitat type [factors: coffee plantation, forest fragment, reserve]	6	107.77	7.17	0.02	0.99	-43.69
log(island size [ha]) + isolation distance [km]	6	109.91	9.31	0.01	1.00	-44.76
isolation distance [km]	5	113.26	12.65	0.00	1.00	-48.90
Null [intercept]	4	114.67	14.06	0.00	1.00	-51.67
Model structure for predicting: Estimated species evenness (Pielou)	K	AICc	ΔAICc	AICcW	CumW	LL
Countryside ecosystem						
Null [intercept]	4	-53.24	0.00	0.56	0.56	32.05
isolation distance [km]	5	-50.19	3.05	0.12	0.69	32.40
broad habitat type [factors: coffee plantation, forest]	5	-49.59	3.65	0.09	0.78	32.10
total forest area within 1 km [%]	5	-49.49	3.75	0.09	0.86	32.05
log(fragment size [ha])	5	-49.49	3.75	0.09	0.95	32.05
general habitat type [factors: coffee plantation, forest fragment, reserve]	6	-47.58	5.66	0.03	0.98	33.29
log(fragment size [ha]) + isolation distance [km]	6	-46.12	7.12	0.02	1.00	32.56
Island ecosystem						
isolation distance [km]	5	-7.99	0.00	0.77	0.77	11.72
log(island size [ha]) + isolation distance [km]	6	-4.71	3.27	0.15	0.92	12.56
Null [intercept]	4	-3.24	4.74	0.07	0.99	7.29
total forest area within 1 km [%]	5	2.25	10.24	0.00	0.99	6.60
general habitat type [factors: coffee plantation, forest fragment, reserve]	6	3.01	11.00	0.00	1.00	8.70
broad habitat type [factors: coffee plantation, forest]	5	3.38	11.37	0.00	1.00	6.04
log(island size [ha])	5	3.91	11.89	0.00	1.00	5.77
Model structure for predicting: Assemblage Abundance Shift Index	K	AICc	ΔAICc	AICcW	CumW	LL
Countryside ecosystem						
In(total forest within 150 m [%])	6	-874.88	0.00	0.91	0.91	443.59
total forest area within 150 m [%]	6	-870.21	4.67	0.09	1.00	441.26
general habitat type [factors: coffee plantation, forest fragment, reserve]	7	-852.71	22.17	0.00	1.00	433.56
broad habitat type [factors: coffee plantation, forest]	6	-851.33	23.55	0.00	1.00	431.82
log(fragment size [ha])	6	-847.65	27.23	0.00	1.00	429.98
log(fragment size [ha]) + isolation distance [km]	7	-846.02	28.86	0.00	1.00	430.22
isolation distance [km]	6	-838.98	35.90	0.00	1.00	425.64
Null [intercept]	4	-671.68	203.20	1.00	1.00	339.91
Island ecosystem						
log(island size [ha])	6	-241.10	0.00	0.37	0.37	126.99
broad habitat type [factors: island, mainland]	6	-240.48	0.62	0.27	0.64	126.68
total forest area within 350 m [%]	6	-239.24	1.86	0.14	0.78	126.06
log(island size [ha]) + isolation distance [km]	7	-238.82	2.28	0.12	0.90	127.01
general habitat type [factors: island, mainland edge, mainland interior]	7	-238.17	2.93	0.08	0.98	126.68
isolation distance [km]	6	-233.82	7.28	0.01	0.99	123.35
Null [intercept]	5	-233.53	7.57	0.01	1.00	122.08

The models used were those predicting estimated bat species richness (green heading), bat species evenness (orange heading) and the Assemblage Abundance Shift Index (purple heading), using a series of landscape metrics as explanatory variables. All models are generalized linear mixed-effects models with Gaussian error structures and identity links. In addition, all models include a 'corRatio' correlation structure based on each site's or net's UTM coordinates. Net-level analyses included site identity as a random effect in all models.

Extended Data Table 4 | Regression coefficients and relevant statistics generated from best-fit models from Extended Data Table 3

Estimated species richness (Chao1)	Estimate	SE	t-value	p-value
Countryside ecosystem				
(Intercept)	18.389	1.425	12.900	0.000
broad habitat type (forest) [factors: coffee plantation, forest]	6.235	1.723	3.618	0.002
Island ecosystem				
(Intercept)	8.953	1.309	6.837	0.000
total forest area within 1 km [%]	18.680	3.202	5.834	0.000
Estimated species evenness (Pielou)				
Countryside ecosystem				
(Intercept)	0.818	0.011	76.064	0.000
Island ecosystem				
(Intercept)	0.575	0.045	12.758	0.000
isolation distance [km]	-0.114	0.031	-3.738	0.002
Assemblage Abundance Shift Index				
Countryside ecosystem				
(Intercept)	0.055	0.011	5.105	0.000
ln(total forest area within 150 m [%])	0.063	0.009	7.366	0.000
Island ecosystem*				
(Intercept)	0.030	0.012	2.557	0.012
broad habitat type (island) [factors: island, mainland]	-0.046	0.015	-3.169	0.006

*The second most competitive model is presented for predicting the Assemblage Abundance Shift Index in the island ecosystem. Island size and broad habitat types in the island ecosystem (i.e., islands and mainland) are confounded. Moreover, island size did not explain the community shift index when mainland sites were excluded from analysis (regression statistics for islands only: $t = 0.561$, $P = 0.588$, $N = 66$). Therefore, we concluded that island size is not a better predictor of community shift than broad habitat type. Model coefficients and statistics correspond with the best-fit lines in panel c of Figure 3 in the main text.

The models explain ecosystem-specific relationships between three dimensions of bat biodiversity and the remaining landscape variables after model optimization. Model performance and comparisons are listed in Extended Data Tables 1–3, in which the summarized models are identifiable in the list by bold text. After model selection, best-fit models were rerun and are presented here using restricted maximum likelihood. Additional, less competitive models using island size and isolation distance to predict estimated species richness are also presented for the island ecosystem because of their relevance to island biogeographic theory.

Extended Data Table 5 | Regression coefficients and relevant statistics generated from best-fit models accounting for species richness in the Abundance-Based Assemblage Similarity Index

Abundance-Based Assemblage Similarity Index	Estimate	SE	t-value	p-value
Countryside ecosystem				
(intercept)	0.000	0.020	0.000	1.000
ln(observed number of species)	0.114	0.008	13.810	0.000
Island ecosystem				
(intercept)	0.414	0.035	11.868	0.000
ln(observed number of species)	0.158	0.019	8.381	0.000

The models explain relationships between the Abundance-Based Assemblage Similarity Index and observed species richness for each net (see Methods). Relationships are plotted in Extended Data Fig. 2 and were used to calculate the Assemblage Abundance Shift Index used throughout analyses and results.

Extended Data Table 6 | Observed diurnal roosts in deforested habitats in the countryside ecosystem

Species	Common name	Roost structure	Offspring observed
<i>Glossophaga commissaris</i> ‡	Commissaris' long-tongued bat	Abandoned building on farm	Yes
<i>Glossophaga soricina</i> *†‡	Common long-tongued bat	Abandoned building on farm	Yes
<i>Carollia castanea</i> ‡	Chestnut short-tailed bat	Abandoned building on farm	Yes
<i>Carollia perspicillata</i> * †‡	Seba's short-tailed bat	Abandoned building on farm	Yes
<i>Carollia sowelli</i> ‡	Sowell's short-tailed bat	Abandoned building on farm	Yes
<i>Artibeus jamaicensis</i> *	Jamaican fruit-eating bat	Live fence of "Caña India" or <i>Dracaena fragrans</i>	No
<i>Artibeus lituratus</i>	Great fruit-eating bat	Ornamental, non-native palm tree on farm	Yes
<i>Uroderma bilobatum</i> *†‡	Common tent-making bat	Live fence of "Caña India" or <i>Dracaena fragrans</i>	Yes
<i>Thyroptera tricolor</i>	Spix's disk-winged bat	<i>Heliconia pendula</i> planted near house	No

* Indicates that roost was found by diurnal location of individuals fitted with radio telemetry transponders.

† Indicates that individuals fitted with radio telemetry transponders were originally captured inside forest fragments, but roosted in deforested habitat.

‡ Indicates that roost was used by the same species at least 12 months after initial discovery.

Casual observations of bat roosts were recorded during bat sampling and related field work in Costa Rica. Some roosts were located using 0.25-g radio telemetry transponders, temporarily attached to some animals in a related study. Radio transponders were temporarily attached using techniques adapted from birds³³. All roosts were found between 24 January and 28 March from 2009 to 2012 and were checked occasionally for use and offspring. The only species whose roost was not used over multiple days was *Thyroptera tricolor*. All roosts hosted multiple individuals of the species listed.