

Combining high biodiversity with high yields in tropical agroforests

Yann Clough^{a,1}, Jan Barkmann^b, Jana Jührbandt^b, Michael Kessler^c, Thomas Cherico Wanger^{a,d,e}, Alam Anshary^f, Damayanti Buchori^{g,h}, Daniele Cicuzza^c, Kevin Darras^{i,j}, Dadang Dwi Putra^k, Stefan Erasmil^l, Ramadhani Pitopang^m, Carsten Schmidtⁿ, Christian H. Schulze^o, Dominik Seidel^l, Ingolf Steffan-Dewenter^p, Kathrin Stenchly^a, Stefan Vidalⁿ, Maria Weist^a, Arno Christian Wielgoss^{a,p}, and Teja Tschardt^a

^aAgroecology, Department of Crop Sciences, ^lInstitute of Geography, Cartography, Geographic Information System, and Remote Sensing Department, and ⁿInstitute of Plant Pathology and Plant Protection, Georg-August-Universität Göttingen, D-37077 Göttingen, Germany; ^bEnvironmental and Resource Economics, Department of Agricultural Economics and Rural Development, Georg-August-Universität Göttingen, D-37073 Göttingen, Germany; ^cInstitute of Systematic Botany, University of Zürich, CH-8008 Zürich, Switzerland; ^dEnvironment Institute and School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia; ^eDepartment of Biological Sciences, National University of Singapore, Singapore 117543; ^fFaculty of Agriculture, University of Tadulako, Palu, Central Sulawesi 94118, Indonesia; ^gPeka Indonesia Foundation (Indonesian Nature Conservation Foundation)-Wildlife Trust Alliance, Bogor, West Java 16680, Indonesia; ^hDepartment of Plant Protection, Bogor Agricultural University, Kampus Darmaga Bogor, West Java 16680, Indonesia; ⁱMaster Ecologie, Biodiversité, Evolution, Université Pierre et Marie Curie, F-75005 Paris, France; ^jDépartement de Biologie, Ecole Normale Supérieure, F-75230 Paris, France; ^kCelebes Bird Club, Palu, Central Sulawesi, Indonesia; ^lHerbarium Celebense, Tadulako University, Kampus Bumi Tadulako Palu, Central Sulawesi 94118, Indonesia; ^mDepartment of Population Ecology, Faculty Center of Biodiversity, University of Vienna, A-1030 Vienna, Austria; and ^pDepartment of Animal Ecology and Tropical Biology (Zoology III), Biozentrum, University of Würzburg, D-97074 Würzburg, Germany

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Local and landscape-scale agricultural intensification is a major driver of global biodiversity loss. Controversially discussed solutions include wildlife-friendly farming or combining high-intensity farming with land-sparing for nature. Here, we integrate biodiversity and crop productivity data for smallholder cacao in Indonesia to exemplify for tropical agroforests that there is little relationship between yield and biodiversity under current management, opening substantial opportunities for wildlife-friendly management. Species richness of trees, fungi, invertebrates, and vertebrates did not decrease with yield. Moderate shade, adequate labor, and input level can be combined with a complex habitat structure to provide high biodiversity as well as high yields. Although livelihood impacts are held up as a major obstacle for wildlife-friendly farming in the tropics, our results suggest that in some situations, agroforests can be designed to optimize both biodiversity and crop production benefits without adding pressure to convert natural habitat to farmland.

agroecosystems | ecosystem services | ecology-economy trade-offs | endemic species richness | shade trees

Worldwide demand for food is likely to double by 2050 (1) and demand for bioenergy crops is sharply increasing (2), which fuels expansion of farming activities at the expense of natural habitat. Further pressure on biological diversity is added through intensification of existing agricultural systems by increases in inputs and landscape homogenization (3). Conservation of biodiversity in human-modified landscapes is necessary to protect rare and common species of aesthetic and cultural interest (4) and to maintain ecosystem services, which are ensured by high species diversity (5).

Wildlife-friendly farming is an approach based on the reduction of management intensity, especially in terms of inputs, which has been proposed to enable coexistence of agricultural activity and biodiversity in the same landscapes (6, 7). This type of farming has been criticized for being ineffective at larger scales because lower yields expected under wildlife-friendly farming would increase land conversion if agricultural demand is to be satisfied. Its opponents suggest sparing land for natural habitat by intensifying existing agricultural systems (6–10). This argument may be overly simplistic. Global food provisioning is certainly central to human well-being (11), but does not capture more complex aspects, such as ecosystem resilience, overall monetary, and nonmonetary ecosystem service provision (12–14). In these respects, wildlife-friendly farming may outperform input-based intensified farming. Moreover, in some situations and especially

in the tropics, yields may be higher under wildlife-friendly farming than under conventional practices (15).

The availability of empirical biodiversity/yield relationships is important for the investigation and resolution of these issues. They can be used to evaluate (*i*) if it is possible to combine both high species diversity and high yields (16–19) and (*ii*) along which sections of the management intensity gradient cost-effective opportunities for wildlife-friendly farming arise, if at all (19). Despite the importance of this relationship, datasets integrating biodiversity data with measures of yield or income are scarce (18). Here, we investigate the relationship between yield and species richness along a gradient from low-intensity tropical agroforestry systems to intensively managed tree-crop plantations. Tropical agroforests have a high biological conservation potential (20), as their vegetation structure can mimic natural forest habitat, and are one of the most important tropical agricultural systems covering over 6.4 million km² or 13% of total agricultural land (21).

Our study had a field component and a survey component. In the field component of the study, we collected data on yield and species richness of nine taxonomic groups, including plants, endophytic fungi, vertebrates, and invertebrates during 2 y in 43 smallholder cacao agroforestry systems situated around Lore Lindu National Park in Sulawesi, Indonesia (*Methods*). Cacao agroforests consist of 3- to 6-m high *Theobroma cacao* trees, as well as herbaceous and shade tree strata. Mature plots (10–20 y since establishment) were selected to include a gradient of shading intensities, and received experimental weeding treatments. Other management actions were standardized among plots. As the biodiversity–yield relationship cannot be assumed to be the same in agricultural landscapes dominated by disturbed habitat and in landscapes with a larger proportion of natural or near-natural habitat (22), we also tested whether distance to natural forest changes the biodiversity–yield relationship.

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¹To whom correspondence should be addressed. E-mail: yclough@gwdg.de.

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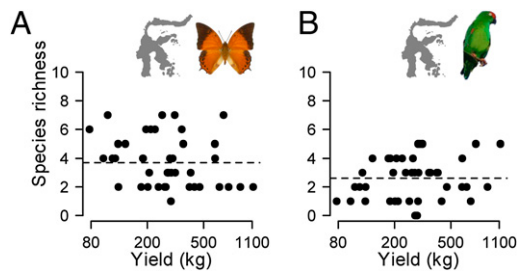


Fig. 2. Endemic species richness and cacao yield do not covary. Relation between species richness of (A) butterflies and (B) birds endemic to the Sulawesi region and yield in smallholder cacao agroforestry plots. Broken lines are intercept-only linear models (regression not significant at the 95% level). $n = 43$ for butterfly and bird data.

such as weeding, pruning of cacao and shade trees, and removal of diseased pods. The inputs were pesticides and herbicides. Our analysis revealed black pod disease *Phytophthora palmivora* to be the most important cause of yield loss in the study region. Interestingly, expenses for pesticides, which include both insecticides and fungicides, were correlated positively with yield (Pearson's $r = 0.34$, $t_{58} = 2.71$, $P = 0.008$), but neither correlated with the incidence of the main pest, the cacao pod borer *Conopomorpha cramerella* (Pearson's $r = 0.12$, $t_{58} = 0.91$, $P = 0.36$) nor with the incidence of the main disease, caused by *P. palmivora* (Pearson's $r = 0.05$, $t_{58} = 0.37$, $P = 0.72$).

Shade Trees, Yield, and Birds. Based on data on yield and percentage cover by shade trees from the field and survey components of the study, we found that expected yield decreased linearly with increasing shade (Fig. 3A). Maximal yield levels conditional on percentage cover by shade trees follow a non-linear pattern, similar to the effect of shading as predicted by the ecophysiological SUCROS-Cocoa model (24), with a decrease of marginal effects of shade reduction with decreasing shade tree cover (Fig. 3A). We contrasted shade quality and quantity effects on yield and species richness of birds, a shade-tree-dependent group. Shade quantity was represented by percentage cover by shade trees, and number of tall trees and number of forest tree species were taken as surrogates for shade quality. The hierarchical partitioning of shade effects on yield showed that almost all of the negative effect of shade on yield could be ascribed to shade tree cover, rather than qualitative aspects of shade (Fig. 3B). For birds, however, both quantitative and qualitative variables played an important role, with the number of tall trees being responsible for most of the shade-related variability in species richness, followed by forest tree species richness and percentage cover by shade trees (Fig. 3C).

Discussion

Biodiversity–Yield Relationship. The debate about land-sparing and wildlife-friendly farming approaches is contentious (6–11). The main argument put forward against wildlife-friendly farming is based on the assumption that it results in lower yields compared with conventional farming, thereby increasing pressure to convert natural habitat to farmland to compensate for the production deficit. Although this argument has already been criticized for oversimplifying the food security issue (11), we set out to investigate its main premise: that is, that yield is negatively related to biodiversity. Using one of the most comprehensive datasets on biodiversity in tropical human-dominated landscapes, we show for smallholder agroforests that supporting species-rich agroforests need not result in a decrease in agricultural output. This finding is remarkable because win-win situations based on biodiversity–yield relationships have not been identified so far. In many agricultural systems, such as in temperate grasslands and arable fields, yields are maintained at a high level through agricultural inputs, which at the same time decrease biodiversity (25). The same finding may apply to large-scale tropical plantation crops. Conserving biodiversity in these systems is therefore associated with costs (26), either in the form of reduced income because of lower yields or increased opportunity costs (27), entailing tradeoffs between conservation and agricultural production (28). In the tropical countryside however, intensity and efficiency of plot management is often low allowing for joint improvement of yield and biodiversity (15).

Agroforests and Conservation. It may be argued that species richness is already strongly depleted in cacao agroforests compared with undisturbed forest, irrespective of management. Indeed, in our study region, many endangered forest species, including the dwarf buffalo anoa (*Bubalus* spp.) and the babirusa (*Babirusa celebensis*), are likely restricted to less disturbed sites, and therefore conserving near-primary forest should be a priority. Our finding that several taxa recorded in agroforests have higher species richness near natural forest also emphasizes the importance of conserving natural habitats. However, the conservation value of agroforests—often the only forested habitat at lower altitudes—can be considerable (20). For example, Sulawesi agroforests host a substantial fraction of forest species, and may host more generalist species than near-primary and secondary forests (23). A potential caveat may be that species richness levels in the agroforests are not yet at equilibrium (29, but see ref. 30), potentially biasing the results. Because long-term data on change in species communities within these agroforests are not yet available, we resorted to choosing well-established, mature agroforests in this study to reduce that risk, yet still acknowledging the need for further monitoring of temporal change in species communities.

Table 1. Overview of the directions of effects of management variables on total species richness observed and yield based on field study plots

Management variables	Species richness	Yield
Percent cover by shade trees	Herbs – Endemic birds –	—
Number of tall trees (>10 m tall)	Butterflies (–) Birds +	
Forest tree species richness	Herbs +	
Frequent weeding	Herbs – Birds –	
Leaf-litter thickness	Amphibians and reptiles + Endemic birds (+)	
Dead wood	Herbs + Amphibians and reptiles (+)	(–)
Distance to forest	Trees – Endemic birds –	(+)
Labor	(Not available)	+
Inputs (pesticides, herbicides)	(Not available)	+

Details can be found in Tables S1 and S3. Effects in parentheses were marginally significant ($0.05 \leq P < 0.10$).

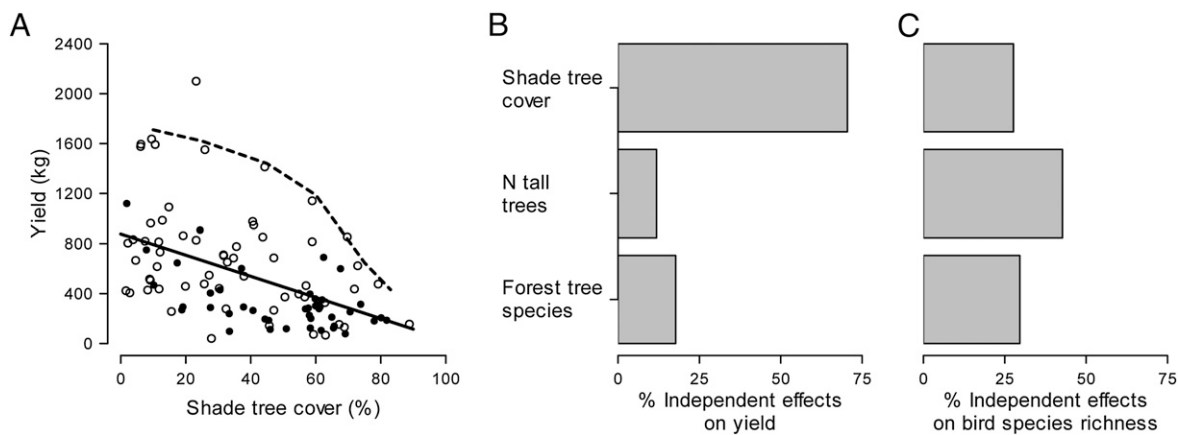


Fig. 3. Shade quantity and quality effects. (A) Expected yield based on data from the field and survey components (closed and open circles, respectively) decreases linearly with increasing percentage cover by shade trees (solid line), but maximum values conditional on shade are nonlinearly related to shade; the broken line is the simulated shade effect prediction from the SUCROS-Cocoa model (24). (B) Partitioning the negative effect of shade on yield shows most of the effect is a result of percentage cover by shade trees, with shade quality variables; that is, number of tall shade trees (>10 m height) and number of tree species, having only very small effects. (C) Bird tree species richness also benefits from the percentage cover by shade trees, but here most of the variability is explained by the above-mentioned shade-quality variables.

Implications for Management. Although our study was not designed to disentangle the effects of all types of management actions, analyses of the determinants of biodiversity and yield helped understand the lack of relationship between species richness and yield in agroforests (Table 1 and Table S3). Although a tradeoff between managing percentage cover by shade trees for biodiversity and yield is apparent (Fig. 3A and Table 1), marginal effects of shade reduction on attainable yield may be relatively weak below 30% to 40% cover by shade trees (Fig. 3A). Qualitative shade variables, such as number of forest tree species and number of tall trees, rather than absolute shade, are important for species richness, especially for trees and birds (Fig. 3). This finding implies that shade reduction, if driven by information on which types of shade trees are particularly valuable for diversity, could be accomplished in a way that is less harmful for biodiversity than is currently the case. In addition, variables related to the management of the plantation floor (reduced weeding frequency, leaf-litter thickness) were associated with species richness of several species groups, without being significantly correlated with yield, suggesting further opportunities for improving biodiversity without reducing yields.

Two important variables correlating positively with yield as determined in the survey component (labor and pesticide use) were standardized in the field component, and thus their impact on biodiversity could not be analyzed. Although labor could be expected to be either biodiversity-neutral or supportive of biodiversity if it replaces pesticide inputs, pesticide use can be expected to have strong negative impacts on biodiversity. Use of pesticides in Sulawesi cacao has been strongly increasing (31), despite little effectiveness against pests (32). Our results reflected this as pesticides were not correlated with pest and disease incidence, suggesting a bias toward higher pesticide expenses in productive plots rather than an actual reduction in crop losses. This example highlights the importance of good agricultural practices (see below), both for biodiversity and agricultural productivity.

Implications for Policy. Our finding that biological conservation and agricultural production can be combined does not mean that the challenges for implementing conservation in agroforestry landscapes should be underestimated (33): Although recent studies have shown that farmers, on average, appreciate a certain amount of shade (~25–30%) (23, 34), this level is often lower than the current level of shading. Farmers are currently unlikely to maintain shade trees in their plantations when they perceive their

removal, which results in short-term yield increases, as an effective way of improving their management. Indeed, current trends clearly indicate ongoing shade tree removal (Fig. S1) (35). If this removal persists, loss of many species of relevance for conservation and ecosystem functioning from agricultural landscapes is inevitable. Surely, more research will be needed to systematically design agroforestry systems, which optimize both the number of species and yield (19), and scientifically sound evaluation of the results of wildlife-friendly certification will have a major role to play. It may be even more important to demonstrate to local smallholder farmers that their economic aspirations can be met by a wildlife-friendly farming approach (33). Moderate shade, high inputs of labor per unit area, and an effective approach to control pests and diseases relying on manual and cultural control are critical for increasing yields and maintaining production in the long term, but are not widely implemented (36–38). An important role may be played by communicating and demonstrating the functional role of shade trees, which increase the productive lifetime of cacao trees (36) and increase the diversity of beneficial organisms, such as insectivorous bird species that may deliver natural pest control (39, 40). Maintaining tropical biodiversity in agroforests through shade tree diversity and habitat complexity requires mechanisms directly aimed at promoting these attributes, rather than simply the number of trees per se. This process may require very different systems than solutions aimed primarily at increasing carbon sequestration or timber resources, which may favor few exotic, fast-growing species (41).

Conclusion

Smallholder agroforests, such as cacao agroecosystems, offer the opportunity to combine high agricultural yield and high biodiversity goals on-farm. The yield–biodiversity relationship and underlying patterns presented here show that suggested tradeoffs (23) are less strong than expected, even for endemic species, and that substantial yield increases and on-farm biodiversity conservation in smallholder agroforestry landscapes may be achieved without increasing pressure on remaining natural forest habitat.

Methods

Biodiversity Plots. Plots 40 × 40 m in size were established in 2006, and monitored and harvested twice a week from November 2006 to September 2008. Twenty-one plots were weeded manually every 3 mo, and another 22 plots every 6 mo. Mean leaf-litter thickness and the number of log piles were recorded. The percentage of shade tree canopy cover was based on hemi-

spheric pictures obtained above the cacao canopy, distance to forest on satellite images of the study area. For details, see *SI Methods*.

Biodiversity Data. Surveys were conducted in all plots (except where specified below) using standard methods whenever available. Trees were recorded in 50 × 50-m plots containing the focal plot. Herb species were recorded in two 5 × 5-m quadrats per plot. Endophytic fungi were recorded from sections cut out of four surface-sterilized leaves from five trees in each of 22 plots, isolated and identified to morphospecies based on spore and mycelium characteristics. Butterflies were caught using banana-baited traps hanging 1 m above the soil. Ants were surveyed in each plot using standardized tuna and sugar baits on 10 cacao trees, as well as the ground 1.5 m from the tree trunks, and identified to morphospecies. Spiders were sampled on a monthly basis using five pitfall traps in each of 22 plots, and identified to morphospecies; immature spiders were excluded from the analyses. Birds were recorded on two mornings per plot. Birds flying overhead were excluded from the analyses. Rats were trapped using live traps (25 on the ground, 15 on the trees) during two three-night sessions per plot. Amphibians and reptiles were surveyed six times during day and night hours. For details on the biodiversity surveys, see *SI Methods*.

Cacao Management Documentation Survey. The cacao agroforestry survey was conducted in 2007 in five villages of the project region. In each village, a sample of one cacao plot of each of 12 cocoa-producing households was selected, resulting in a total sample size of 60 cacao plots. The plots were chosen to represent the entire intensification gradient of high- to low-canopy closure values. Percentage cover by shade trees, plot owner perceptions about soil fertility, patterns of input use, and adoption of agricultural innovations, as well as the impact of pests, diseases, dryness, and tree age on cocoa production were recorded. During 2007, plot owners recorded inputs and outputs as well as structural changes in plot vegetation. For details on the cacao management documentation survey, see *SI Methods*.

Data Analysis. The relationship between yield and total number of species observed per plot was investigated using generalized linear models with yield (log-transformed), distance to forest (square-root-transformed) and account for the decreasing effect of the forest with increasing distance), and region-fitted to the observed species numbers. A small number of very high-yielding plots inflated leverage of these plots, justifying log-transformation of yield. Analyses based on the raw yield gave results similar in terms of strength and direction of effects. Given that species richness data are positive discrete but contains fewer zeros than count data, even at low average species richness, we assumed normal errors instead of Poisson errors and confirmed adequacy with residual plots. Model adequacy of full and best models, including normality, homoscedasticity of the residuals, and whether a linear relationship was likely to be appropriate, was checked graphically using diagnostic plots (42). The Pearson values for the pairwise correlations of all of the explanatory variables were below $r = 0.61$ (number of tall trees and percentage cover by

shade trees in the biodiversity plots). The variance inflation factors were below 3 (42). Models with all possible combinations of the explanatory variables were then generated, and the best model chosen on the basis of the Akaike Information Criterion (AIC) with a correction for small sample sizes (AICc) (43). We repeated this analysis with estimated species richness from individual-based rarefaction, applied to taxonomic groups for which abundance data were available. Samples were rarefied to 5 individuals for trees, 13 individuals for all butterflies, 29 for spiders, 5 for trees, 5 for amphibians and reptiles (six low-abundance sites excluded), and 5 for endemic butterflies (21 low-abundance sites excluded). Abundance of rats was very low throughout the sites, so we omitted this group from the analysis.

We used the same approach to identify the predictors of observed species richness. Generalized linear models were fitted with observed number of species (or morphospecies) as a dependent variable, and as explanatory variables weeding intensity, number of forest tree species, number of tall trees, percent cover by shade trees, volume of dead wood, leaf-litter thickness, altitude, and region, as well as distance to forest (square-root transformed) and its interaction with all other variables. Number of forest tree species, dead wood, and leaf litter were omitted from models fitted to number of forest tree species as a dependent variable. The drivers of yield were analyzed as follows: for the experimental plots ($n = 43$), we used dry yield as a dependent variable and the same explanatory variables as for the analysis of biodiversity (see above), including their interaction with distance to forest. For the survey plots ($n = 60$), we used the explanatory variables, percent cover by shade trees, the expenses for synthetic pesticides and fertilizer (in Indonesian Rupiah, log_e-transformed), labor (in hours, log_e-transformed), the number of forest trees, the incidence of the main disease (*Phytophthora palmivora*), the incidence of the main pest (*Conopomorpha cramerella*), distance to forest (square-root-transformed) and its interaction with all other variables. To model the effect of percentage cover by shade trees on yield using the joint data from field and survey components, we used a generalized linear model with percent cover as the only explanatory variable. We compared the data to the predictions of relative yield conditional on percent cover by shade trees as based on the SUCROS-Cocoa model (24). We fixed maximum expected yield in the region at 1,800 kg·ha⁻¹ based on the observed data, ignoring one outlier. To partition the variance in yield and bird species richness that could be ascribed to percentage cover by shade trees, the number of tall shade trees, and the number of shade tree species, we used a hierarchical partitioning approach (44) with root-mean-square prediction error as a goodness-of-fit index.

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- Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. *Nature* 418:671–677.
- Field CB, Campbell JE, Lobell DB (2008) Biomass energy: The scale of the potential resource. *Trends Ecol Evol* 23:65–72.
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: Is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188.
- Gaston KJ, Fuller RA (2008) Commonness, population depletion and conservation biology. *Trends Ecol Evol* 23:14–19.
- Flynn DFB, et al. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecol Lett* 12:22–33.
- Fischer J, et al. (2008) Should agricultural policies encourage land sparing or wildlife-friendly farming? *Front Ecol Environ* 6:380–385.
- Matson PA, Vitousek PM (2006) Agricultural intensification: Will land spared from farming be land spared for nature? *Conserv Biol* 20:709–710.
- Balmford A, Green RE, Scharlemann JPW (2005) Sparing land for nature: Exploring the potential impact of changes in agricultural yield on the area needed for crop production. *Glob Change Biol* 11:1594–1605.
- Ewers RM, Scharlemann JPW, Balmford A, Green RE (2009) Do increases in agricultural yield spare land for nature? *Glob Change Biol* 15:1716–1726.
- Phalan B, Balmford A, Green RE, Scharlemann JPW (2011) Minimising harm to biodiversity of producing more food globally. *Food Policy* 36:562–571.
- Raudsepp-Hearne C, et al. (2010) Untangling the environmentalist's paradox: Why is human well-being increasing as ecosystem services degrade? *Bioscience* 60:576–589.
- Chapell MJ, Lavalle LA (2011) Food security and biodiversity: Can we have both? An agroecological analysis. *Agric Human Values* 28:3–26.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis* (Island Press, Washington, DC).
- Albrecht G, et al. (2007) Solastalgia: The distress caused by environmental change. *Australas Psychiatry* 15(Suppl 1):S95–S98.
- Badgley C, et al. (2007) Organic agriculture and the global food supply. *Renew Agr Food Syst* 22:86–108.
- Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. *Science* 307:550–555.
- Kleijn D, Sutherland WJ (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *J Appl Ecol* 40:947–969.
- Mattison EH, Norris K (2005) Bridging the gaps between agricultural policy, land-use and biodiversity. *Trends Ecol Evol* 20:610–616.
- Koh LP, Levang P, Ghazoul J (2009) Designer landscapes for sustainable biofuels. *Trends Ecol Evol* 24:431–438.
- Bhagwat SA, Willis KJ, Birks HJB, Whittaker RJ (2008) Agroforestry: A refuge for tropical biodiversity? *Trends Ecol Evol* 23:261–267.
- Zomer RJ, Trabucco A, Coe R, Place F (2009) *Trees on Farm: Analysis of Global Extent and Geographical Patterns of Agroforestry* (ICRAF Working Paper no. 89. Nairobi, Kenya: World Agroforestry Centre).
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecol Lett* 8:857–874.
- Steffan-Dewenter I, et al. (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc Natl Acad Sci USA* 104:4973–4978.
- Zuidema PA, Lefelaar PA, Gerritsma W, Mommer L, Anten NPR (2005) A physiological model for cocoa (*Theobroma cacao*): Model presentation, validation and application. *Agric Syst* 84:195–225.
- Kleijn D, et al. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc Biol Sci* 276:903–909.

26. Nilsson FOL (2009) Biodiversity on Swedish pastures: Estimating biodiversity production costs. *J Environ Manage* 90:131–143.
27. House A, et al. (2008) Integrating production and natural resource management on mixed farms in eastern Australia: The cost of conservation in agricultural landscapes. *Agric Ecosyst Environ* 127:153–165.
28. Hodgson JA, Kunin WE, Thomas CD, Benton TG, Gabriel D (2010) Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecol Lett* 13:1358–1367.
29. Kuussaari M, et al. (2009) Extinction debt: A challenge for biodiversity conservation. *Trends Ecol Evol* 24:564–571.
30. Ranganathan J, Daniels RJR, Chandran MDS, Ehrlich PR, Daily GC (2008) Sustaining biodiversity in ancient tropical countryside. *Proc Natl Acad Sci USA* 105:17852–17854.
31. Wanger TC, Rauf A, Schwarze S (2010) Pesticides and tropical biodiversity. *Front Ecol Environ* 4:178–179.
32. Wood BJ, Fee CG, Cheong SS, Foh CC (1992) Trials on control of the cocoa pod borer *Conopomorpha cramerella* (Snellen) in Sabah by regular complete harvesting. *Trop Pest Manage* 38:271–278.
33. Garcia CA, et al. (2010) Biodiversity conservation in agricultural landscapes: Challenges and opportunities of coffee agroforests in the Western Ghats, India. *Conserv Biol* 24:479–488.
34. Barkmann J, et al. (2008) Confronting unfamiliarity with ecosystem functions: The case for an ecosystem service approach to environmental valuation with stated preference methods. *Ecol Econ* 65:48–62.
35. Tschardt T, et al. (2011) Multifunctional shade-tree management in tropical agroforestry landscapes. *J Appl Ecol* 10.1111/j.1365-2664.2010.01939.x.
36. Ahenkorah Y, Akrofi GS, Adri AK (1974) The end of the first cocoa shade and manurial experiment at the Cocoa Research Institute of Ghana. *J Hort Sci* 49: 43–51.
37. Jührbandt J, Duwe T, Barkmann J, Gerold G, Marggraf R (2010) *Tropical Rainforests and Agroforests under Global Change*, eds Tschardt T, et al. (Springer, Heidelberg), pp 115–140.
38. Clough Y, Faust H, Tschardt T (2009) Cacao boom and bust: Sustainability of agroforests and opportunities for biodiversity conservation. *Cons Lett* 2:197–205.
39. Philpott SM, et al. (2009) Functional richness and ecosystem services: Bird predation on arthropods in tropical agroecosystems. *Ecol Appl* 19:1858–1867.
40. Clough Y, Dwi Putra D, Pitopang R, Tschardt T (2009) Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biol Conserv* 142:1032–1041.
41. Ghazoul J (2007) Challenges to the uptake of the ecosystem service rationale for conservation. *Conserv Biol* 21:1651–1652.
42. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York), 1st Ed.
43. Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York), 2nd Ed.
44. Chevan A, Sutherland M (1991) Hierarchical partitioning. *Am Stat* 45:90–96.