Impact of cocoa agricultural intensification on bird diversity and community composition

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Keywords: cacao, biodiversity, avian, farm, land sparing, sustainable, meta-analysis, chocolate

Running head: Birds in cocoa farms

Article impact statement: Loss of tree and understory plant diversity on cocoa farms and landscapes reduces diversity of endemic, frugivore, and insectivore birds.

Abstract:

Cocoa (*Theobroma cacao*) agriculture threatens tropical biodiversity to meet growing demand for chocolate, but cocoa sustainability initiatives largely overlook biodiversity conservation. To inform these initiatives, we analyzed how cocoa agriculture impacts bird diversity at farm and landscape scales with a global meta-analysis of 23 studies. Bird diversity declined sharply in intensified, low shade cocoa. Cocoa with >30% canopy cover from diverse trees retained similar bird diversity to forest, but composition changed: diversity...
of “agriculture avoiders” – endemics, frugivores, and insectivores – declined, while diversity of “agriculture associates” – habitat generalists, migrants, nectarivores, and granivores – increased. As forest decreased on the landscape, the difference in bird community composition between forest and cocoa also decreased, indicating agriculture associates replaced agriculture avoiders in forest patches. Our results emphasize the need to conserve forested landscapes (land sparing) and invest in mixed-shade agroforestry (land sharing), with each strategy benefiting a diverse and distinct biological community.

Introduction:

Global biodiversity peaks in tropical regions and is threatened by increasing demand for agricultural commodities (Laurance et al. 2014). With most tropical deforestation driven by agriculture, supply chains face pressure to minimize biodiversity loss while maximizing production and profitability, leading companies to commit to sustainable agricultural practices (Rueda et al. 2017, Curtis et al. 2018). However, such sustainability commitments may not prioritize or ensure tropical biodiversity conservation, given the wide range of environmental, economic, and social issues that fall under the sustainability umbrella (Freidberg 2017). Even programs that explicitly prioritize biodiversity conservation face challenges to identify best practices because biodiversity responses often vary between regions, landscapes, and farming systems (De Beenhower et al. 2013). Quantitative syntheses that account for such variation in responses are critical to guide sustainability initiatives.

Cocoa (*Theobroma cacao*) is an important tropical commodity farmed on 11.8 million hectares of land, primarily in biodiversity hotspots within West Africa, South America, and Southeast Asia (FAOstat 2019, Fig 1). When cocoa is grown under a native tree canopy, biodiversity of the agroforest can match that of adjacent forest (Faria et al. 2007). Such
agroforestry systems contribute to landscape-level biodiversity by connecting forest patches, facilitating plant and animal dispersal, and providing wildlife habitat (Jose 2012) and can sustain the productivity of cocoa trees indefinitely (Saj et al. 2017). However, increasing demand for cocoa drives tropical deforestation (Barima et al. 2016; Kroeger et al. 2017). An estimated 2-3 million ha of tropical forest were converted to cocoa from 1988-2008 (Kroeger et al. 2017), and many cocoa agroforestry systems have been intensified through tree reduction or elimination (Clough et al. 2009a). The resulting monocultures tend to collapse under the combined pressures of diseases, pests, and soil degradation, thereby pushing cocoa agriculture into forests with better soils (Ruf & Schroth 2004; Clough et al. 2009a) and leaving behind impoverished land, biological communities, and human inhabitants (Leaky 2018).

Despite these troubling trends, the cocoa industry is uniquely positioned to adopt and implement global sustainability standards, given high supply chain consolidation (Carodenuto 2019) and high sustainability certification rates (Uribe-Leitz & Ruf 2019). Thirty-three companies and three governments recently published plans to increase cocoa sustainability and end cocoa-driven deforestation (Carodenuto 2019). These plans adopt a sustainable intensification paradigm, calling for increased cocoa yields without additional deforestation or negative environmental impact (Andres & Bhullar 2016). Intensifying production would theoretically decrease pressure on forests, but explicit biodiversity conservation planning is absent from these plans, especially at the farm level (Cocoa & Forests Initiative 2019).

Greater clarity about cocoa intensification’s effect on biodiversity is needed, given current deforestation rates and projected increases in cocoa demand (Kozika et al. 2018). Unfortunately, cocoa is poorly represented in quantitative biodiversity reviews compared with coffee and other tropical tree crops (Najera & Simonetti 2010; Şekercioğlu 2012; De
Beenhouwer et al. 2013; Jeezer et al. 2017). Case studies show that cocoa management intensity and surrounding forest composition can impact biodiversity (Faria et al. 2007, Bisseleua et al. 2009), yet no study quantitatively synthesizes the impact of cocoa intensification at both farm and landscape scales (e.g. De Beenhouwer et al. 2013). Nearby forest may control the presence of forest-dependent species in cocoa farms (Clough et al. 2009b), while diversity and structure of the tree canopy may impact species diversity at the farm level (Van Bael et al. 2007). Variation in habitat requirements can also lead to major differences in how taxonomic and functional groups respond to intensification (Clough et al. 2009b; Kessler et al. 2009). For example, cocoa agroforests can retain the same species richness and abundance of birds as nearby forest (Faria et al. 2007), yet bird species composition may vary dramatically between the two habitats (Greenler & Ebersole 2015). Global reviews of bird responses to agroforestry suggest full community and insectivore diversity declines across an intensification gradient of forest to agroforest to monoculture, while frugivore, nectarivore, and migratory bird diversity is generally greatest in structurally complex agroforestry systems (Najera & Simonetti 2010; Şekercioğlu 2012). Accounting for such guild-level responses to landscape and farm management is critical to understand how the proposed sustainable intensification of cocoa will impact biodiversity.

Here we present a quantitative meta-analysis and review of bird responses to cocoa agriculture that account for intensity of farm management and landscape composition. We focus on birds because they are well studied at guild and community levels within cocoa growing regions and are strong indicators of ecosystem health (Renwick et al. 2012). We test two hypotheses: 1) diversity of full bird communities and some guilds decline over a gradient of agricultural intensification (rustic cocoa, mixed shade cocoa, low shade cocoa, and annual monoculture) relative to nearby native forest; and 2) avian diversity is correlated with both farm- and landscape-scale habitat features. We also compare bird responses to intensification

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among geographic regions and biodiversity indicator metrics, as response to intensification may vary among regions (De Beenhowser et al. 2013) or the indicator metrics employed in the analysis (Kessler et al. 2009; Santini et al. 2017). We use these results to provide specific recommendations to conserve biodiversity within cocoa agricultural areas.

**Methods:**

**Literature review**

We searched relevant Web of Science databases (CABI, ZOOREC, WOS, SCIELO, BCI, BIOSIS, CCC) for literature from 1995 to 2019 using TS=(“cocoa” OR “cacao”) AND (avi* OR bird* OR biodivers*). Databases accessed full time span except CCC (1998-present) and SCIELO (2002-present). We reviewed titles and abstracts of the 952 returns and excluded studies that did not report bird community or diversity metrics in a cocoa agricultural system. We reviewed the full text and cited and citing literature of 42 retained articles in English and Spanish. We identified 4 additional articles that met inclusion criteria and excluded 23 studies if they only reviewed other studies or lacked error estimates for reported biodiversity metrics. Sixteen studies were retained for meta-analysis that compared bird biodiversity indicator metrics (e.g. species richness, abundance, diversity and community similarity indices) between forest and at least one adjacent cocoa system. Fourteen studies were retained that reported relationships between bird indicator metrics and continuous habitat covariates at the cocoa farm or landscape scale (see Appendix S1 for PRISMA flow diagram).

**Data compilation**

We compiled a dataset for meta-analysis with comparisons of bird biodiversity indicator metrics and variances among forest and adjacent agricultural systems (directly adjacent to a few km away) that included cocoa. We retained three biodiversity indicator
metrics—species richness, abundance, and Shannon’s index—and excluded metrics not reported from multiple studies (e.g. evenness and functional diversity indices). We preferentially retained estimated metrics over observed metrics to account for sampling biases if studies reported both. We used the online Web Plot Digitizer (Rohatgi 2019) to extract numerical values from figures, including supplemental information and appendices. Nearly all community similarity analyses reported index values without metrics of variance or ordination analyses with non-comparable axes, so we compiled a separate dataset with similarity indices, excluding ordinations. Finally, we compiled a dataset with signs and significance values of correlations between bird biodiversity and continuous habitat covariates for qualitative analysis. We determined this dataset was inappropriate for meta-analysis given a lack of comparable correlation coefficients, variance metrics, and habitat covariates assessed across studies. We retained data from farm-level habitat covariates that described the shade canopy above cocoa—canopy cover, canopy height, tree density, Shannon’s index of trees, tree species richness, and vertical structural diversity—and the cocoa understory—leaf litter, herbaceous ground cover, Shannon’s index of understory plants, and understory species richness. We also retained landscape-level covariates that described distance to forest or percent forest on the landscape. We excluded other habitat covariates given low management relevance.

Data classification

For each comparison in the meta-analysis dataset, we classified the bird group studied as full community or guild. We excluded guilds based on family, genera, or foraging strata due to low representation (reported in ≤ 2 studies). The retained foraging guilds are comprised of unique species (frugivore, granivore, insectivore, nectarivore, omnivore) but may include species from retained life history guilds (biome or regional endemics, forest
specialists, habitat generalists, migrants). We classified land cover as native forest based on author descriptions (including intact primary, disturbed primary, and mature secondary forest) or one of the following agricultural systems: rustic cocoa agroforestry (cocoa under a native shade canopy of retained primary forest trees; typically > 60% canopy cover), mixed cocoa agroforestry (cocoa under a mix of planted shade and fruit trees with some retained forest trees, typically 30-50% canopy cover), low shade cocoa (intensified cocoa plantation with 0-2 species of nitrogen-fixing, fruit, or timber trees; typically 0-20% canopy cover), or annual monoculture (annual commodity crops cultivated without shade). Cocoa classifications follow Rice and Greenberg (2000) but divide the “planted shade cocoa” category into “mixed shade” (analogous to commercial polyculture; Perfecto et al. 2007) and “low shade,” which includes mono-specific timber shade and legume service shade (Somarriba & Beer 2011). Abandoned cocoa was excluded given low industry applicability. We classified landscapes as high forest (>40% native primary forest in a 10 km radius around study site) or low forest (<39.9% forest) based on author descriptions. If landscape composition was not reported, we extracted the study location from the study text or maps and calculated forest cover in a 10 km buffer around a study location in ESRI ArcMap 10.6 using the Primary Humid Tropical Forest raster for the year 2001 (Turubanova et al. 2018) and subtracting forest loss pixels from the University of Maryland Forest Loss raster between the year 2000 and the study year (Hansen et al. 2013). Finally, we classified each study as belonging to one of three regions: Latin America, Southeast Asia, and West Africa. In total, we identified 214 comparisons of biodiversity indicator metrics between forest and adjacent agriculture and 14 comparisons of bird community similarity between land cover classes (Appendix S2).

Data analysis
We calculated a bias-corrected, Hedges’ $g^*$ statistic of effect size (Borenstein et al. 2011) for each comparison between a native forest baseline and an adjacent agricultural system. We tested heterogeneity of the full data set and subsets of bird and habitat groups with fixed-effect meta-analysis prior to analysis. $I^2$ and Q values indicate substantial heterogeneity for all groups, justifying random effects and meta-regression (Appendix S3). We thus fit sets of linear mixed effects models with study as a random effect and inverse-variance weighted Hedges’ $g^*$ as the dependent variable, using packages ‘meta’ version 4.9.9 (Balduzzi et al. 2019) and ‘metafor’ version 2.1.0 (Viechtbauer 2010) in program ‘R’ (R Core Team 2017). For all models, we calculated fit statistics with package ‘dmetar’ version 0.0.9 (Harrer et al. 2019), used a $\Delta AIC_c$ cutoff of 2 to identify supported models (Burnham and Anderson 2004), and assessed unexplained heterogeneity of supported models with $I^2$ and QE statistics.

To determine if diversity of the full bird community varied significantly between each agricultural system and if response varied among biodiversity metrics, we compared a null model and models with agricultural system, biodiversity metric, and the interaction as independent variables. We pooled biodiversity metrics if the model gave no support for variation in effect size among metrics. We tested if guilds responded differently to agricultural systems by comparing a set of models with guild, biodiversity metric, agricultural system, and the interactions as independent variables. In this model set, the interaction between agricultural system and guild was supported (Appendix S7), but interaction models do not provide useable confidence intervals around Hedges’ $g$ estimates around categorical comparisons. We therefore fit no-intercept models for each guild with agricultural system as the predictor and to determine if Hedges’ $g^*$ for each category differed from zero. Using the results of this analysis, we classified each guild as an “agriculture avoider” if Hedges’ $g^*$ estimates were greater than zero at $P<0.05$ or an “agriculture associate” if estimates were
significantly less than zero for at least one agricultural system. These designations indicate average guild trends and do not imply that all species within the guild respond similarly to cocoa agriculture. Next, we tested if guilds respond differently to cocoa in high and low forest landscapes using an intercept model with landscape composition as the independent variable for full bird communities and agriculture avoider and associate groups. Finally, we tested if birds respond differently to agriculture among regions by comparing a model set with a null, region, agricultural system, and the interaction as predictors. We report the inverse of Hedges’ $g^*$ in all figures such that positive values indicate higher diversity in the agricultural system than the forest baseline.

For the community similarity dataset, case studies reported multiple indices, precluding a direct comparison across all values. Sorensons’ Index was the most reported metric of similarity, and we compared those values with a non-parametric Kruskal-Wallis rank sum test across agricultural systems ordered by intensification. For the habitat correlation dataset, we plotted number of case studies reporting positive, negative, or non-significant relationships with on-farm habitat features. Correlations with landscape-level covariates (e.g. distance to forest) were rarely analyzed, so we report those qualitatively in the discussion section.

**Results:**

Sixteen studies reported comparisons of bird biodiversity metrics between forest and cocoa agriculture ($N=45$ comparisons for full bird communities, $N=169$ comparisons for guilds). For full bird communities, model selection indicated that biodiversity varied significantly among agricultural systems regardless of the biodiversity indicator metric used (Appendix S4). In the supported model, biodiversity indicator metrics in rustic and mixed cocoa agroforestry systems were similar to nearby forest baselines, while low shade cocoa and...
monoculture had significantly lower biodiversity indicator metrics than forest (Fig. 2, Appendix S5).

Community Similarity

Seven studies reported 14 comparisons of bird community similarity between native forest and agricultural systems. The Sorensens’ Similarity Index was used in 67% of comparisons and showed decreasing community similarity relative to forest with increasing land use intensification: average Sorensens’ Index (SE) = 0.68 (.10) for rustic shade cocoa, 0.60 (.14) for mixed shade cocoa, and 0.35 (.10) for annual monocultures (Appendix S6). A Kruskal-Wallis rank sum test indicates a trend of decreasing community similarity with intensification (Chi= 5.54, df=2, P=0.06).

Bird Guilds

The changes in community similarity are reflected by the divergent responses of bird guilds to cocoa agriculture, with both additive and interaction models supported between guilds and agricultural system (Appendix S7). As for full communities, models testing if bird response varied with indicator metric were not supported (Appendix S7). The top model showed diversity of endemic birds and frugivores was significantly lower in all agricultural systems than nearby forest baselines (Fig. 3 A). Insectivore diversity declined significantly in all agricultural systems except rustic cocoa, which maintained similar diversity to forest (Fig. 3 A). Granivores, generalists, migrants, and nectarivores showed similar or greater diversity in agriculture than forest (Fig. 3 B). Generalists were more diverse in rustic and mixed shade cocoa agroforests than forest, while granivore diversity was greater than forest in mixed shade and monoculture, but not rustic cocoa (Fig. 3 B). Migrant and nectarivore diversity was only greater than forest in mixed shade cocoa (Fig. 3 B). We found no support for differences in diversity of forest specialists and omnivores between agricultural systems and forest.
although forest specialists were unstudied in low shade cocoa and monoculture (Fig. 3 C, Appendix S8). Heterogeneity in effect sizes among cases was well explained by the models for endemics and granivores ($I^2 < 31\%$), but all other guilds retained substantial unexplained heterogeneity after models were fit ($I^2 > 87\%$; Appendix S8). High heterogeneity is expected due to differences in sites, data collection methods, analysis methods, and bird community composition, but high heterogeneity supports interpretation of results as general trends rather than precise effect size differences that would hold in all cases.

**Farm-Level Habitat**

Fourteen studies reported relationships between on-farm habitat features and bird diversity. Full bird communities and agriculture avoiders (endemics, frugivores, and insectivores) were well studied (N=51 and N=44 cases respectively) compared with agriculture associates (habitat generalists, migrants, nectarivores, and granivores; N=24). Diversity of full bird communities was positively correlated with canopy metrics in 70% of studied cases, understory metrics in 60% of cases, and with both tree and understory plant diversity in all cases (Fig. 4A). Understory plant metrics were poorly studied compared to canopy metrics across bird groups, although understory plant richness and diversity were positively correlated with all bird groups in all studied cases (Fig. 4). Canopy tree richness and vertical structural diversity were also positively correlated with diversity for all bird groups (Fig. 4). Basal area was the only canopy metric that never positively correlated with bird diversity, and it was negatively associated with agriculture associates in half of the cases (Fig. 4).

**Landscape Effects**

Magnitude of effect size differences in bird diversity between cocoa systems and forest was conditional on landscape composition for both agriculture avoider and agriculture associate groups (Fig 5; Appendix S9). Relative to nearby forest baselines, agriculture associates
gained significantly more diversity in agricultural landcovers when forest comprised > 40% of the landscape composition (Fig. 5, Appendix S10). Agriculture avoiders showed the opposite pattern, with significantly lower diversity in cocoa relative to forest when landscapes were highly forested (Fig. 5). Landscape was not a supported covariate for full bird communities (Fig. 5, Appendix S9).

**Geographic Region**

Region was a supported covariate in models to explain bird responses to cocoa agriculture for full bird communities but not for agriculture avoider or associate groups (Appendix S11). However, estimates of mean effect size differences in full bird community metrics between forest and agriculture did not show meaningful, regional differences for full bird communities (Appendix S12). For full communities, sampling of agricultural systems was uneven between regions, with rustic cocoa primarily studied in Latin America, low shade cocoa studied exclusively in SE Asia, and West Africa being underrepresented in general (Appendix S12).

**Discussion:**

Our results show that intensification of cocoa agroforestry into low or no shade systems causes large losses in bird diversity, while mixed shade and rustic cocoa agroforestry maintain similar bird diversity to forest. However, some forest species are lost in any cocoa agricultural system, as even rustic cocoa only retained an average of 68% community similarity to nearby forests. Differences in community composition resulted from divergent responses of bird guilds to cocoa intensification. Relative to forest, the diversity of endemic, frugivore, and insectivore birds declined in rustic and mixed shade cocoa, while generalist, migrant, nectarivore, and granivore diversity increased. This compensatory mechanism appears absent in low shade cocoa plantations, given large declines in bird diversity relative to native forest. Low shade, intensified cocoa therefore possesses low biodiversity.

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conservation potential, while intermediate to high shade systems may support a diverse but
distinct biological community relative to native forest.

Habitat structure of the shade canopy and understory positively predicted bird
diversity on cocoa farms in most cases. Positive correlations with canopy tree density,
richness, and diversity were particularly well documented for full communities and
agriculture avoider guilds, as was understory plant richness for avoider guilds. Interestingly,
canopy cover was a poorly studied predictor of bird diversity, despite being an evaluation
metric in several third-party sustainability certifications (Waldron et al. 2015, Newsom et al.
2017). All but two studies found linear relationships between bird diversity and canopy
metrics, but in Ecuador, bird species richness peaked in cocoa with 35-40% shade cover
(Waldron et al. 2012), while >20% native tree cover in Indonesian cocoa was required to
retained forest birds (Sohdi et al. 2005). Although the relative importance of distinct canopy
metrics varies among locations (Clough et al. 2011, Van Bael et al. 2007), most studies
agreed that bird diversity increased linearly with the richness, diversity, and density of
canopy trees. This finding stresses the conservation importance of managing cocoa farms as
multi-species and multi-strata agroforestry systems.

Landscape composition around cocoa farms affected the bird guild diversity
relationships between cocoa and nearby forest. The diversity differences in agriculture
associate and agriculture avoider guilds between cocoa and forest were less pronounced in
landscales with low forest composition than landscapes with high forest. In cocoa farms
within highly forested landscapes, agriculture avoider guilds had significantly less diversity
than in forest while agriculture associate guilds showed greater diversity. As the diversity
relationship between cocoa and forest did not vary with landscape for the full bird
community, these findings suggest that agriculture avoiders were lost from the forest patches
in low forest landscapes and replaced by agriculture associates. The alternative explanation—
agriculture avoiders preferentially select cocoa farms in low-forest landscapes and vice
versa—is improbable given the habitat correlations we documented between agriculture
avoider guilds and tree diversity and density. These findings highlight the importance of
conserving not just forest patches, but highly forested landscapes for guilds that generally
avoid cocoa agriculture. Cocoa industry commitments to zero-deforestation support this
conservation action (Carodenuto 2019) and could maximize their impact by focusing on
landscapes that retain at least 40% forest.

Findings from case studies further support the importance of highly forested
landscapes for guilds that avoid cocoa agriculture. In Brazil, forest specialists, frugivores and
insectivores declined sharply in landscapes with less than ~50% primary forest cover
(Morante-Filho et al. 2016), while ~74% forest was required to retain those guilds in
Cameroon (Kupsch et al. 2019). Research from Ghana and Indonesia report linear declines in
those guilds and surprisingly nectarivores (which we found have equal or greater diversity in
cocoa than forest) as distance to forest increases (Clough et al. 2009b; Clough et al. 2011;
Deikumah et al. 2017). Given differences in the methodologies and spatial scales of these
studies, we recommend further research to quantify the interactions and critical thresholds
between forest cover, cocoa cover, and biodiversity across cocoa regions to help further tailor
industry zero-deforestation or reforestation commitments to the scales and landscape
configurations with greatest potential to conserve endemic, at-risk, and forest dependent
species.

The conservation value of cocoa agriculture depends on the diversity, composition,
and fitness of the biological community that occupies it. As with shade coffee, mixed shade
cocoa retained a greater diversity of migratory birds than forest (Philpott et al. 2008). In the
Americas, migratory birds have declined continuously since at least 1970, making them a group of conservation concern (Rosenberg et al. 2019). Migratory bird abundance and species richness in cocoa was positively correlated with vertical canopy structure (Estrada & Coates-Estrada 2005), indicating that cocoa agroforestry can be managed to conserve members of this guild and other species of conservation concern with similar habitat requirements. However, agroforests may contain ecological traps (Sanchez-Clavijo et al. 2020), thus future studies that quantify the survival and demographics of the species or guilds that occupy these agroforests would greatly increase our understanding of the potential benefits and consequences they pose to biodiversity.

Among guilds that avoided agriculture, frugivores and endemic species were particularly sensitive to cocoa agriculture. Frugivore diversity in other tropical agroforestry systems can exceed forest (Najera & Simonetti 2010; Şekeçicioğlu 2012), suggesting frugivores are uniquely sensitive to cocoa agriculture perhaps due to their species composition in cocoa regions or unique habitat features of cocoa agroforests. Insectivores, which provide important pest regulation services (Van Bael et al. 2007), maintained similar diversity in rustic cocoa and forest. However, understory insectivores are highly sensitive to tropical forest disturbance ( Şekeçicioğlu et al. 2012; Van Bael et al. 2007), suggesting species composition within the guild likely shifted between forest and rustic plantations. Agriculture avoider diversity was also positively associated with manageable features of cocoa farming systems including understory plant diversity and richness. However, active weed suppression on cocoa farms may hinder the adoptability of recommendations to retain understory plants, and off-farm conservation areas are likely required to maintain a diverse understory bird assemblage. Forest specialists were remarkably underrepresented in our metanalyses as an artifact of the guilds that case studies chose to report. Although we found no difference in their diversity between forest and rustic cocoa, broader reviews show agricultural
intensification drives biodiversity loss of forest specialists (De Beenhowser et al. 2013), which cautions against overinterpretation of this result.

In conclusion, our results reveal two complimentary strategies by which cocoa sustainability initiatives can support biodiversity conservation. The first is targeting zero deforestation commitments at highly forested landscapes that still retain high diversity of species and guilds that generally avoid cocoa agriculture or agricultural landscapes. The aggressive zero-deforestation commitments by industry groups have already started the process and achieved government support in several countries that lead global cocoa production (Carodenuto 2019, Cocoa & Forests Initiative 2019). Achieving similar commitments in other cocoa producing countries, and most importantly, achieving successful and permanent implementation of these policies, should continue to be a priority for all participants in cocoa supply chains. The second strategy is protecting and implementing rustic and mixed shade agroforestry systems that maintain a diversity of tree species and vegetation structures. This strategy conserves different birds than zero-deforestation policies and may be at odds with the industry push towards sustainable intensification. Cocoa agricultural intensification has led to widespread prevalence of cocoa monocultures with low biodiversity value (Clough et al. 2009a), and it is currently unclear if sustainable intensification commitments will change that trend. Prior industry efforts to maximize cocoa yields have been criticized for overlooking farmer initiatives to diversify production within the farming area that could increase the ecological diversity and economic viability of the farm unit (Mithofer et al. 2017). Indeed, industry and government extension programs can drive canopy tree cover well below optimal levels for cocoa production (Waldron et al. 2015; Asare et al. 2019), with negative impacts for farmers and biodiversity. In contrast to intensification, farm-diversification programs can re-incorporate timber species and native
trees that produce non-timber products with market value into cocoa agroforests, creating wins for both farmer livelihoods and biodiversity (Sonwa et al. 2014).

Potential tradeoffs between cocoa production and shade cover may limit industry interest in retaining and implementing rustic and mixed shade cocoa agroforestry systems. This trepidation may be unfounded, however, as case studies suggest 30-60% shade tree cover optimizes the tradeoff between cocoa yields and biodiversity conservation (Bisseleua et al. 2009; Waldron et al. 2015; Jeezer et al. 2017; Blaser et al. 2018). Similarly, a canopy cover of 30-40% either optimizes or negligibly impacts cocoa yields in many regions (Clough et al. 2011; Blaser et al. 2018; Asare et al. 2019), although careful configuration of shade trees and farmer extension programs may be required to achieve maximum yield benefits (Waldron et al. 2015; Andres & Bhullar 2016). Additionally, mixed and rustic shade agroforestry systems provide greater ecological resilience and ecosystem services than low shade cocoa (Jacobi et al. 2013; Mortimer et al. 2018). As cocoa industry groups and national governments launch programs to meet zero-deforestation and sustainable intensification commitments, a focus on incorporating a diversity of trees into the cocoa farm system will be critical to linking the conservation of on-farm biodiversity with landscape-level biodiversity.

Supporting Information

PRISMA flow diagram for study selection (Appendix S1), number of paired comparisons between agriculture and forest by guild (Appendix S2), heterogeneity among effect sizes (Appendix S3), model selection comparing Hedges’ g* in full bird community biodiversity by habitat and metric (Appendix S4), model estimates for the top model in S4 (Appendix S5), bird community similarity index values between native forest and agriculture (Appendix S6), model selection comparing Hedges’ g* in biodiversity of nine bird guilds by habitat and metric (Appendix S7), Model estimates for top model in S7 (Appendix S8), model selection...
comparing Hedges’ $g^*$ in bird biodiversity by landscape (Appendix S9), model estimates for top model in S9 (Appendix S10), model selection comparing Hedges’ $g^*$ in bird biodiversity by region (Appendix S11), and model estimates for top model in S11 (Appendix S12). All data files, R codes, and case study metadata are available at https://osf.io/fd6kc/. Queries (other than absence of the material) should be directed to the corresponding author.

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**Figures**

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Figure 1: Land used for cocoa agriculture by country with overlay of biodiversity hotspots and locations of all studies used in meta-analysis. Cocoa data from FAOstat 2019.
Figure 2: Mean effect size differences in three bird biodiversity metrics between native forest and four farming systems of increasing intensity. Values above zero indicate greater biodiversity values in the farming system than forest and vice versa. Asterisks indicate the model estimate of Hedges’ $g^*$ is significantly different than zero at $P < 0.001$. Model estimate tails show 95% CIs, and the number of comparisons analyzed for each agricultural system in parentheses. Compiled from 16 studies.
Figure 3: Mean effect size differences in biodiversity metrics between native forest and four farming systems of increasing intensity for nine functional bird groups that are classified as
A) “agriculture avoiders” if response metrics are lower in agricultural systems than forest, B) “agriculture associates” if response metrics are greater in agricultural systems than forest, or C) “neutral” if no difference was recorded between forest and agriculture. Values above zero indicate greater biodiversity in the farming system than forest and vice versa. Asterisks indicate the estimated Hedges’ g* is significantly different than zero at * P< 0.05, ** P< 0.01, *** P < 0.001. Model estimate tails show 95% CIs.
Figure 4: Number of significant correlations between bird biodiversity metrics and habitat features managed on cocoa farms for A) full bird communities, B) guilds that avoid agriculture (endemics, frugivores, and insectivores), and C) guilds associated with agriculture (generalists, migrants, granivores, and nectarivores). Positive (pink) and negative (dark blue) relationships reported significant at P < 0.05, with number of nonsignificant cases in italics at bottom of each plot. Asterisks indicate a significant effect (P < 0.05) across studies with binomial exact test. All habitat variables continuous and compiled from 14 studies.
Figure 5: Mean effect size differences in bird biodiversity metrics between native forest and cocoa agriculture for all birds, guilds that avoid agriculture (endemics, frugivores, insectivores), and agriculture associates (granivores, generalists, migrants and nectarivores) in landscapes with high (>40%) and low (<40%) amounts of primary forest in a 10 km radius around the study site. Asterisks indicate the estimated Hedges’ $g^*$ values are significantly different between landscapes for each group at * $P < 0.05$, and *** $P < 0.001$. Tails show 95% CIs around model estimates. Compiled from 16 studies.