Using land-use history and multiple baselines to determine bird responses to cocoa agroforestry

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Abstract

Agroforests can play an important role for biodiversity conservation in complex landscapes. A key factor distinguishing among agroforests is land-use history – whether agroforests are established inside forests or on historically forested but currently open lands. The disparity between these land-use histories means that the appropriate biodiversity baselines may differ, which should be accounted for when assessing the conservation value of agroforests. Specifically, comparing against multiple baselines in forest and open land could enrich our understanding of species responses by contextualizing them. Here, we implemented this approach using data from a recently published meta-analysis on the response of bird diversity to various kinds of cocoa (*Theobroma cacao*) agroforestry (rustic, mixed shade cocoa, low shade cocoa). First, we re-grouped cocoa agroforests based on land-use history into forest-derived and open-land derived agroforests. Second, we compared forest- and open-land-derived agroforests to forest and open land, representing two alternative baselines. We found that forest-derived agroforests hosted bird diversity similar to

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forests. Open-land-derived agroforests were significantly less diverse than forests and comparable to open lands. There are two key contributions of this work: first, given the biodiverse forest baseline, we highlight the risk of forest degradation through cocoa agroforest establishment. Moreover, we emphasize rehabilitation opportunities through open-land-derived cocoa agroforestry on historically forested open land, but more studies are needed to determine how birds may benefit. Second, comparing against multiple baselines offers the opportunity to discuss relative contributions of agroforestry to bird conservation on a landscape-scale.

Introduction

A careful baseline choice is pivotal for studies on the effect of land system change on biodiversity. Such research commonly relies on control-impact (i.e., space-for-time) designs which heavily depend on chosen baselines (i.e., controls; De Palma et al., 2018). Here, heterogeneous controls can represent a major source of bias (De Palma et al., 2018), and varying controls between studies pose a challenge for synthesis research (Gerstner et al., 2017). To partly address this issue, working with more than one control and producing multiple comparisons can be useful. For example, by comparing vanilla agroforests in Madagascar to little used old-growth-forest and heavily used forest fragments, Fulgence et al., (2021) show that amphibian communities in agroforests are significantly less species rich than old-growth forests but comparable to forest fragments; highlighting both opportunities and limitations of amphibian conservation in agroforestry systems.

In agroforestry research, different baselines – various kinds of forest, perennial monoculture, and open land – are commonly used (Mupepele et al., 2021), but rarely in combination within the same study (Martin et al., 2020). In this context, considering multiple baselines may be particularly beneficial since agroforests can differ in land-use history (Martin et al., 2020), meaning they originate from different baselines (forests or open lands; **Fig. 1**). A non-quantitative review highlights the importance of land-use history for ecosystem services and biodiversity in tropical agroforests (Martin et al., 2020). The paper suggests that forest-derived agroforests typically degrade forests, while open-land derived agroforests typically rehabilitate open lands. This path-dependency leads to contrasting outcomes for ecosystem services and biodiversity. Taking the land-use history of focal agroforests and multiple baselines into account may thus enrich our understanding of the value of agroforests for biodiversity and ecosystem services.

One crop commonly farmed in agroforestry systems is cocoa, the most important ingredient of chocolate. Practiced across multiple tropical biodiversity hotspots (FAO, 2020), cocoa agroforestry has been acknowledged for its value for biodiversity (Bisseleua et al., 2009; Jarrett et al., 2021) and ecosystem services (De Beenhouwer et al., 2013). This value has also been recognized in new

quantitative syntheses on biodiversity (Bennett et al., 2022; Maney et al., 2022) and ecosystem services (Niether et al., 2020) across various types of cocoa agroforestry. Nonetheless, cocoa agroforestry expansion into forest is a key driver of forest loss in West Africa (Tutu Benefoh et al., 2018) and contributes to forest degradation in Latin America and South-East Asia (Rice & Greenberg, 2000). But cocoa agroforests can also be established on historically forested open land: for example, on Sulawesi, Indonesia, 50% of cocoa plantations were established on open lands and 50% inside forests (Rice & Greenberg, 2000). Land-use history may also affect biodiversity (Kessler et al., 2009; Maney et al., 2022), ecosystem services (Nijmeijer et al., 2019), and labor requirements (Ruf, 2001) in cocoa agroforestry, and might be itself influenced by policy (Orozco-Aguilar et al., 2021). Importantly, benefits of open-land-derived agroforestry would likely turn into trade-offs if agroforests were established on naturally open land, such as savannas. However, given the climatic niche of cocoa (Schroth et al., 2016), encroachment into forests appears to be a far greater risk than encroachment into naturally open lands (Tutu Benefoh et al., 2018).

In this light, a recent meta-analysis by Bennett et al. (2022) makes an important contribution to our understanding of bird responses to cocoa agroforestry. Their synthesis brings together data from 23 papers to compare 'rustic cocoa', 'mixed shade cocoa', 'low shade cocoa', and 'annual monoculture' to a forest baseline, thereby combining studies with space-for-time designs (De Palma et al., 2018) and a single baseline (i.e., forest). In a first analysis, they compared species richness, abundance and Shannon Index, before refining their analysis for various functional guilds. Additionally, the authors looked at how various habitat features and landscape composition influence bird communities in cocoa agroforests.

Here, we reanalyse data presented by Bennett et al. (2022) to demonstrate how considering landuse history and multiple baselines enriches our understanding of the conservation value of cocoa agroforests for birds. Specifically, we searched underlying original studies for information on the land-use history of focal agroforests and regrouped agroforests into two new categories: 'forestderived cocoa agroforest' and 'open-land-derived cocoa agroforest'. In a second step, we compared outcomes to forests and historically forested open lands, representing two alternative baselines.

Methods

To separate bird diversity estimates between forest- and open-land-derived agroforests, we gathered information on the land-use history of focal agroforests in the introduction and method sections of 16 papers underlying the comparison of three bird biodiversity metrics (Richness, Abundance, Shannon's Index) in the meta-analysis by Bennett et al. (2022). Additionally, we extracted information on the human influence (e.g., selective logging, secondary vs. primary forest,

fragmentation) on forest baselines from the introduction and methods sections of the same studies (**Appendix S1**). We also renamed the land-use category 'annual monoculture' from (Bennett et al., 2022) to 'open land', in line with (Martin et al., 2020). According to the underlying papers, the open land category includes predominantly annual crops, but also plantain (Harvey & González Villalobos, 2007) and pasture (Estrada et al., 1997; Estrada & Coates-Estrada, 2005; **Appendix S1**).

The separation based on land-use history revealed that ten studies compared forest-derived agroforests to forests while four studies contrasted open-land-derived agroforests to forests. Two studies directly compared forest- and open-land-derived cocoa agroforests (Kessler et al., 2009; Reitsma et al., 2001). We then used the data made available by Bennett et al. (2022) to provide additional results under the consideration of land-use history and multiple alternative baselines.

We first excluded two studies (Schulze et al., 2004; Waltert et al., 2011) which used the same underlying data as other studies (Waltert et al., 2004, 2005) included in the meta-analysis by (Bennett et al., 2022), leading to pseudoreplication (**Appendix S1**). We also excluded Reitsma et al. (2001), since the study encompasses forest-and open-land-derived agroforests without separating the two during data collection and analysis, preventing the calculation of separate effect sizes. Furthermore, two studies took place at the same sites but with different data (Estrada et al., 1997; Estrada & Coates-Estrada, 2005), one including only Neotropical migrants (Estrada & Coates-Estrada, 2005). In this case, we followed Bennett et al. (2022) and included both. Lastly, we excluded three studies without whole community diversity measures. This left us with ten studies (**Appendix S1**).To directly compare open-land-derived agroforests to open land, we calculated hedges' g^* for this comparison using the same approach as Bennett et al. (2022). This was possible for only two effect sizes of different metrics from the same study (Waltert et al., 2004; **Appendix S2**). We also calculated the Hedge's g^* statistic of effect size for the two types of cocoa agroforests and the open lands against the available forest baselines. We operationalized this using the same methods and R-scripts as Bennett et al. (2022).

Before fitting the Hedge's *g** into a model, we first ran a test of the heterogeneity of the data of the full community with fixed-effect meta-analysis using 'metacont' function with the R-package *meta* version 5.0.2 (Balduzzi et al., 2019). In line with Bennett et al. 2022, we found significant heterogeneity between the studies for the comparison of all land-use systems to the forests (**Appendix S3**). Thus, we used a linear mixed effect model to determine the difference between the three land systems (forest-derived agroforest, open-land-derived agroforest, and open land) and the forests using 'metareg' function with the R-package *metafor* version 3.0.2 (Viechtbauer, 2010) running the study key as a random effect. We did not find significant heterogeneity for the

comparison of open-land-derived agroforest to open-land (**Appendix S3**). Therefore, to compare open-land derived agroforests to open land, we used a simple linear model.

Results

In our re-analysis, we found that forest-derived agroforests and the available forest baselines host a comparable bird diversity (hedges' g^* estimate (SE) = -0.3144 (0.3416), p-value = 0.36, Fig. 2A, Appendix S4, based on 19 diversity measures from seven studies). Open-land-derived agroforests had a species diversity comparable to open lands (hedges' g^* estimate (SE) = -0.1529 (0.5035), p-value = 0.76, Fig. 2B, Appendix S5, based on two diversity measures from one study). Directly comparing forest- and open-land-derived agroforests to each other was not possible because only Kessler et al. (2009) included an estimate for forest- and open-land-derived agroforests. However, when comparing both to the available forest baselines, open-land-derived agroforests had significantly lower bird diversity measures than forests (hedges' g^* estimate (SE) = 1.4312 (0.6308), p-value = 0.023, based on 11 diversity measures from four studies, Fig. 2A, Appendix S5).

The assessment of forest baselines in underlying studies in Bennett et al. (2022), revealed that only three studies compared agroforests to 'near-primary forest' or 'mature forest', while 13 studies compared agroforests to fragmented, selectively logged, disturbed, used, or secondary forests (**Appendix S1**).

Discussion

Our analysis shows that considering the land-use history of focal agroforests along with multiple baselines offers an opportunity to draw nuanced conclusions about the bird conservation value of different cocoa agroforestry systems.

Our findings are in line with Bennett et al. (2022) for 'rustic' and 'mixed shade' forest-derived agroforests – these systems host a bird diversity comparable to available forest baselines (**Fig. 2**, **Appendix S3**). However, the recommendation of "implementing 'rustic' and 'mixed shade' agroforestry systems" (Bennett et al., 2022) is controversial, as rustic agroforests are by-definition forest-derived (Moguel & Toledo, 1999), so establishing new ones will contribute to forest degradation and associated species turnover – as documented by Bennett et al. (2022). Considering multiple taxa, a recent analysis by Maney et al. (2022) also documents significant decreases in diversity under the conversion of primary forest to forest-derived cocoa agroforestry.

In our study, the forest baselines included in the underlying papers are representing fragmented (Faria et al., 2006), disturbed (Davies et al., 2015), partly secondary (Reitsma et al., 2001; Van Bael et

al., 2007), or selectively logged forests (Greenler & Ebersole, 2015; Harvey & González Villalobos, 2007; comprehensive list for all studies in **Appendix S1**). Such forests will typically have lower bird diversity than less disturbed primary forests – which may themselves lose species (Stouffer et al., 2021) – suggesting shifting baseline syndrome and an overestimated value of forest-derived agroforests for bird diversity. Nonetheless, we agree with the recommendation of maintaining already established biodiverse forest-derived agroforests, in line with Martin et al. (2020) and Raveloaritiana et al. (2021).

For 'low shade intensified' cocoa, we show that the non-consideration of land-use history and the comparison with forest, as done by Bennett et al. (2022), comes with various interpretation challenges that should be carefully considered. We find that all 'low shade intensified' agroforests included in Bennett et al. (2022) were established on open lands (**Appendix S1**). Considering those agroforests as the last step of an intensification from forest via 'rustic' and 'mixed shade' cocoa to 'low shade intensified' cocoa is thus inaccurate. Instead, these open-land-derived 'low shade intensified' agroforests could have rehabilitated the open lands on which they were established, leading to possible gains of biodiversity. One study (Waltert et al., 2004) included with two estimates in the bird diversity meta-analysis also collected data on bird diversity in open lands (i.e., annual cropping in Bennett et al. (2022)), enabling a direct comparison to an alternative baseline. This comparison reveals a similar diversity in open-land-derived agroforests as in open lands (**Fig. 2**, **Appendix S3**), but estimates are uncertain given the small sample size. However, Waltert et al. (2004) shows species turnover between the two land uses and much lower diversity in cocoa compared with forests, suggesting distinct bird communities in open-land-derived agroforests.

The single study included in the meta-analysis by Bennett et al. (2022) that directly compared forestand open-land-derived agroforests (Kessler et al., 2009) shows higher bird diversity in forest-derived than in open-land-derived agroforests, underlining the importance of considering land-use history. However, Kessler et al. did not compare their open-land-derived agroforests with open lands, prohibiting conclusions on the role of land-use history. Similarly, Reitsma et al. (2001) mention that focal agroforests differed in land-use history, but did not consider this difference in their analysis.

Extrapolating to the landscape scale, our additional meta-analysis suggests that the benefits of cocoa agroforestry for bird conservation can be best harnessed under the consideration of land-use history. Seeing open-land-derived agroforests as a rehabilitation opportunity (Martin et al., 2020), rather than a degradation state (Bennett et al., 2022), may help to improve management practices so that agroforests deliver for conservation and production goals. For example, the rehabilitation lens could help to identify historically forested but currently open lands as priority areas for

agroforestry promotion (Martin et al., 2020), or could steer programs to increase shade tree diversity in open-land-derived agroforests (Osen et al., 2021) with potential benefits for birds (Gordon et al., 2007). Here, additional studies focusing on open-land-derived agroforests will be valuable. On the other hand, forest-derived agroforests could serve as buffer zones around protected areas or could be maintained as biodiverse elements within agricultural landscapes (Tscharntke et al., 2011). Evaluating the benefits of agroforestry in response to both principal baselines, forests and open lands, can help to make agroforestry a key element of complex agricultural landscapes.

Given these important findings, we argue that future (meta-)analyses on biodiversity and ecosystem services in agroforestry systems should consider land-use history and multiple baselines. Here, going beyond 'forest' and 'open land' as broad categories may offer an interesting research avenue. Specifically, comparing forest-derived agroforests to old-growth forests as well as selectively logged or secondary forests could give a more nuanced picture on the value of agroforests for biodiversity, possibly showing that they are less diverse than old-growth forests but comparable to logged or secondary forests. However, for 'open land' we were already short in available estimates, so a further differentiation in various kinds of open lands would require additional empirical studies in cocoa agroforests.

We conclude that open-land-derived cocoa agroforests should not be dismissed simply because they have a lower bird diversity than forest-derived cocoa agroforests. Rather, by being established on historically forested open land, they will contribute to agricultural production within working landscapes, without worsening the status quo for biodiversity. Moreover, while forest-derived cocoa agroforests have higher bird diversity, they should not be the preferred form of cocoa production, especially if this entails the further transformation of intact forests. Considering alternative baselines thus allows for more nuanced policies in the cocoa sector.

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References

- Balduzzi, S., Rücker, G., & Schwarzer, G. (2019). How to perform a meta-analysis with R: A practical tutorial. *Evidence-Based Mental Health*, *22*(4), 153–160. https://doi.org/10.1136/ebmental-2019-300117
- Bennett, R. E., Sillett, T. S., Rice, R. A., & Marra, P. P. (2022). Impact of cocoa agricultural intensification on bird diversity and community composition. *Conservation Biology*, 36(1), e13779. https://doi.org/10.1111/cobi.13779
- Bisseleua, D. H. B., Missoup, A. D., & Vidal, S. (2009). Biodiversity Conservation, Ecosystem
 Functioning, and Economic Incentives under Cocoa Agroforestry Intensification.
 Conservation Biology, 23(5), 1176–1184. https://doi.org/10.1111/j.1523-1739.2009.01220.x
- Davies, T. E., Clarke, R. H., Ewen, J. G., Fazey, I. R. A., Pettorelli, N., & Cresswell, W. (2015). The effects of land-use change on the endemic avifauna of Makira, Solomon Islands: Endemics avoid monoculture. *Emu - Austral Ornithology*, *115*(3), 199–213. https://doi.org/10.1071/MU14108
- De Beenhouwer, M., Aerts, R., & Honnay, O. (2013). A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. *Agriculture, Ecosystems & Environment, 175,* 1–7. https://doi.org/10.1016/j.agee.2013.05.003
- De Palma, A., Sanchez-Ortiz, K., Martin, P. A., Chadwick, A., Gilbert, G., Bates, A. E., Börger, L., Contu, S., Hill, S. L. L., & Purvis, A. (2018). Challenges With Inferring How Land-Use Affects Terrestrial Biodiversity: Study Design, Time, Space and Synthesis. In *Advances in Ecological Research* (Vol. 58, pp. 163–199). Elsevier. https://doi.org/10.1016/bs.aecr.2017.12.004
- Estrada, A., & Coates-Estrada, R. (2005). Diversity of Neotropical migratory landbird species assemblages in forest fragments and man-made vegetation in Los Tuxtlas, Mexico. *Biodiversity & Conservation*, 14(7), 1719–1734. https://doi.org/10.1007/s10531-004-0696-x

Estrada, A., Coates-Estrada, R., & Meritt, D. A. (1997). Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity & Conservation*, *6*(1), 19–43. https://doi.org/10.1023/A:1018328930981

FAO. (2020). FAOSTAT. Food and Agriculture Organisation of the United Nations. http://www.fao.org/faostat/en/#home

Faria, D., Laps, R. R., Baumgarten, J., & Cetra, M. (2006). Bat and Bird Assemblages from Forests and Shade Cacao Plantations in Two Contrasting Landscapes in the Atlantic Forest of Southern Bahia, Brazil. *Biodiversity & Conservation*, *15*(2), 587–612. https://doi.org/10.1007/s10531-005-2089-1

- Fulgence, T. R., Martin, D. A., Randriamanantena, R., Botra, R., Befidimanana, E., Osen, K., Wurz, A., Kreft, H., Andrianarimisa, A., & Ratsoavina, F. M. (2021). Differential responses of amphibians and reptiles to land-use change in the biodiversity hotspot of north-eastern Madagascar. *BioRxiv*. https://doi.org/10.1101/2021.03.18.435920
- Gerstner, K., Moreno-Mateos, D., Gurevitch, J., Beckmann, M., Kambach, S., Jones, H. P., & Seppelt,
 R. (2017). Will your paper be used in a meta-analysis? Make the reach of your research
 broader and longer lasting. *Methods in Ecology and Evolution*, 8(6), 777–784.
 https://doi.org/10.1111/2041-210X.12758
- Gordon, C., Manson, R., Sundberg, J., & Cruz-Angón, A. (2007). Biodiversity, profitability, and vegetation structure in a Mexican coffee agroecosystem. *Agriculture, Ecosystems & Environment*, 118(1), 256–266. https://doi.org/10.1016/j.agee.2006.05.023

Greenler, S. M., & Ebersole, J. J. (2015). Bird communities in tropical agroforestry ecosystems: An underappreciated conservation resource. *Agroforestry Systems*, *89*(4), 691–704. https://doi.org/10.1007/s10457-015-9805-y

Harvey, C. A., & González Villalobos, J. A. (2007). Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. *Biodiversity and Conservation*, 16(8), 2257– 2292. https://doi.org/10.1007/s10531-007-9194-2

Jarrett, C., Smith, T. B., Claire, T. T. R., Ferreira, D. F., Tchoumbou, M., Elikwo, M. N. F., Wolfe, J.,
 Brzeski, K., Welch, A. J., Hanna, R., & Powell, L. L. (2021). Bird communities in African cocoa
 agroforestry are diverse but lack specialized insectivores. *Journal of Applied Ecology*, *58*(6),
 1237–1247. https://doi.org/10.1111/1365-2664.13864

Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D., Putra, D. D., Gradstein, S. R., Höhn, P., Kluge, J.,
Orend, F., Pitopang, R., Saleh, S., Schulze, C. H., Sporn, S. G., Steffan-Dewenter, I.,
Tjitrosoedirdjo, S. S., & Tscharntke, T. (2009). Alpha and beta diversity of plants and animals
along a tropical land-use gradient. *Ecological Applications*, *19*(8), 2142–2156.
https://doi.org/10.1890/08-1074.1

- Maney, C., Sassen, M., & Hill, S. L. L. (2022). Modelling biodiversity responses to land use in areas of cocoa cultivation. Agriculture, Ecosystems & Environment, 324, 107712. https://doi.org/10.1016/j.agee.2021.107712
- Martin, D. A., Osen, K., Grass, I., Hölscher, D., Tscharntke, T., Wurz, A., & Kreft, H. (2020). Land-use history determines ecosystem services and conservation value in tropical agroforestry. *Conservation Letters*, *13*(5), e12740. https://doi.org/10.1111/conl.12740
- Moguel, P., & Toledo, V. M. (1999). Biodiversity Conservation in Traditional Coffee Systems of Mexico. *Conservation Biology*, *13*(1), 11–21. https://doi.org/10.1046/j.1523-1739.1999.97153.x
- Mupepele, A.-C., Keller, M., & Dormann, C. F. (2021). European agroforestry has no unequivocal effect on biodiversity: A time-cumulative meta-analysis. *BMC Ecology and Evolution*, 21(1), 193. https://doi.org/10.1186/s12862-021-01911-9
- Niether, W., Jacobi, J., Blaser, W. J., Andres, C., & Armengot, L. (2020). Cocoa agroforestry systems versus monocultures: A multi-dimensional meta-analysis. *Environmental Research Letters*, 15(10), 104085. https://doi.org/10.1088/1748-9326/abb053
- Nijmeijer, A., Lauri, P.-E., Harmand, J.-M., Freschet, G. T., Essobo Nieboukaho, J.-D., Fogang, P. K., Enock, S., & Saj, S. (2019). Long-term dynamics of cocoa agroforestry systems established on

lands previously occupied by savannah or forests. *Agriculture, Ecosystems & Environment,* 275, 100–111. https://doi.org/10.1016/j.agee.2019.02.004

- Orozco-Aguilar, L., López-Sampson, A., Leandro-Muñoz, M. E., Robiglio, V., Reyes, M., Bordeaux, M., Sepúlveda, N., & Somarriba, E. (2021). Elucidating Pathways and Discourses Linking Cocoa Cultivation to Deforestation, Reforestation, and Tree Cover Change in Nicaragua and Peru. *Frontiers in Sustainable Food Systems*, *5*. https://doi.org/10.3389/fsufs.2021.635779
- Osen, K., Soazafy, M. R., Martin, D. A., Wurz, A., März, A., Ranarijaona, H. L. T., & Hölscher, D. (2021).
 Land-use history determines stand structure and tree diversity in vanilla agroforests of northeastern Madagascar. *Applied Vegetation Science*, *24*(1), e12563.
 https://doi.org/10.1111/avsc.12563
- Raveloaritiana, E., Wurz, A., Grass, I., Osen, K., Soazafy, M. R., Martin, D. A., Faliniaina, L.,
 Rakotomalala, N. H., Vorontsova, M. S., Tscharntke, T., & Rakouth, B. (2021). Land-use
 intensification increases richness of native and exotic herbaceous plants, but not endemics,
 in Malagasy vanilla landscapes. *Diversity and Distributions*, *27*(5), 784–798.
 https://doi.org/10.1111/ddi.13226
- Reitsma, R., Parrish, J. D., & McLarney, W. (2001). The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. *Agroforestry Systems*, 53(2), 185–193. https://doi.org/10.1023/A:1013328621106
- Rice, R. A., & Greenberg, R. (2000). Cacao Cultivation and the Conservation of Biological Diversity. *Ambio*, *29*(3), 167–173. https://doi.org/10.1579/0044-7447-29.3.167

Ruf, F. (2001). Tree crops as deforestation and reforestation agents: The case of cocoa in Côte d'Ivoire and Sulawesi. In A. Angelsen & D. Kaimowitz (Eds.), *Agricultural technologies and tropical deforestation*. CABI Publishing. https://doi.org/10.1079/9780851994512.0291

Schroth, G., Läderach, P., Martinez-Valle, A. I., Bunn, C., & Jassogne, L. (2016). Vulnerability to climate change of cocoa in West Africa: Patterns, opportunities and limits to adaptation.

Science of The Total Environment, 556, 231–241.

https://doi.org/10.1016/j.scitotenv.2016.03.024

- Schulze, C. H., Waltert, M., Kessler, P. J. A., Pitopang, R., Veddeler, D., Mühlenberg, M., Gradstein, S.
 R., Leuschner, C., Steffan-Dewenter, I., & Tscharntke, T. (2004). Biodiversity Indicator Groups of Tropical Land-Use Systems: Comparing Plants, Birds, and Insects. *Ecological Applications*, *14*(5), 1321–1333.
- Stouffer, P. C., Jirinec, V., Rutt, C. L., Bierregaard Jr, R. O., Hernández-Palma, A., Johnson, E. I., Midway, S. R., Powell, L. L., Wolfe, J. D., & Lovejoy, T. E. (2021). Long-term change in the avifauna of undisturbed Amazonian rainforest: Ground-foraging birds disappear and the baseline shifts. *Ecology Letters*, 24(2), 186–195. https://doi.org/10.1111/ele.13628
- Tscharntke, T., Clough, Y., Bhagwat, S. A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J.,
 Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., & Wanger, T. C. (2011).
 Multifunctional shade-tree management in tropical agroforestry landscapes—A review. *Journal of Applied Ecology*, 48(3), 619–629. https://doi.org/10.1111/j.1365-2664.2010.01939.x
- Tutu Benefoh, D., Villamor, G. B., van Noordwijk, M., Borgemeister, C., Asante, W. A., & Asubonteng,
 K. O. (2018). Assessing land-use typologies and change intensities in a structurally complex
 Ghanaian cocoa landscape. *Applied Geography*, *99*, 109–119.
 https://doi.org/10.1016/j.apgeog.2018.07.027
- Van Bael, S. A., Bichier, P., Ochoa, I., & Greenberg, R. (2007). Bird diversity in cacao farms and forest fragments of western Panama. *Biodiversity and Conservation*, 16(8), 2245–2256. https://doi.org/10.1007/s10531-007-9193-3
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

- Waltert, M., Bobo, K. S., Kaupa, S., Montoya, M. L., Nsanyi, M. S., & Fermon, H. (2011). Assessing
 Conservation Values: Biodiversity and Endemicity in Tropical Land Use Systems. *PLoS ONE*,
 6(1), e16238. https://doi.org/10.1371/journal.pone.0016238
- Waltert, M., Bobo, K. S., Sainge, N. M., Fermon, H., & Mühlenberg, M. (2005). From forest to farmland: Habitat effects on afrotropical forest bird diversity. *Ecological Applications*, 15(4), 1351–1366. https://doi.org/10.1890/04-1002
- Waltert, M., Mardiastuti, A., & Mühlenberg, M. (2004). Effects of Land Use on Bird Species Richness in Sulawesi, Indonesia. *Conservation Biology*, *18*(5), 1339–1346.

https://doi.org/10.1111/j.1523-1739.2004.00127.x

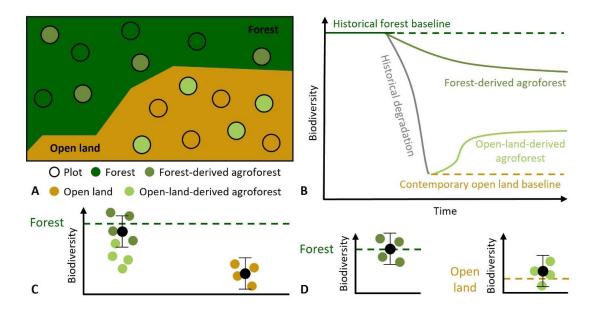


Fig. 1: Concept of land-use history in agroforestry systems. **A:** Forest-derived agroforests are established inside forests by thinning out trees and replacing the understory with agroforestry crops, while open-land-derived agroforests are established on historically forested open lands by planting agroforestry crops alongside planted or naturally regenerating shade trees. **B:** Hypothesized outcomes of agroforest establishment under the consideration of land-use history. Forest-derived agroforests are likely more biodiverse, but represent a degradation of forest, whereas open-land-derived agroforests may increase biodiversity compared to a contemporary open land baseline. **C:** Hypothetical analysis of biodiversity in agroforests are not separated and collectively compared with the forest baseline (horizontal line), as is open land. **D:** Hypothetical analysis of biodiversity in agroforests are not separated agroforests are compared with forest, while open-land-derived agroforests are compared with open land.

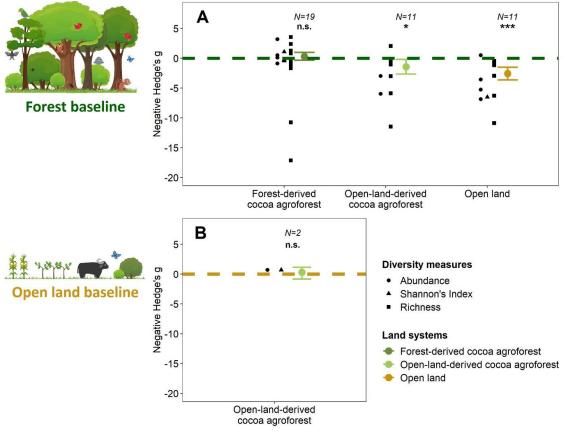


Fig. 2: Comparison of multiple bird diversity measures across land systems. **A:** Comparison of forestderived cocoa agroforests, open-land-derived cocoa agroforests, and open lands to forest baseline (horizontal line). **B:** Comparison of open-land-derived cocoa agroforests to open land baseline (horizontal line). Asterisks indicate that the estimated Hedges' g^* differ significantly from the baseline at *p< 0.05 or ***p< 0.001; n. s. stands for 'not significant'.