Land-use trajectories for sustainable land system transformations: Identifying leverage points in a global biodiversity hotspot

Dominic Andreas Martin[a,1,2], Fanilo Andrianisaina[b], Thio Rosin Fulgence[c,d], Kristina Osen[e], Anjaharinony Andry Ny Aina Rakotomalala[f], Estelle Raveloaritiana[g], Marie Rolande Soazafy[d,h], Annemarie Wurz[i], Rouvah Andriafanomezantsoa[c], Harilala Andriamaniraka[b], Aristide Andrianarimisa[c], Jan Barkmann[j,k], Saskia Dröge[a,l], Ingo Grass[m], Nathaly Guerrero-Ramirez[a], Hendrik Hänke[k], Dirk Hölscher[e,n], Bakolimalala Rakouth[g], Hery Lisy Tiana Ranarijaona[h], Romual Randriamanantena[d], Fanomezana Mihaja Ratsoavina[c], Lala Harivelo Raveloson Ravaomanarivo[f], Dominik Schwab[i], Teja Tscharntke[i,n], Delphine Clara Zemp[a,n,o], and Holger Kreft[a,n]

[a]Biodiversity, Macroecology, and Biogeography, University of Goettingen, 37077 Goettingen, Germany; [b]Department of Tropical Agriculture and Sustainable Development, Higher School of Agronomic Sciences, University of Antananarivo, Antananarivo 101, Madagascar; [c]Zoology and Animal Biodiversity, Faculty of Sciences, University of Antananarivo, Antananarivo 101, Madagascar; [d]Natural and Environmental Sciences, Regional University Centre of the SAVA Region, Antalaha 206, Madagascar; [e]Tropical Silviculture and Forest Ecology, University of Goettingen, 37077 Goettingen, Germany; [f]Entomology Department, Faculty of Science, University of Antananarivo, Antananarivo 101, Madagascar; [g]Plant Biology and Ecology Department, University of Antananarivo, Antananarivo 101, Madagascar; [h]Biodiversity and Conservation, University of Mahajanga, Mahajanga 401, Madagascar; [i]Agroecology, University of Goettingen, 37077 Goettingen, Germany; [j]Department of Social Sciences, Risk, and Sustainability Sciences, Hochschule Darmstadt, University of Applied Sciences, 64295 Darmstadt, Germany; [k]Research Unit Environmental and Resource Economics, Department of Agricultural Economics and Rural Development, University of Goettingen, 37073 Goettingen, Germany; [l]Division of Forest, Nature, and Landscape, Department of Earth and Environmental Sciences, KU Leuven, 3000 Leuven, Belgium; [m]Ecology of Tropical Agricultural Systems, University of Hohenheim, 70599 Stuttgart, Germany; [n]Centre for Biodiversity and Sustainable Land Use, University of Goettingen, 37077 Goettingen, Germany; and [o]Laboratory of Conservation Biology, Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland

Edited by Arun Agrawal, School for Environment and Sustainability, University of Michigan, Ann Arbor, MI; received April 30, 2021; accepted January 7, 2022

Sustainable land-system transformations are necessary to avert biodiversity and climate collapse. However, it remains unclear where entry points for transformations exist in complex land systems. Here, we conceptualize land systems along land-use trajectories, which allows us to identify and evaluate leverage points, i.e., entry points on the trajectory where targeted interventions have particular leverage to influence land-use decisions. We apply this framework in the biodiversity hotspot Madagascar. In the northeast, smallholder agriculture results in a land-use trajectory originating in old-growth forests and spanning from forest fragments to shifting hill rice cultivation and vanilla agroforests. Integrating interdisciplinary empirical data on seven taxa, five ecosystem services, and three measures of agricultural productivity, we assess trade-offs and cobenefits of land-use decisions at three leverage points along the trajectory. These trade-offs and cobenefits differ between leverage points: Two leverage points are situated at the conversion of old-growth forests and forest fragments to shifting cultivation and agroforestry, resulting in considerable trade-offs, especially between endemic biodiversity and agricultural productivity. Here, interventions enabling smallholders to conserve forests are necessary. This is urgent since ongoing forest loss threatens to eliminate these leverage points due to path dependency. The third leverage point allows for the restoration of land under shifting cultivation through vanilla agroforests and offers cobenefits between restoration goals and agricultural productivity. The co-occurring leverage points highlight that conservation and restoration are simultaneously necessary to avert collapse of multifunctional mosaic landscapes. Methodologically, the framework highlights the importance of considering path dependency along trajectories to achieve sustainable land-system transformations.

agroforestry | conservation | restoration | path dependency | Madagascar

Ecosystem degradation and climate change call for land-system transformations that improve human well-being and reverse biodiversity loss through conservation and restoration (1). Such transformations could be enabled by policies and interventions that influence land-use decisions in ways that result in multifunctional land systems that work for people and nature (2–4). To study how various land-use types contribute to biodiversity conservation, ecosystem services, and agricultural production, scientists commonly compare multiple land-use types with each other (5). However, such comparisons often fail to consider which conversions between land-use types are

Significance

Finding entry points where policy has strong leverage to transform land systems for people and nature is pivotal. We develop an innovative framework to identify and evaluate such leverage points along land-use trajectories that account for path dependency. Applied to the biodiversity hotspot Madagascar, the framework reveals three leverage points: Two leverage points are associated with trade-offs between biodiversity, ecosystem services, and agricultural productivity, while the third entails cobenefits. Swift policy action is required, as path dependency caused by forest loss may soon put two leverage points out of reach. We argue that such closing windows of opportunity may be common, but often overlooked, calling for a wider consideration of path dependency in land-system science.

Author contributions: D.A.M., F.A., T.R.F., K.O., A.A.N.A.R., E.R., M.R.S., A.W., H.A., A.A., J.B., I.G., H.H., D.H., B.R., H.L.T.R., F.M.R., L.H.R.R., T.T., and H.K. designed research; D.A.M., F.A., T.R.F., K.O., A.A.N.A.R., E.R., M.R.S., A.W., R.A., S.D., H.H., R.R., and D.S. performed research; D.A.M. analyzed data with assistance from E.R., I.G., N.G.-R., D.C.Z., and H.K.; and D.A.M. wrote the paper with assistance from F.A., T.R.F., K.O., A.A.N.A.R., E.R., M.R.S., A.W., R.A., H.A., A.A., J.B., S.D., I.G., N.G.-R., H.H., D.H., B.R., H.L.T.R., R.R., F.M.R., L.H.R.R., D.S., T.T., D.C.Z., and H.K.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

[1]Present address: Wyss Academy for Nature, University of Bern, 3011 Bern, Switzerland.

[2]To whom correspondence may be addressed. Email: dominic.martin@wyssacademy.org.

This article contains supporting information online at http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2107747119/-/DCSupplemental.

Published February 14, 2022.

SUSTAINABILITY SCIENCE

ECOLOGY

realistic and which are unrealistic on policy-relevant timescales (6). For example, conversions from open land to old-growth forest are typically not realistic.

Here, we propose a framework that overcomes this problem by understanding land systems along actually observed land-use trajectories (Fig. 1, steps 1 to 3). Various land-use types are organized along distinct stages that may be converted into each other, following the trajectory downstream. Importantly, the different stages vary in the number of conversion steps they are away from the historical land cover (for example old-growth forest), but may all occur simultaneously in a single landscape.

The framework also allows identifying leverage points for land-system transformations (Fig. 1, step 4) (7). In this context, leverage points are entry points along the trajectory where land uses with realistic conversion potential to other land uses are situated, offering leverage for interventions that can steer conservation and conversion decisions. At each leverage point, such interventions can be informed by biodiversity, ecosystem service, and agricultural productivity data (Fig. 1, step 5) that can be combined to evaluate cobenefits and trade-offs between the current land system and various conversion options (Fig. 1, step 6). Furthermore, various leverage points along the land-use trajectory can be compared, helping to find those promising the best cost-to-benefit ratio. This trajectory framework also takes path dependency into account (8). This is because available leverage points depend on prior decisions, and future leverage points will be limited by current decisions. Considering path dependency may also uncover windows of opportunity, as current decisions influence the leverage points available in the future.

We apply our framework to a smallholder mosaic landscape in Madagascar (Fig. 2). In such landscapes, possible leverage points for land-system transformations exist at deforestation frontiers, where large swaths of biodiverse old-growth forest can be conserved (9, 10), as well as within mosaic landscapes, where smallholders may benefit from increased food security, higher incomes, and improved resilience to economic and environmental shocks (3, 11, 12). Madagascar is a biodiversity hotspot (13) that has lost 44% of its forest cover from 1953 to 2014 (14) without ensuring basic needs for many rural people (15, 16). This underlines the urgency of a transformation toward sustainable land systems. Smallholder subsistence agriculture, predominantly through shifting cultivation, remains the main driver of forest loss in the northeastern part of the country (17). The region is also the most important area for vanilla growing globally, with vanilla providing a livelihood for an estimated 70,000 to 80,000 farmers (18). These smallholders produce vanilla as a cash crop for the international market and largely rely on family labor (19). The spice is derived from the orchid *Vanilla planifolia* locally farmed in agroforestry systems (20).

We identified the land-use history of the predominant land-use types of northeastern Madagascar, building on published literature (17, 21, 22), local knowledge accessed through a transdisciplinary approach (19), and field experience of our multidisciplinary research team. By combining the histories of all land-use types, we revealed a trajectory shaped by shifting cultivation and various forms of forest transformation. Old-growth forests (stage 0; historic baseline; Fig. 2) can be burned for shifting hill rice cultivation (stage 1). Alternatively, old-growth forests may be fragmented and heavily used for timber extraction, resulting in forest fragments (stage 1). These fragments can, in turn, be converted to shifting hill rice cultivation or to forest-derived vanilla agroforests (stage 2). Irrespective of previous use, hill rice fields are left fallow and usually develop into woody fallows within a few years (stage 3). Woody fallows can again be converted, either through an additional cycle of shifting hill rice cultivation or through the establishment of fallow-derived vanilla agroforests (stage 4). Vanilla, therefore, plays a role at two distinct points along the land-use trajectory: if forest-derived, vanilla agroforestry contributes to forest degradation; if fallow-derived, vanilla agroforestry has the potential to restore fallow land (23). On this trajectory, we identify three leverage points at which smallholders make key land-use decisions and where policy interventions may have strong leverage: old-growth forest, forest fragment, and woody fallow (Fig. 2). Rice paddies are another prevalent land-use type in the region,

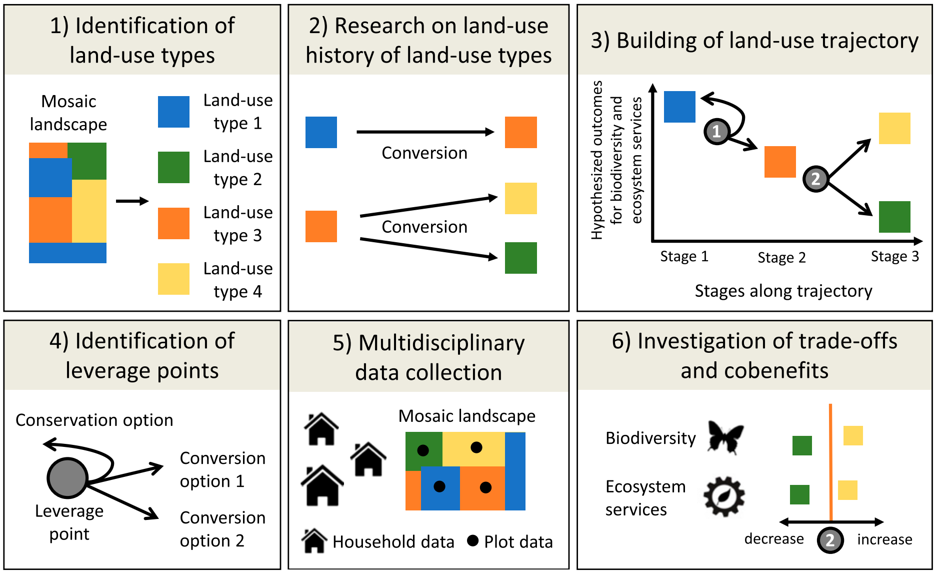

Fig. 1. Methodological framework to identify leverage points along land-use trajectories. The framework starts with 1) the identification of relevant land uses within a mosaic landscape, followed by 2) multidisciplinary research (interviews, surveys, and literature) on the land-use history. With this knowledge, 3) a land-use trajectory is built, aligning conversions across multiple stages, following the trajectory downstream. Now, 4) multiple leverage points can be identified, depending on the complexity of the trajectory. Next, 5) data on biodiversity, ecosystem services, and agricultural productivity of each land-use type is collected. Then, 6) trade-offs and cobenefits of conversion options can be evaluated against the current land use at leverage points (here, leverage point 2). This knowledge can inform interventions, showcasing which cobenefits can be harnessed and which trade-offs need to be mitigated under various conservation and conversion options at each leverage point.

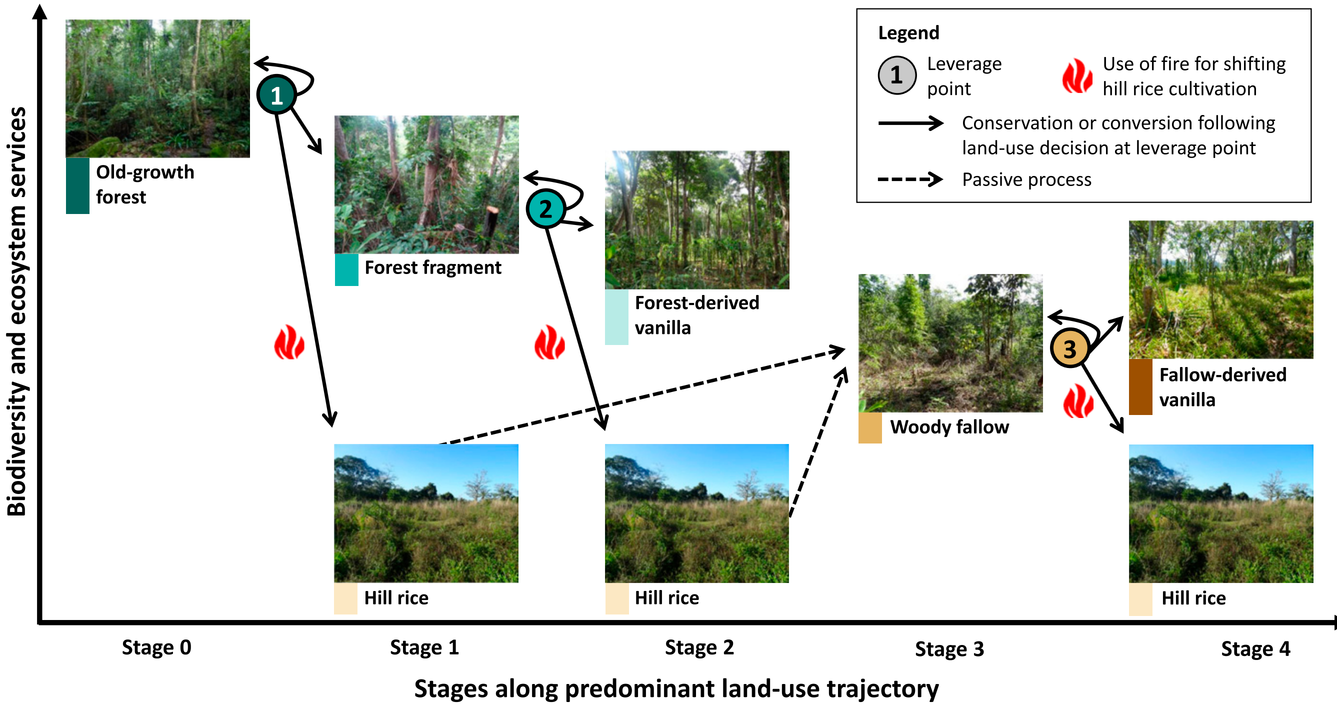

Fig. 2. Hypothesized outcomes for ecosystem services and biodiversity along the predominant land-use trajectory in northeastern Madagascar, with leverage points 1 to 3. We define leverage points as distinct points along a land-use trajectory, where land users face alternative land-use options with potentially contrary outcomes. At each leverage point, the current land use could be conserved or converted into one of multiple alternatives, suggesting strong leverage for interventions targeted to these points. Importantly, we can then evaluate the conversion options against the conservation option and against each other in terms of ecosystem services, biodiversity, and agricultural productivity. The relative position on the *y* axis for each land-use type represents hypothesized outcomes for ecosystem services and biodiversity.

SUSTAINABILITY SCIENCE

ECOLOGY

but are not part of the predominant trajectory, as they are typically established in floodplains and wetlands (20).

To test our methodological framework and hypotheses, we collected multidisciplinary data on seven taxa (trees, herbaceous plants, birds, amphibians, reptiles, butterflies, and ants), five ecosystem service indicators (above-ground carbon, soil organic carbon, predation rate, natural product provisioning, and water regulation), and three parameters of agricultural productivity (profit per person-day, profit per hectare, and yield mass per hectare) across the seven predominant land-use types of northeastern Madagascar (old-growth forest, forest fragment, forest-derived vanilla agroforest, fallow-derived vanilla agroforest, herbaceous fallow, woody fallow, and rice paddy). We collected data on seven taxa and three ecosystem services (above-ground carbon, soil organic carbon, and predation rate) from 70 plots of all six land-use types that form part of the trajectory, as well as on rice paddy (10 plots per land-use type, except 20 plots for fallow-derived vanilla). Additionally, we interviewed 322 households about ecosystem services (water regulation and natural product provisioning) gained from each land-use type and followed 109 households through a year-long longitudinal study to record data on agricultural productivity of rice paddies, hill rice, and vanilla agroforestry.

We combine these data by calculating (endemic) multidiversity and ecosystem service multifunctionality [hereafter ES-multifunctionality sensu Manning et al., 2018 (24)]. These combined measures enable us to summarize the ability of each land-use type to simultaneously host a suite of (endemic) taxa and to provide multiple ecosystem services into only three integrated measures. Following the well-established threshold-based ES-multifunctionality approach (24), we calculate ES-multifunctionality as the proportion of services crossing a certain threshold, which we defined as the mean of the top five maximum values measured in our study. Similarly, we calculate (endemic) multidiversity as the proportion of taxa crossing a certain threshold of the observed maximum (endemic) species richness. We show results for an intermediate threshold (50%) in the main text (Figs. 3 and 4) and show results for low (20%) and high (80%) thresholds in *SI Appendix*, Fig. S2. Additionally, we compare the three parameters of agricultural productivity across the seven land-use types (Fig. 4).

Results and Discussion

While no land-use decision at any leverage point maximizes all outcome variables, we find cobenefits between ecosystem services, biodiversity, and agricultural productivity under conversion of fallow land into fallow-derived vanilla agroforestry. Trade-offs prevail under forest conversion to shifting hill rice cultivation. Throughout this section, we refer to higher species richness, greater ecosystem service supply, and better agricultural productivity as desirable outcomes.

Leverage Point 1: Trade-Offs in Old-Growth Forest Conservation. Our results reveal that the conversion of old-growth forests in northeastern Madagascar is associated with a marked loss of plot-level species richness of most taxa (except for butterflies and herbaceous plants) and a 2.6-times-higher loss of endemic species richness across all taxa evaluated, highlighting the leverage for biodiversity conservation at this point on the trajectory (Figs. 3 and 4). These stronger losses for endemic species indicate that endemic species are more negatively affected by land-use change than nonendemic species (25). Our finding also underlines the need to protect the last remaining old-growth forests in Madagascar (26), a conclusion that would likely be strengthened by the inclusion of biodiversity variables at

https://doi.org/10.1073/pnas.2107747119

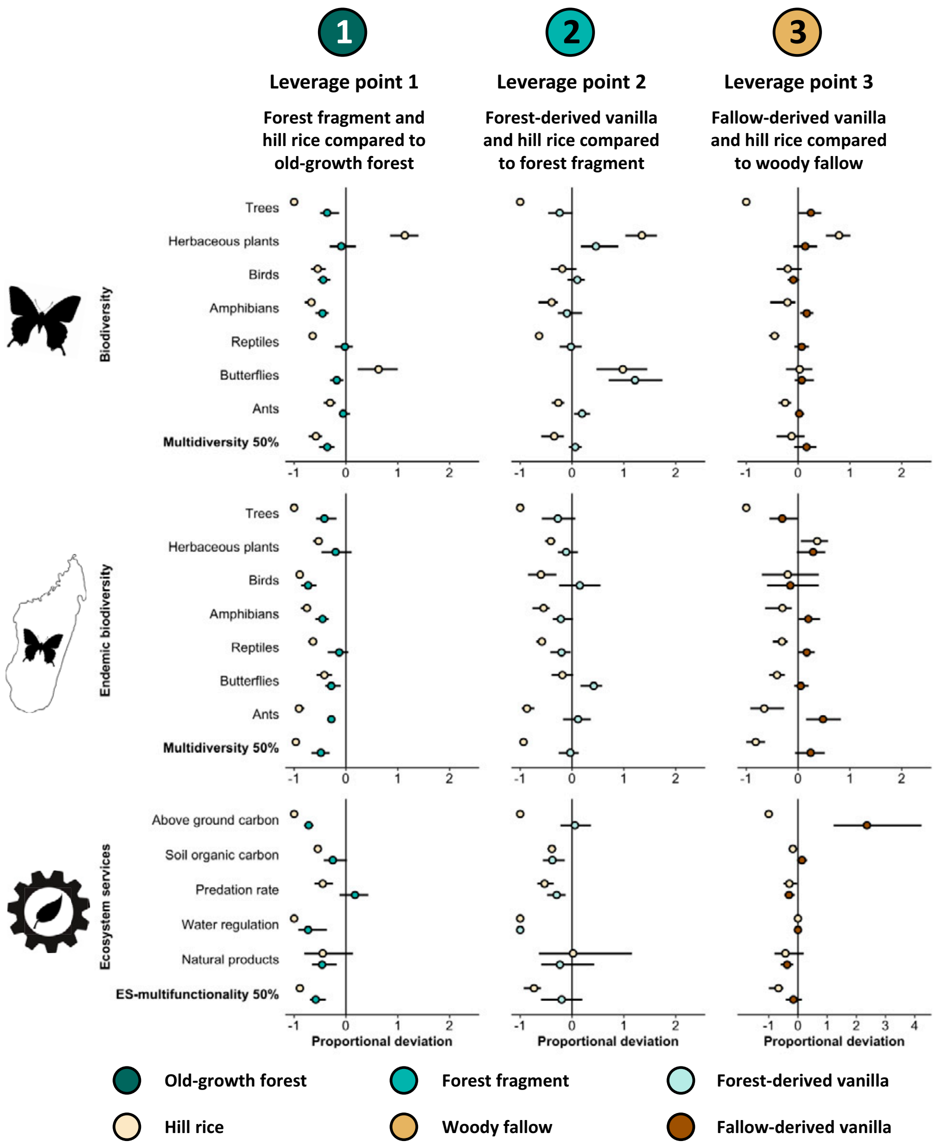

Fig. 3. Comparison of biodiversity, endemic biodiversity, and ecosystem services at leverage points 1 to 3 along the predominant land-use trajectory of northeastern Madagascar. Leverage point 1: conserving old-growth forest is necessary to retain many endemic taxa and ecosystem services. Conversion to shifting hill rice cultivation has overall stronger negative effects than conversion to forest fragments. Leverage point 2: conserving forest fragments is important to retain biodiversity and ecosystem services, but the lack of agricultural productivity encourages their conversion. After conversion, forest-derived agroforests outperform shifting hill rice cultivation across variables. Leverage point 3: cobenefits are possible under conversion of fallow land to fallow-derived vanilla agroforestry, given stable multidiversity and ES-multifunctionality and a strong increase in profitability. Dots and lines (mean and 95% CI) represent proportional deviation in biodiversity or ecosystem services resulting from land-use conversion. If the 95% CI does not include zero, this indicates significant differences between land-uses. Values of −1 indicate a 100% decrease (complete loss), and values of 1 indicate a 100% increase in biodiversity or ecosystem services when compared with old-growth forest, forest fragments, or woody fallow.

broader temporal and spatial scales (such as beta diversity, gamma diversity, and extinction debts).

Losses of biodiversity are particularly strong when old-growth forests enter the shifting cultivation cycle for hill rice production—i.e., when they are cleared under the use of fire (Figs. 3 and 4). Here, multidiversity drops by 58% and endemic multidiversity by 97%. The fragmentation into forest fragments and the extraction of timber and other natural products also result in a loss of (endemic) species, but to a lesser extent, reducing multidiversity by 36% and endemic multidiversity by 48%. Our assessment of leverage point 1 shows, however, the considerable benefits that smallholders gain from old-growth forest conversion. Hill rice cultivation has average yields of 1,082 $kg \cdot ha^{-1} \cdot y^{-1}$ (referring to a year farmed not including fallow periods; vs. 2,692 $kg \cdot ha^{-1} \cdot y^{-1}$ in rice paddy) and generates profits of \$51 $ha^{-1} \cdot y^{-1}$ and \$1.60 $person\text{-}day^{-1}$ (referring to a year farmed not including fallow periods; vs. \$751 $ha^{-1} \cdot y^{-1}$ and \$21 $person\text{-}day^{-1}$ in rice paddy). Most importantly, however, shifting hill rice cultivation is essential to satisfy subsistence needs, particularly for poorer households who own little or no paddy rice (19), thus contributing to local food security (15). These findings are in line with recent research from northeastern Madagascar, which has demonstrated trade-offs between global demands—such as biodiversity conservation—and local needs—such as food-crop production (27).

Old-growth forest conversion offers clear individual benefits, so smallholders need clear economic alternatives to forest conversion or need to be compensated for losses they experience

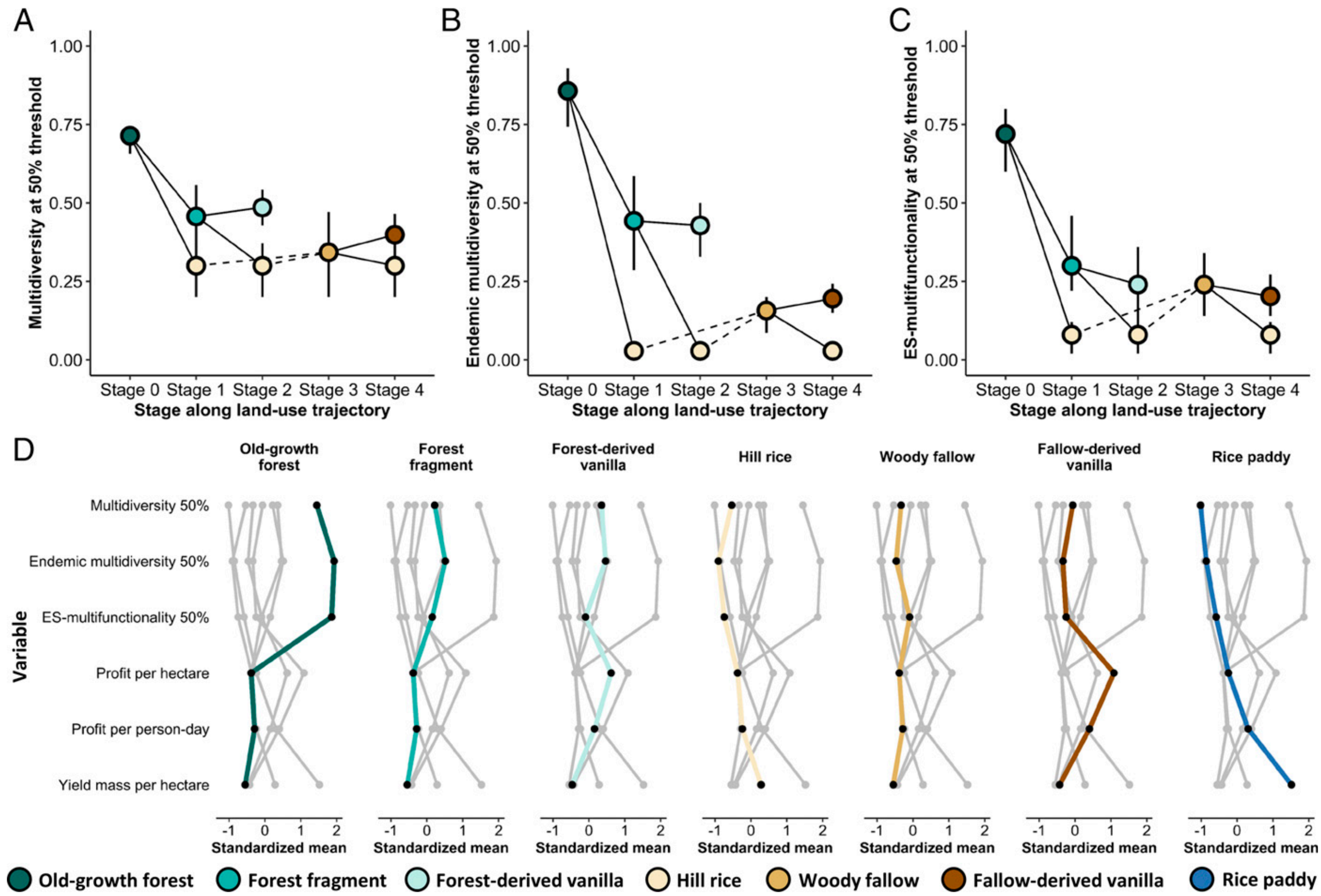

Fig. 4. Variation along the land-use trajectory for multidiversity (*A*), endemic multidiversity (*B*), and ES-multifunctionality (*C*) and their trade-off with agricultural productivity (*D*) in northeastern Madagascar. Losses of multidiversity (*A*), and to a greater extent endemic multidiversity (*B*), happen after old-growth forest conversion. Changes at later transitions within the land-use trajectory (leverage points 2 and 3) are less strong. ES-multifunctionality (*C*) follows the same pattern. Trade-offs with agricultural productivity (*D*) become apparent as the most biodiverse and multifunctional land uses (old-growth forests and forest fragments) have no farming outcomes, while the most high-yielding land use (rice paddy) has the lowest value for biodiversity and services. Vanilla agroforests offer a compromise. Multidiversity (*A* and *B*) and ES-multifunctionality (*C*) are calculated as the proportion of taxa or services that reach 50% of the species richness or value of the five best-performing plots (50% threshold). Points colored according to the land-use type represent the mean value for each land-use type, while error bars are 95% CIs. The parallel coordinate plots (*D*) each depict one focal land-use type (color) in relation to the other six land-use types (gray). To enable comparison across variables, values are standardized so that zero represents the mean across all seven land-use types. Values at the 20% and 80% thresholds are displayed in *SI Appendix*, Fig. S2. Multidiversity and ES-multifunctionality are positively correlated (*SI Appendix*, Fig. S3).

under strict forest protection. These opportunity costs for restricted forest use and conversion are estimated at 27 to 84% of total annual income for median-income households (28) at the forest frontier in eastern Madagascar.

Leverage Point 2: Conserving Forest Fragments and Favoring Forest-Derived Agroforestry over Shifting Cultivation. Comparing outcomes under the conversion of forest fragments to shifting hill rice cultivation at leverage point 2 shows that conserving forest fragments benefits (endemic) biodiversity and ecosystem services (Figs. 3 and 4). Specifically, multidiversity drops by 34% under this conversion, with endemic species particularly affected (ranging from −100% for trees to −19% for butterflies; −94% for endemic multidiversity). These results underpin past research (29) on the high value of rapidly vanishing tropical forest fragments (9) for biodiversity and ecosystem services. However, the conversion of forest fragments to forest-derived vanilla agroforestry, where understory trees and shrubs are used as support structures for the vanilla vines while most of the canopy stays intact, does not cause significant change for many taxa and ecosystem services of forest fragments (6% increase in multidiversity and 3% decrease in endemic multidiversity; both with CIs overlapping zero). This slight increase in overall species richness is mostly due to nonendemic herbaceous plants, birds, butterflies, and ants that are more species-rich in forest-derived agroforests (30–32).

The high profitability of vanilla farming, both per person-day and per hectare (Fig. 4), strongly incentivizes the conversion of forest fragments into forest-derived vanilla agroforests. Indeed, profits generated through vanilla farming can be remarkable under high vanilla prices, as observed between 2014 and 2019: forest-derived vanilla agroforests bear mean profits of \$5,250 $ha^{-1}·y^{-1}$ and \$16 person-day^{-1}. Under these conditions, forest-derived agroforestry established inside (already degraded) forest fragments appears justifiable as an alternative to shifting cultivation in terms of biodiversity, ecosystem services, and profits. This is further supported by a chronosequence within vanilla agroforests (23). The study shows increasing canopy cover in forest-derived vanilla agroforests over time, suggesting that forest-derived agroforests may sustain trees also in the long run.

Leverage Point 3: Cobenefits under the Conversion of Fallow Land into Fallow-Derived Vanilla Agroforests. The third leverage point along the trajectory occurs on fallow land. Fallows form part of the shifting cultivation cycle (22) succeeding crop cultivation.

https://doi.org/10.1073/pnas.2107747119

Smallholders who own fallow land essentially face three options. First, they may keep the land under shifting cultivation by initiating another rice-cultivation cycle through slash-and-burn. This is associated with a short-term loss of biodiversity (−12% multidiversity and −82% endemic multidiversity) before fallow vegetation recovers (Figs. 3 and 4). Importantly, this recovery only happens if the land stays fallow for several years prior to this cycle of shifting cultivation (22). Otherwise, the land may enter a degradation cycle associated with nonnative plants and a loss of soil fertility (22, 33). A shortening of fallow periods can, however, be observed in eastern Madagascar as land becomes scarce (33) and, in part, degraded (22).

The transformation of fallow land to fallow-derived vanilla agroforests represents the second option. This conversion is associated with strong gains in profitability (to \$7,684 $ha^{-1} \cdot y^{-1}$ and \$25 person-day^{-1}) and stable or moderately increasing plot-level species richness (ranging between −9% for birds and +25% for trees), including endemic multidiversity (raising from 0.03 in woody fallows to 0.17 in fallow-derived vanilla agroforests; Figs. 3 and 4). Similarly, fallow-derived agroforests also feature levels of ecosystem services that are not significantly different to fallow land (−16% ES-multifunctionality), but significantly higher than hill rice (+153% ES-multifunctionality). We thereby show that the restoration of fallow land through vanilla agroforestry is a win–win–win opportunity to simultaneously achieve positive outcomes for biodiversity, ecosystem services, and agricultural productivity. Many of these benefits, such as carbon storage (34), are likely accumulating over time, further underlining the advantages of fallow-derived vanilla agroforestry.

Despite likely benefits, various factors may inhibit smallholders from converting their fallow land into vanilla agroforests. There are the benefits of fallow land—namely, as a land resource for future shifting hill rice cultivation and as a source of natural products (such as firewood or medicinal plants). But problems associated with vanilla growing may also hinder vanilla agroforest establishment: firstly, labor input for vanilla is high (19), necessitating hired labor or the reduction of other farming activities (35), such as rice cultivation, under the expansion of vanilla agroforestry. Secondly, vanilla yields only 3 y after planting (36), thereby creating a time lag between resource investment and pay-off. Thirdly, vanilla prices fluctuate strongly (19), making a specialization on vanilla farming risky and undesirable (35), a circumstance that is worsened by prevalent vanilla theft (37). Fourthly, sustainability certification schemes (e.g., Rainforest Alliance or Organic) require diverse and native shade-tree cover, a criterion that may be more difficult to meet in fallow-derived agroforestry compared to forest-derived agroforestry [see Martin et al., 2020 (6) for an extended discussion of the topic]. Interventions that aim at increasing smallholder fallow-derived vanilla agroforestry should thus focus on smallholders who currently struggle to establish high-yielding agroforestry systems due to the competing labor demand with shifting hill rice cultivation. For those farmers, food or cash aid for the 3 y until the first vanilla yields could act as a catalyst enabling vanilla cash cropping in addition to subsistence agriculture.

The third possible land-use option for smallholders owning fallow land is to stop shifting cultivation and allow secondary forest to regenerate. However, secondary forests are extremely rare in eastern Madagascar (38), the reason for which they do not form part of our land-use trajectory. The lack of secondary forests may be due to accidental fire escapes (22, 39), depleted seed banks, invasive plants (22), land scarcity, limited land tenure (40), and the absence of targeted policies (9).

Despite a common perception of fallows as wasteland among researchers and policymakers (41), our analysis highlights fallow land conversion as a prime leverage point for achieving positive outcomes for people and nature. It may thus be advantageous to focus policy interventions on leverage point 1, where old-growth forest can be conserved, and on leverage point 3, where cobenefits may be realized. Here, conceptualizing the landscape along the trajectory was key to understanding and analyzing realistic land-use options and therefore likely trade-offs and cobenefits.

Policy Recommendations Informed by Leverage Points. From the analysis of three leverage points along the predominant land-use trajectory of northeastern Madagascar, we derive four key policy recommendations. Firstly, the paramount role of old-growth forest in maintaining (endemic) biodiversity and ecosystem services requires strict protection of the remaining contiguous forests (Figs. 3 and 4). However, apparent trade-offs between old-growth forest conservation and agricultural production (Fig. 4) confirm the importance of considering smallholder livelihoods in land-use policies (42). Secondly, fallow-derived vanilla agroforestry should be favored over forest-derived agroforestry, given cobenefits between ecosystem services, biodiversity, and agricultural productivity (Figs. 3 and 4). Thirdly, forest-derived agroforestry should only be encouraged as an alternative to complete deforestation of forest fragments and should play no role in old-growth forest degradation. Fourthly, while shifting hill rice cultivation may not be economically profitable at first sight (Fig. 4), its contribution to local food security (15) and natural product provisioning is considerable. This is mainly because households relying on hill rice are, on average, poorer and may lack the means to invest in land preparation and irrigation, even if suitable land for paddy rice cultivation would be available (19). This illustrates the motivations for shifting cultivation, despite low yields.

Interventions should thus encourage more sustainable smallholder subsistence agriculture also on land not suitable for paddy rice cultivation, potentially including shifting cultivation with long fallow periods that sustain yields in the long term (22). However, disadvantaged households depend heavily on shifting hill rice cultivation and are often forced to apply short fallow periods. Sustainable smallholder agriculture may only be possible if disadvantaged households are empowered—for example, through training, credit, or land tenure—to establish productive vanilla agroforestry and rice paddies. Such rice paddies have higher yields and higher profits than shifting hill rice cultivation, but have limited value for ecosystem services and biodiversity (Fig. 3). Importantly, implementing these interventions will rely on close collaborations between various local and global actors (42).

Our framework provides a basis for future research, with three promising avenues. Firstly, our approach could be refined by data on currently unmeasured, but potentially important, ecosystem services—for example, climate regulation, erosion control, soil fertility, pollination, or cultural value. Secondly, analysis across spatial scales could highlight the relationships between ecosystem services, biodiversity, and agricultural productivity from local to landscape scales (43). Thirdly, elucidating stakeholder preferences about future landscape trajectories (24) would generate target knowledge that could further inform interventions at multiple leverage points. This could help to ensure that conservation and restoration interventions are locally desired (42), likely improving their efficacy and permanence.

Broader Applications: Land-Use Trajectories as a Tool to Identify Leverage Points in Land Systems. We demonstrate that the conceptualization of landscapes along land-use trajectories, and the associated path dependency, offers the opportunity to identify multiple leverage points, which each have distinct land-use options and outcomes (Fig. 2). These can then be evaluated in terms of any given indicator; in our case, these are biodiversity, ecosystem services, and agricultural productivity (Figs. 3 and 4).

Our framework may be particularly useful in diverse and dynamic mosaic landscapes, where many different land uses coexist. Here, the occurrence of multiple land-use types may lead to overall higher multifunctionality of mosaic landscapes compared to simplified ones (3), so maintaining land-use diversity is important. The multiple, simultaneously occurring leverage points in such landscapes suggest that a suite of interventions specific to each leverage point may be ideal. Importantly, these interventions may either work on the conservation side—for example, in old-growth forest conservation—or on the conversion side—for instance, by promoting restorative agroforestry on shifting cultivation fallows. If successfully implemented, this would lead to a forest transition (44) with increasing landscape-scale tree cover. In this light, our methodological framework can also inform large-scale forest-restoration activities by considering previous land use, as well as current biodiversity, ecosystem service supply, and agricultural productivity of target areas.

Focusing on realistic land conversions along land-use trajectories, instead of just comparing all different land-use types (5, 11), further avoids evaluating theoretical contrasts between land-use types that, due to path dependency, cannot be converted into each other. For example, dozens of studies contrast forest-derived agroforests to open land, reporting higher biodiversity and ecosystem services in forest-derived agroforests (6). However, such agroforests cannot be established on open land over policy-relevant timescales, so comparing them to open land may lead to inapplicable or even misleading policy recommendations.

The strong path dependency revealed in our case study also implies that windows of opportunity close as leverage points become inaccessible due to current decisions, limiting the scope of interventions in the future. For example, in the study region in northeastern Madagascar, remnant forest fragments within the mosaic landscape are disappearing quickly (9), indicating that the window of opportunity for forest fragment conservation is closing. This suggests that, if faced with resource limitations, nongovernmental organizations and state actors may better concentrate on forest conservation. Nonetheless, restoration activities through agroforestry (6) or payments for ecosystem services (45) could improve livelihoods, which is a prerequisite for forest conservation (28). This highlights again that multiple leverage points need to be addressed in concert.

We conclude that identifying and analyzing leverage points along land-use trajectories can, firstly, focus the lens of researchers to ensure that realistic land-use options are evaluated, leading to more applicable research findings. Secondly, the approach enables the quantification of trade-offs and cobenefits of various conservation and conversion options at each leverage point, elucidating the motivations of land users to make certain decisions, as well as the consequences these decisions have for biodiversity and ecosystem services. Thirdly, by comparing various leverage points, policymakers aiming at landscape-scale conservation and restoration can focus on those leverage points that promise desired outcomes or those that promise the best cost-to-benefit ratio.

Materials and Methods

Study Region. Our study was based in the central part of the Sambava, Antalaha, Vohemar, and Andapa (SAVA) region in northeastern Madagascar (map in *SI Appendix*, Fig. S1), a global biodiversity hotspot (13). The area has retained more forest than any other part of the eastern Madagascar rainforest biome, but also suffers from ongoing forest loss (9, 14), mainly due to shifting hill rice cultivation practiced by smallholders (17). The SAVA region is also the historic and current center of global vanilla production (19), producing the majority of Madagascar's 40% share of the world market (46). A recent price boom for vanilla (19) has led to an expansion of vanilla agroforests (21) and has contributed to the development of the region relative to other regions of Madagascar [Human Development Index of 0.57 for 2018, third-highest among the 22 Malagasy regions (16)].

Study Design: Biodiversity and Ecosystem Service Indicators. We sampled data on biodiversity and ecosystem services in a replicated, plot-based, space-for-time design spanning 80 circular plots of 25-m radius (1,963.5 m^2). We sampled the most prevalent land-use types of the study region. These are old-growth forest (inside Marojejy National Park), forest fragments, forest-derived vanilla agroforests, hill rice, woody fallow, fallow-derived vanilla agroforests, and rice paddy (*SI Appendix* for more details, Fig. 2 for example photos and the land-use trajectory, and *SI Appendix*, Fig. S1 for a map of the study region, the old-growth forest sites, and the villages).

Biodiversity. We collected all biodiversity data between October 2017 and February 2019. We did so on all 80 plots, except for the tree data, which we collected on all land-use types with tree presence (i.e., all but hill rice and rice paddy, for which we set tree species richness to zero; $n = 20$ plots), except for two fallow-derived vanilla agroforest plots, where we were denied plot access (47). For data analysis, we used total (endemic) species richness per taxa per plot as input data. Endemism categorization sources are available in *SI Appendix*, Table S1.

We inventoried all trees with free-standing stems with ≥8 cm of diameter at breast height, including arborescent palms, herbs, and tree ferns, but excluding lianas (47). Based on field characteristics and collected herbarium material, we identified all trees to species or morphospecies level. We sampled herbaceous plants within eight 4-m^2 subplots per plot (32). In each subplot, we assessed all vascular plant species that did not have apparent wood at maturity. Based on field characteristics and collected herbarium material, we identified all herbaceous plants to species or morphospecies level. We counted birds during dry and low-wind conditions at two 40-min point counts per plot conducted at two points in time (30). We excluded observations in flight and outside the plot. We sampled amphibians and reptiles during three diurnal and three nocturnal time-standardized search walks of 45 min by two observers in each plot (48), covering both the wettest and driest seasons. Upon encountering an individual, we stopped the standardized search time and identified the individual to species level. For individuals where morphological identification proved difficult, we took DNA samples that we used to determine the species. We sampled butterflies with fruit trapping and time-standardized netting. We baited eight fruit traps (cylindrical nets) with fermented bananas and deployed them for 24 h. During the time-standardized netting, we caught butterflies for 30 min while walking at a slow and steady speed in a zig-zag line from plot edge to plot center to cover the plot area equally and interrupted the 30-min search time when handling butterflies. We only performed time-standardized netting in dry and non-windy conditions, either in the morning (8:00 to 12:00) or afternoon (13:00 to 17:00). Irrespective of the sampling method, we collected all captured butterflies, dried them, and took them to the laboratory for identification (moths excluded). We sampled ants with five bait (sardine and sugar) and five pitfall traps (31). We left pitfalls open for 48 h, but retrieved bait traps 30 min after installation. We preserved ant specimens in a tube with 70% alcohol for further identification. We identified ant specimens to (morpho-) species level.

Ecosystem Service Indicators. We estimated above-ground carbon stocks ($Mg \cdot ha^{-1}$) based on above-ground biomass values derived from the tree-inventory data (34). To calculate these, we used the pantropical allometric model with diameter at breast height, tree height, and wood density as input data (*SI Appendix*). To measure soil organic carbon concentration, we took two mixed soil samples at 0- to 15-cm depth per plot using a soil corer and followed established laboratory methods (*SI Appendix*). We assessed predation rates using artificial caterpillars made from plasticine (49). We deployed the dummy caterpillars for 48 h in the plots and calculated predation rates for each plot based on the ratio of dummies that were attacked by predators to the number of dummies that remained untouched.

We interviewed 322 households in 10 villages (*SI Appendix*, Fig. S1) to quantify perceived ecosystem services (natural products and water regulation). We interviewed mainly randomly selected households that participated in our baseline study [233 of 322 (19)]. To assess natural product use, we first asked the head of each household if they had access to each land-use type (same land-use types as for plots, except for vanilla, which we did not separate into fallow- and forest-derived for these interviews). We then asked the respondent to name all natural products (charcoal, firewood, plants for construction, weaving materials, lianas for string making, livestock fodder, wild food, honey, and medicinal plants) they gained from each land-use type. We then derived a single measure for all natural products by summing up the number of different products derived from each land-use type in each village and divided the sum by the number of households that had access to that land-use type. To assess perceived water-regulation services, we considered all responses related to water (water retention, water infiltration, and

SUSTAINABILITY SCIENCE

ECOLOGY

https://doi.org/10.1073/pnas.2107747119

interception of precipitation), as we expected these values to vary between land-use types (50). Because these water-regulation services were not access-related, we divided the number of people who cited water-regulation services from each land-use type by the number of households interviewed in that village. The resulting value is thus the proportion of people interviewed who perceived to gain water-regulation services from a particular land-use type.

Agricultural Productivity: Profitability and Yields. We calculated three parameters of agricultural productivity: 1) yield in kilograms per hectare, 2) profit per hectare, and 3) profit per person-day from a longitudinal study (October 2017 through October 2018), a recall study (October 2018 through March 2019), and a baseline study. We calculated profit as the difference between gross income and total costs over 1 y, where gross income was yield (kilograms) multiplied by the median farmgate price surveyed (Malagasy ariary [MGA] 165,000 kg^{-1} for green vanilla pods and MGA 1,300 kg^{-1} for brown rice). Costs included values of seeds, fertilizers, and pesticides used; hired labor wages; in-kind costs for labor; other cash costs directly related to production; and depreciation of materials. We did not include nonpaid labor (family labor and exchange labor) as costs, but calculated profit per person-day by dividing profit by nonpaid labor and similarly calculated profit per hectare by dividing profit by field size. To make the profit calculations more accessible, we converted the profits from MGA to dollars using an exchange rate of MGA 3,333 to $1. See *SI Appendix* for details.

Multidiversity, Endemic Multidiversity, and ES-Multifunctionality. We calculated (endemic) multidiversity and ES-multifunctionality to unify multiple indicators for biodiversity, endemic biodiversity, and ecosystem services into a single value. We computed multidiversity and endemic multidiversity for each land-use type based on raw plot-level species-richness data of seven taxonomic groups (trees, herbaceous plants, birds, amphibians, reptiles, butterflies, and ants) covering plants, vertebrates, and invertebrates. For calculating endemic biodiversity, we included only species classified as endemic to the country of Madagascar (*SI Appendix*, Table S1 for endemism sources for all taxa). We calculated ES-multifunctionality for each land-use type by combining three ecosystem services (above-ground carbon, soil organic carbon, and predation rate) measured on the plot level and two ecosystem services (natural product provisioning and water regulation) assessed through interviews at the village level. To connect these data, we linked each measured ecosystem service to the corresponding land-use type in each village. For example, we linked the perceived value for water-regulation service of forest fragments in a village to the forest-fragment plot of the same village. For the 10 old-growth forest plots that are by design not situated in a village, we randomly associated each plot to one of the perceived ecosystem service values from one of the 10 villages. Compared to alternative approaches of ES-multifunctionality calculation (24), our approach allowed us to derive a single measure of ES-multifunctionality that considers multiple services from local to landscape scales. By including only a single indicator from each underlying dataset (e.g., only one soil variable), we provide a more robust measure of ES-multifunctionality (51).

We calculated multidiversity, endemic multidiversity, and ES-multifunctionality using a thresholding approach (24). The basic idea behind this approach is that to fulfill a function or service, a taxon or function needs to occur to a sufficient extent to provide that service. Multidiversity or ES-multifunctionality is then expressed as the proportion of functions or taxonomic groups that exceed an a priori defined threshold, as compared with the maximum reached performance level (24). To circumvent the definition of an arbitrary threshold, researchers often use a multithreshold approach, running the analysis for various thresholds between 0% and 100% (24). Here, we computed multidiversity and ES-multifunctionality at the 20%, 50%, and 80% threshold, but chose to display the 50% threshold result in the main text (Fig. 3). We did this since diversity effects on ecosystem functioning peak at the 50% threshold (52). However, we display the results at the 20% and 80% thresholds in *SI Appendix*, Fig. S2. To operationalize this approach, we calculated the maximum reached performance level as the average of the 5 highest recorded values across all 80 plots, allowing us to reduce the influence of potential outliers. Importantly, the five highest recorded values were not limited to a single land-use type, so the average of the five highest recorded values may stem from, for example, three old-growth forest and two forest-fragment plots. Furthermore, the plots with the five highest recorded values may differ between multidiversity, endemic multidiversity, and ES-multifunctionality. We then calculated how many evaluated taxa and ecosystem functions reached the threshold on each plot, resulting in three values per plot (multidiversity, endemic multidiversity, and ES-multifunctionality). For instance, in a plot that reached a multidiversity value of 0.75 at the 50% threshold, 75% of all evaluated taxa reached a minimum of 50% of species richness compared to the average of the five plots of any land-use type with most species of that taxa. These calculations follow Grass et al., 2020 (11).

Assessment of Leverage Points and Trade-Offs with Agricultural Productivity. We identified three leverage points along the land-use trajectory (Fig. 2), i.e., points at which policy interventions may have large leverage for more sustainable outcomes since land users face conservation and conversion options with contrary outcomes. Importantly, the three leverage points exist at the same point in time due to various current land-use types that are placed at different stages along the trajectory. On our land-use trajectory, each leverage point has three possible outcomes: conservation of the present state and two conversion options. Therefore, decisions at each leverage point can result in vastly different outcomes, highlighting the leverage that interventions at these points may have. The frequency at which each leverage point occurs may vary through time: as old-growth forest vanishes, leverage point 1, where old-growth forest is at risk for being converted, will become less common, signifying a closing window of opportunity.

We investigated multiple taxa and ecosystem services at each leverage point to comprehensively assess trade-offs and cobenefits (Fig. 3). For each taxon or ecosystem service, we considered the difference to the current land use as the outcome of a land-use decision. We thus calculated the proportional deviation and 95% adjusted bootstrap CIs as follows:

$$\textit{Proportional deviation} = \frac{\textit{Conversion option} - \overline{\textit{Current land use}}}{\overline{\textit{Current land use}}}.$$

Conversion option is the value of biodiversity or ecosystem functioning in the conversion option, and $\overline{\textit{Current land use}}$ is the mean of the biodiversity or ecosystem functioning under the conservation option associated with each leverage point, i.e., old-growth forest, forest fragment, or woody fallow. Values of −1 thus indicate a 100% decrease (complete loss), and values of 1 indicate a 100% increase in biodiversity or ecosystem functioning compared to the current land use—that is, old-growth forest at leverage point 1, forest fragment at leverage point 2, or woody fallow at leverage point 3. We then calculated 95% CIs of the proportional deviation using 10,000 bootstrap replicates [R-package *boot* (53), adjusted percentile bootstrap (bca-type)]. If the 95% CI did not include zero, this indicated significant differences between the conversion option and the current stage.

To compare multidiversity, endemic multidiversity, and ES-multifunctionality along the land-use trajectory (Fig. 4 *A*–*C*), we calculated means and 95% adjusted bootstrap CIs (CI type "bca") of the variable for each land-use type at the corresponding stage (stage 0 to 4) as implemented in the R-package *boot* (53) with 10,000 bootstrap replicates. Two land-use types along the trajectory are considered to be different in terms of multidiversity, endemic multidiversity, and multifunctionality when their 95% CIs do not overlap.

To visualize multidiversity, endemic multidiversity, ES-multifunctionality, and individual measures of agricultural productivity per land-use type (Fig. 4*D*), we standardized all variables to a common scale by subtracting the mean value of the variable across all land-use types and dividing through the SD of the variable across all land-use types:

$$\textit{Standardized value} = \frac{\textit{Value} - \overline{\textit{Value}}}{\textit{Standard deviation}(\textit{Value})}.$$

We then calculated the mean for each variable for each land-use type (Fig. 4) to provide an overview across the seven land-use types. We processed all data in R (version 3.6.2) (54).

Data Availability. The data and code to reproduce the figures are available on Zenodo (https://doi.org/10.5281/zenodo.5554864).

ACKNOWLEDGMENTS. We thank members of the Diversity Turn in Land Use Science project for discussions; all involved farmers and Chef de Fokontany for their support; and the Ministry of Environment and Sustainable Development for research permits (N°100/17/MEEF/SG/DGF/DSAP/SCB.Re, N°163/17/MEEF/SG/DGF/DSAP/SCB.Re, N°18/18/MEEF/SG/DGF/DSAP/SCB.Re, and N°254/18/MEEF/SG/DGF/DSAP/SCB.Re). We are grateful to Theudy Alexis, Patrice Antilahimena, Soavita Fenohaja Babarezoto, Evrard Benasoavina, Claudine Bemamy, Jean Chrysostome Bevao, Ronik Botra, Dietrich Hertel, Harriet Lambert, David Lees, Marie Berthine Maminirina, Thorien Rabemanantsoa, Julien Randriampenomanana, Cédric Randrianantenaina, Nantenaina Herizo Rakotomalala, Eric Rakotomalala, Gatien Rasolofonirina, Joel Razafinantenaina, Grimo Jaona Sedric, Jacqueline Estenie Soa, Sáfián Szabolcs, Guillaume Velotody, Miguel Vences, and Maria S. Vorontsova, who contributed to logistics, data collection, sample identification, sample processing, or feedback on the manuscript. We thank the two anonymous reviewers whose constructive feedback strongly improved this manuscript. We acknowledge funding by Niedersächsisches Vorab of Volkswagen Foundation (Grant 11-76251-99-35/13 [ZN3119]) and the German Academic Exchange Service within the "Partnerships for Supporting Biodiversity in Developing Countries" initiative (Project 57449386). N.G.-R. thanks the Dorothea Schlözer Postdoctoral Program of the University of Goettingen. Portions of this paper were developed from a dissertation chapter of D.A.M.

1. D. Leclère *et al.*, Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature* **585**, 551–556 (2020).
2. O. E. Freeman, L. A. Duguma, P. A. Minang, Operationalizing the integrated landscape approach in practice. *Ecol. Soc.* **20**, 24 (2015).
3. C. Kremen, A. M. Merenlender, Landscapes that work for biodiversity and people. *Science* **362**, eaau6020 (2018).
4. B. L. Turner, 2nd, E. F. Lambin, P. H. Verburg, From land-use/land-cover to land system science. *Ambio* **50**, 1291–1294 (2021).
5. Y. Clough *et al.*, Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. *Nat. Commun.* **7**, 13137 (2016).
6. D. A. Martin *et al.*, Land-use history determines ecosystem services and conservation value in tropical agroforestry. *Conserv. Lett.* **13**, e12740 (2020).
7. D. J. Abson *et al.*, Leverage points for sustainability transformation. *Ambio* **46**, 30–39 (2017).
8. A. Röhring, L. Gailing, "Path dependency and resilience—The example of landscape regions" in *German Annual of Spatial Research and Policy 2010: Urban Regional Resilience: How Do Cities and Regions Deal with Change?*, B. Müller, Ed. (Springer, Berlin, 2011), pp. 79–88.
9. T. L. Morelli *et al.*, The fate of Madagascar's rainforest habitat. *Nat. Clim. Chang.* **10**, 89–96 (2020).
10. I. M. D. Rosa, M. J. Smith, O. R. Wearn, D. Purves, R. M. Ewers, The environmental legacy of modern tropical deforestation. *Curr. Biol.* **26**, 2161–2166 (2016).
11. I. Grass *et al.*, Trade-offs between multifunctionality and profit in tropical smallholder landscapes. *Nat. Commun.* **11**, 1–13 (2020).
12. R. Prudhomme *et al.*, Combining mitigation strategies to increase co-benefits for biodiversity and food security. *Environ. Res. Lett.* **15**, 114005 (2020).
13. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
14. G. Vieilledent *et al.*, Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol. Conserv.* **222**, 189–197 (2018).
15. J. N. Andriamparany, H. Hänke, E. Schlecht, Food security and food quality among vanilla farmers in Madagascar: The role of contract farming and livestock keeping. *Food Secur.* **13**, 981–1012 (2021).
16. J. Smits, I. Permanyer, The Subnational Human Development Database. *Sci. Data* **6**, 190038 (2019).
17. J. G. Zaehringer, S. Eckert, P. Messerli, Revealing regional deforestation dynamics in North-Eastern Madagascar—Insights from multi-temporal land cover change analysis. *Land (Basel)* **4**, 454–474 (2015).
18. Sustainable Vanilla Initiative, SVI: Sustainable Vanilla Initiative. https://www.idhsustainabletrade.com/sustainable-vanilla-initiative-svi/. Accessed 12 April 2021.
19. H. Hänke *et al.*, "Socio-economic, land use and value chain perspectives on vanilla farming in the SAVA Region (north-eastern Madagascar): The Diversity Turn Baseline Study (DTBS). July 2019 Edition" (Diskussionsbeitrag No. 1806, Georg-August-Universität Göttingen, Göttingen, Germany, 2018).
20. D. A. Martin, "Smallholder vanilla agroforestry in Madagascar: Biodiversity, ecosystem services and yields in a land-use context." Dissertation, University of Goettingen, Goettingen, Germany (2021).
21. J. C. Llopis *et al.*, Effects of protected area establishment and cash crop price dynamics on sland use transitions 1990–2017 in north-eastern Madagascar. *J. Land Use Sci.* **14**, 1–29 (2019).
22. E. Styger, H. M. Rakotondramasy, M. J. Pfeffer, E. C. M. Fernandes, D. M. Bates, Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agric. Ecosyst. Environ.* **119**, 257–269 (2007).
23. D. A. Martin *et al.*, Shade-tree rehabilitation in vanilla agroforests is yield neutral and may translate into landscape-scale canopy cover gains. *Ecosystems (N. Y.)* **24**, 1253–1267 (2021).
24. P. Manning *et al.*, Redefining ecosystem multifunctionality. *Nat. Ecol. Evol.* **2**, 427–436 (2018).
25. L. Wilmé, "Composition and characteristics of bird communities in Madagascar" in *Biogéographie de Madagascar, Colloques et Séminaires*, W. R. Lourenço, Ed. (ORSTOM, Paris, France, 1996), pp. 349–362.
26. H. Rakotomanana, R. K. B. Jenkins, J. Ratsimbazafy, "Conservation challenges for Madagascar in the next decade" in *Conservation Biology: Voices from the Tropics*, P. H. Raven, N. S. Sodhi, L. Gibson, Eds. (John Wiley & Sons, Ltd., Hoboken, NJ, 2013), pp. 33–39.
27. J. C. Llopis *et al.*, Year-to-year ecosystem services supply in conservation contexts in north-eastern Madagascar: Trade-offs between global demands and local needs. *Ecosyst. Serv.* **48**, 101249 (2021).
28. M. Poudyal *et al.*, Who bears the cost of forest conservation? *PeerJ* **6**, e5106 (2018).
29. I. M. Turner, Species loss in fragments of tropical rain forest: A review of the evidence. *J. Appl. Ecol.* **33**, 200–209 (1996).
30. D. A. Martin *et al.*, Bird diversity and endemism along a land-use gradient in Madagascar: The conservation value of vanilla agroforests. *Biotropica* **53**, 179–190 (2021).
31. A. A. N. A. Rakotomalala *et al.*, Tropical land use drives endemic vs. exotic ant communities in a global biodiversity hotspot. *Biodivers. Conserv.* **30**, 4417–4434 (2021).
32. E. Raveloaritiana *et al.*, Land-use intensification increases richness of native and exotic herbaceous plants, but not endemics, in Malagasy vanilla landscapes. *Divers. Distrib.* **27**, 784–798 (2021).
33. R. M. Laney, Disaggregating induced intensification for land-change analysis: A case study from Madagascar. *Ann. Assoc. Am. Geogr.* **92**, 702–726 (2002).
34. M. R. Soazafy *et al.*, Aboveground carbon stocks in Madagascar's vanilla production landscape—Exploring rehabilitation through agroforestry in the light of land-use history. *Glob. Ecol. Conserv.* **31**, e01853 (2021).
35. R. Laney, B. L. Turner, 2nd, The persistence of self-provisioning among smallholder farmers in northeast Madagascar. *Hum. Ecol. Interdiscip. J.* **43**, 811–826 (2015).
36. D. Havkin-Frenkel, F. C. Belanger, Eds., *Handbook of Vanilla Science and Technology* (Wiley, Hoboken, NJ, ed. 2, 2018).
37. B. Neimark, S. Osterhoudt, L. Blum, T. Healy, Mob justice and 'The civilized commodity'. *J. Peasant Stud.* **48**, 734–753 (2019).
38. K. Klanderud *et al.*, Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. *Biodivers. Conserv.* **19**, 187–204 (2010).
39. C. A. Kull, Madagascar aflame: Landscape burning as peasant protest, resistance, or a resource management tool? *Polit. Geogr.* **21**, 927–953 (2002).
40. J. P. G. Jones *et al.*, Human migration to the forest frontier: Implications for land use change and conservation management. *Geo* **5**, e00050 (2018).
41. O. Mertz, The relationship between length of fallow and crop yields in shifting cultivation: A rethinking. *Agrofor. Syst.* **55**, 149–159 (2002).
42. O. R. Andriamihaja, F. Metz, J. G. Zaehringer, M. Fischer, P. Messerli, Identifying agents of change for sustainable land governance. *Land Use Policy* **100**, 104882 (2021).
43. F. van der Plas *et al.*, Towards the development of general rules describing landscape heterogeneity—Multifunctionality relationships. *J. Appl. Ecol.* **56**, 168–179 (2019).
44. T. K. Rudel, Is there a forest transition? Deforestation, reforestation, and development. *Rural Sociol.* **63**, 533–552 (1998).
45. J. Salzman, G. Bennett, N. Carroll, A. Goldstein, M. Jenkins, The global status and trends of payments for ecosystem services. *Nat. Sustain.* **1**, 136–144 (2018).
46. FAO, "FAOSTAT" (Report, Food and Agriculture Organisation of the United Nations, Rome, 2020).
47. K. Osen *et al.*, Land-use history determines stand structure and tree diversity in vanilla agroforests of northeastern Madagascar. *Appl. Veg. Sci.* **24**, e12563 (2021).
48. T. R. Fulgence *et al.*, Differential responses of amphibians and reptiles to land-use change in the biodiversity hotspot of north-eastern Madagascar. *Anim. Conserv.*, 10.1111/acv.12760 (2021).
49. D. Schwab *et al.*, Decreasing predation rates and shifting predator compositions along a land-use gradient in Madagascar's vanilla landscapes. *J. Appl. Ecol.* **58**, 360–371 (2021).
50. H. J. (Ilja) van Meerveld *et al.*, Forest regeneration can positively contribute to local hydrological ecosystem services: Implications for forest landscape restoration. *J. Appl. Ecol.* **58**, 755–765 (2021).
51. G. Garland *et al.*, A closer look at the functions behind ecosystem multifunctionality: A review. *J. Ecol.* **109**, 600–613 (2020).
52. J. S. Lefcheck *et al.*, Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.* **6**, 6936 (2015).
53. A. Canty, B. Ripley, Package 'boot' (Version 1.3-22, 2017).
54. R Core Team, R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria, Version 3.6.2, 2019).