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Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity

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The conversion of tropical rainforest to agricultural systems such as oil palm alters biodiversity across a large range of interacting taxa and trophic levels. Yet, it remains unclear how direct and cascading effects of land-use change simultaneously drive ecological shifts. Combining data from a multi-taxon research initiative in Sumatra, Indonesia, we show that direct and cascading land-use effects alter biomass and species richness of taxa across trophic levels ranging from microorganisms to birds. Tropical land use resulted in increases in biomass and species richness via bottom-up cascading effects, but reductions via direct effects. When considering direct and cascading effects together, land use was found to reduce biomass and species richness, with increasing magnitude at higher trophic levels. Our analyses disentangle the multifaceted effects of land-use change on tropical ecosystems, revealing that biotic interactions on broad taxonomic scales influence the ecological outcome of anthropogenic perturbations to natural ecosystems.

Expansion and intensification of agricultural landscapes for food production and biofuels have altered many of the Earth's ecosystems[1–3]. In tropical regions, which harbour exceptionally high levels of biodiversity[4], the conversion of rainforest to monoculture cash crops, such as oil palm and rubber, poses a severe threat to biodiversity[1,5–8]. Temperate and tropical research has long focused on how land-use change directly affects one or two trophic groups (for example, plants, butterflies, or birds)[3,9]; an approach that is limited as it often yields widely varying or contrasting results depending on the model taxon. Such studies are also typically conducted without considering possible biotic interactions that can trigger cascading effects via bottom-up or top-down forces. In recent years, however, more attention has turned towards quantifying land-use impacts on multi-trophic systems[10], revealing that biotic interactions underlie the provisioning of ecosystem functioning and that neglecting these interactions may lead to biased inference on the extent of land-use consequences. Even so, research has still predominantly been restricted to only a few trophic levels[10], without considering cascading effects through multiple trophic levels across many higher-level taxa[11,12]. Consequently, there is persisting uncertainty about how land-use impacts alter taxa across multiple trophic levels directly (Fig. 1a) and indirectly via trophic cascades (Fig. 1b).

In recent years, experimental research that manipulates plant diversity and composition has elucidated how primary producers influence the structure of food webs via bottom-up trophic cascades[13–15]. These findings lend credence to the theory that perturbations at particular trophic levels can have profound impacts on the structure of whole ecosystems as these effects ripple across functional groups of organisms that are linked by their trophic interactions[16]. This notion holds crucial implications for the way that land-use change will impact ecosystems, raising the question of how bottom-up cascades impact multi-trophic communities in combination with the direct impacts of management practices in intensified land-use systems. Experimental manipulations of trophic levels have been necessary to understand how trophic cascades operate in simple multi-trophic systems, but these experiments

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are restricted to systems of low trophic complexity due to strong logistical constraints. Multivariate analytical techniques such as structural equation modelling allow for the inference of cascading effects from observational data in more complex systems by analysing the covariance structure of multiple variables[17], thus expanding our ability to explore cascading dynamics in complex systems. On one hand, direct land-use effects could dominate through factors such as pesticide application imposing direct toxic effects on invertebrates and microorganisms in intensively managed plantations (Fig. 1a). In contrast, cascading effects could prevail for consumers that may be more strongly impacted by the depletion of their resources (Fig. 1b), but these effects could also conjointly impact various trophic levels. Identifying and understanding these direct and cascading processes could improve the efficiency of conservation and management efforts in tropical land-use systems by allowing practitioners to target taxa whose manipulation might have especially broad impacts on many other important taxa, such as those that are of conservation concern or that provide important ecosystem services.

Here we investigate the direct (Fig. 1a) and cascading (Fig. 1b) effects of anthropogenic land use by employing a path modelling framework to quantify their isolated and combined impacts on taxa ranging from prokaryotic microorganisms to birds. In an extensive multi-taxon research initiative, we sampled species richness and biomass of plants, bacteria, archaea, litter invertebrates, arboreal ants and birds (see Supplementary Table 1) in lowland forest, jungle rubber, rubber monocultures and oil palm monocultures in Sumatra, Indonesia. To investigate the direct (Fig. 1a) and cascading effects (Fig. 1b) of land-use change, we constructed generalized multilevel path models[18], allowing us to model direct and interactive effects of land use and abiotic variables, as well as biologically relevant, bottom-up trophic effects across taxa. We find that land-use conversion to tropical monocultures imposes direct effects across almost all taxa, with some of these direct impacts eliciting cascading effects to higher trophic levels. Our findings suggest that a combination of direct and cascading effects of land-use change contribute to the increased vulnerability of taxa at higher trophic levels, demonstrating the role of biotic interactions for determining the outcome of ecosystem responses to anthropogenic disturbances.

Results

Land-use change impacts taxa across trophic levels. Conversion of rainforest to oil palm and rubber plantations imposed predominantly direct impacts on almost all trophic levels (Fig. 2; Supplementary Table 2 and Supplementary Fig. 1). Most of these direct effects in the path model (77%) were negative, with a clear overall reduction in species richness and biomass as a result of land-use conversion in these lowland tropical ecosystems (Fig. 2; Supplementary Fig. 1). We also identified bottom-up effects driven by variability in the species richness and biomass of many of the trophic groups (Fig. 2). In a number of cases, bottom-up effects propagated from direct land-use impacts (Fig. 2), demonstrating that in complex multi-trophic systems, both direct and cascading effects alter a wide range of taxa to yield realized net impacts of land-use change on species richness and biomass.

Identifying direct effects and bottom-up cascades. In general, the weakest direct effects of land use were found on invertebrate omnivores (Fig. 2; see Supplementary Table 2), with even positive effects found on the arboreal ant communities. At the lowest trophic level of plants and soil microorganisms, we found the strongest negative effects of land use on plant species richness and biomass (70% shift). Yet, while there was also a strong reduction of microbial biomass (77%), this was coupled with equally high increases in prokaryotic microbial species richness (78%). We also detected both direct and interactive effects from the abiotic variables (for example, microclimate and soil) in the lowest trophic level groups (plants, microorganisms and invertebrate detritivores). Changes in soil characteristics aided in strengthening (soil organic matter) the negative direct effects of land-use conversion on microbial biomass and in weakening (soil nutrient availability) its negative effects on plant communities (Fig. 2). The most consistent direct impacts of land use for any general organism group was detected in the bird communities, with strong negative effects of land use on species

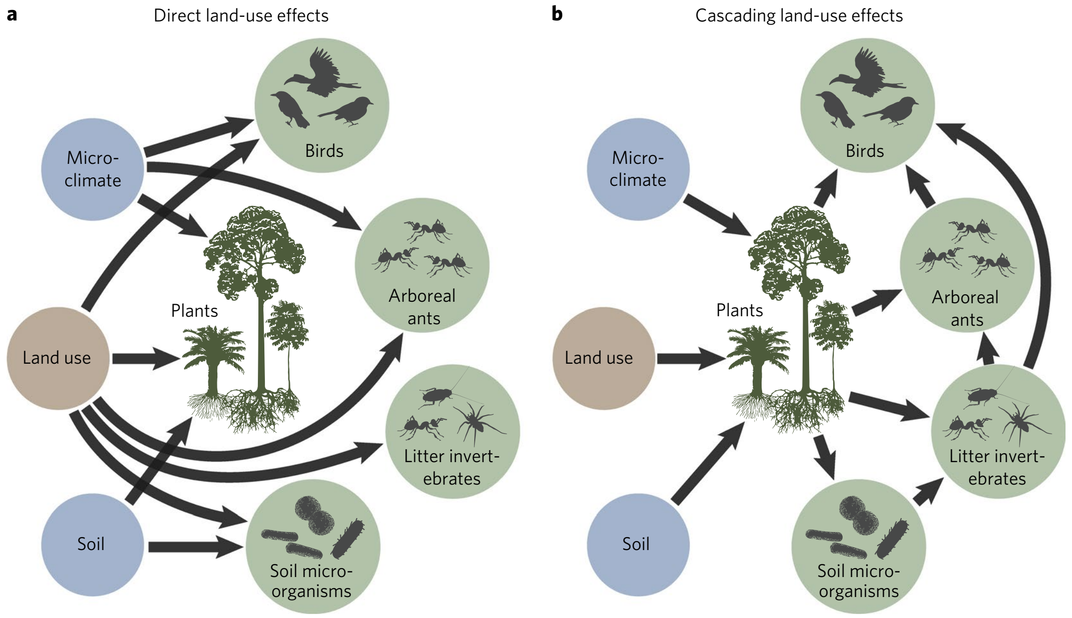

Fig. 1 | How land-use change may directly and indirectly alter whole ecosystems. a, The direct land-use effects hypothesis assumes that land-use change directly impacts all taxonomic groups and trophic levels. **b**, The cascading land-use effects hypothesis assumes that all impacts of land-use change at higher trophic levels propagate via cascading bottom-up processes. Only selected effects are represented for illustrative purposes (see Supplementary Fig. 2 for all hypothesized effects).

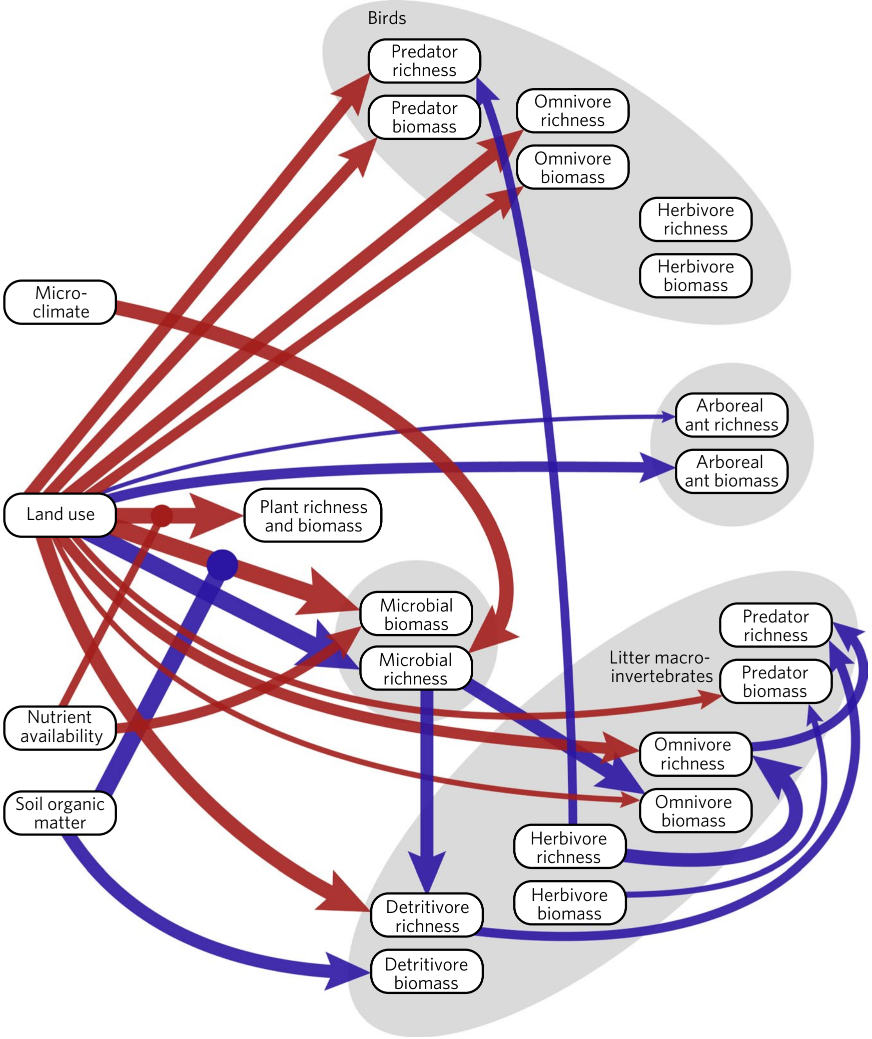

Fig. 2 | Path model of direct and cascading land-use effects in a tropical multi-trophic system. Final selected model ($\chi^2 = 297.40$, d.f. = 338, $P = 0.95$), with red and blue arrows to denote all significant negative and positive effects, respectively. Arrows ending in circular nodes that intersect the arrows originating from land use indicate a mediation of these effects (that is, a statistically significant interaction). Arrow widths are proportional to their absolute range-standardized effect sizes.

richness and biomass of both predatory and omnivorous birds, displaying shifts in their values between 47 and 59% with agricultural land-use conversion (Fig. 2; see Supplementary Table 2).

Within our multi-taxon path model we were also able to detect a number of indirect cascading effects of land-use change that affected up to three succeeding trophic levels (species richness of prokaryotic microorganisms, invertebrate detritivores and invertebrate predators; Fig. 2). Such cascading effects caused unexpected shifts in communities that did not reflect the direct effects of land use. As a specific example, although we found a 66% reduction of detritivore species richness in response to land-use change (holding all detected cascading effects constant), there were positive indirect effects of land use via the effects of increased microbial species richness on detritivore species richness, which yielded a net positive effect (45%; Table 1). This pattern was similarly found for invertebrate omnivore biomass (Fig. 2; Table 1). Not all bottom-up effects, however, influenced the impacts of land-use change. Specifically, species richness and biomass of invertebrate herbivores had positive effects on litter invertebrate omnivores, predators and even bird predators (Fig. 2; Supplementary Table 2); yet, there were no significant responses of these herbivorous invertebrates to land use.

The interplay of direct and cascading effects in multi-trophic communities. We calculated the mean effect sizes of direct and cascading effects, and combined these to estimate the total effects of land-use change on the sampled broad-scale multi-trophic communities. These analyses revealed that, overall, direct land-use impacts were strongly negative (standardized path coefficient of −0.35; Fig. 3a), which was in stark contrast to the positive indirect effects of land use (standardized path coefficient of 0.28; Fig. 3a). Nevertheless, combining these direct and cascading effects at the entire community level showed overall negative impacts of land-use change on the species richness and biomass of sampled taxa (Fig. 3a). By separating these direct and cascading effects into different trophic levels, we found that direct land-use effects were, on average, strongly negative, with the exception of very weak direct effects on the invertebrate omnivore level (Table 1; Fig. 3b). In contrast, we found positive cascading effects of land-use change on the lower trophic levels of invertebrate detritivores and omnivores, but these positive cascading effects shifted to negative effects at the higher trophic level of invertebrate predators (Table 1; Fig. 3b). Interestingly, when looking at the total effects of land use (direct and cascading effect sizes combined), the data suggest increasingly negative effects of land-use change with increasing trophic level,

Table 1 | Summary of direct and cascading land-use effects for each individual trophic group

Response variable	Trophic level	Direct effect size	Cascading effect size
Plant richness and biomass	1	−0.699	
Microbial biomass	1	−0.768	
Microbial richness	1	0.781	
Invertebrate detritivore biomass	2		
Invertebrate detritivore richness	2	−0.663	0.449
Invertebrate herbivore biomass	2		
Invertebrate herbivore richness	2		
Bird herbivore biomass	2		
Bird herbivore richness	2		
Invertebrate omnivore biomass	3	−0.254	0.487
Invertebrate omnivore richness	3	−0.498	
Arboreal ant biomass	3	0.459	
Arboreal ant richness	3	0.187	
Invertebrate predator biomass	4	−0.308	
Invertebrate predator richness	4		−0.291
Bird omnivore biomass	5	−0.467	
Bird omnivore richness	5	−0.587	
Bird predator biomass	5	−0.512	
Bird predator richness	5	−0.542	

Effect sizes are range-standardized path coefficients taken from the final path model (Fig. 2). The 'Cascading effect size' column gives the multiplicative indirect land-use effects summed for each trophic group response variable. Blank cells indicate no detected effects.

with the strongest reductions in species richness and biomass at the invertebrate predator, bird omnivore and bird predator trophic levels (Fig. 3b; see Fig. 2 and Supplementary Table 2 for trophic-group-specific effects).

Discussion

Our findings of direct and cascading ecological impacts of tropical land-use change shed light on the poorly understood role that biotic interactions play in determining impacts of anthropogenic perturbations at the whole-ecosystem level. Land-use conversion of lowland rainforest to plantation monocultures drives large-scale ecological shifts across trophic levels spanning a large range of taxa. In essence, our results suggest that as one moves upward in the food chain, land-use impacts seem to become increasingly negative, but these effects were a combination of both direct and indirect factors that act in concert to yield broad-scale changes in species richness and biomass of these tropical ecosystems. Such indirect effects, however, would remain undetected without considering the role of biotic interactions among trophic levels in ecosystems undergoing land-use change impacts.

By segregating the variance in species richness and biomass responses of different trophic levels between direct impacts of land use and cascading effects through biotic interactions, we identified where direct land-use impacts might be most influential. The strong direct effects found on plant species richness and biomass are indicative of the drastic changes to plant communities that take place when converting rainforest and low-intensity agroforestry systems (that is, jungle rubber plantations) to intensively managed monocultures such as rubber and oil palm plantations[6]. Furthermore, the higher inputs of soil amendments (for example, lime and chemical fertilizers) and herbicides in oil palm monocultures[19] probably drive further reductions in plant species richness[20]. On the contrary, fertilization can increase microbial diversity in these systems[21], but this is coupled with declines in microbial biomass[19], suggesting a community shift towards low biomass–high diversity communities in the oil palm plantations[22,23]. Although there is considerable evidence that microbial communities are dependent on plant diversity and biomass[24,25], we did not detect such effects that mediated land-use impacts (Fig. 2), despite testing for these interactions in the path model (Supplementary Fig. 2). This is probably owing to the dominating effects of the aforementioned land-use practices that override potentially more subtle influences of plant biomass and species richness per se, as well as the fact that diversity of larger plants (that is, trees and palms) varies on a scale far larger than that on which microorganisms operate. Thus, land-use impacts on prokaryotic microorganisms were predominantly direct, with no detectable effects via plant species richness. We did, however, find notably strong cascading effects of altered microbial species richness on litter invertebrate detritivores and omnivores. Considering that species richness of invertebrate detritivores was significantly lower in intensive land-use systems, these impacted detritivore communities seem to rely rather heavily on the increased microbial species richness found in these monoculture land-use systems. This example elucidates the complexity of land-use effects on multi-trophic systems, whereby direct negative effects might be partially counterbalanced by more obscure indirect effects mediated by biotic interactions. In addition to the complexity demonstrated in our analyses, these multi-trophic responses could be even further complicated by potential feedback effects of taxa on environmental properties; such as, for example, soil fauna effects on soil properties. Feedback effects could thus yield even further variability in the responses of various trophic groups to land-use change, although we did not investigate these processes here. Furthermore, we did not explicitly consider shifts in species composition among land-use systems, which is likely to be an important response of various trophic groups as species tend to respond variably to such environmental change drivers[26]. Although changes in biomass and species richness are likely to be the strongest determinants of cascading effects on higher trophic levels, changing species composition of a trophic group could also influence its consumers due to changes in relative densities of consumer food resources. As this is not necessarily captured by analysing biomass and species richness, alone, the influence of compositional shifts will be an important consideration for future studies.

Although most responses to land-use change were negative, various cases such as the large increase found in microbial species richness in oil palm plantations (also previously found in other studies; for example, ref. [21]) demonstrate that certain taxa are likely to mask the expected negative responses of ecosystems to land-use change. For example, we found that omnivorous invertebrates (including both arboreal ants and litter macroinvertebrates) had generally weak negative or positive responses to land-use change, especially when taking into account the positive cascading effect via microbial species richness on omnivorous litter invertebrate biomass (Fig. 2). Interestingly, the strongest negative effect on the invertebrate omnivores was on species richness, but with both direct and cascading positive effects found in their biomass (Fig. 2). This trend indicates a shift towards higher biomass of particular species that are probably generalist feeders and are better able to exploit resources present in new environments[27], such as intensive agricultural systems. It should also be noted that such increases in biomass (or even species richness) within intensified land-use systems can often result from colonization of invasive species, which may be detrimental to native species[6]. Also, an important consideration in agricultural systems, such as oil palm and rubber plantations, is that communities are temporally dynamic due to regular disturbance cycles imposed by plantation establishment and growth[6]. Thus, it is likely that over time, following plantation establishment, there might be high species richness or biomass as previous species assemblages have not yet been completely lost from the converted ecosystem but there

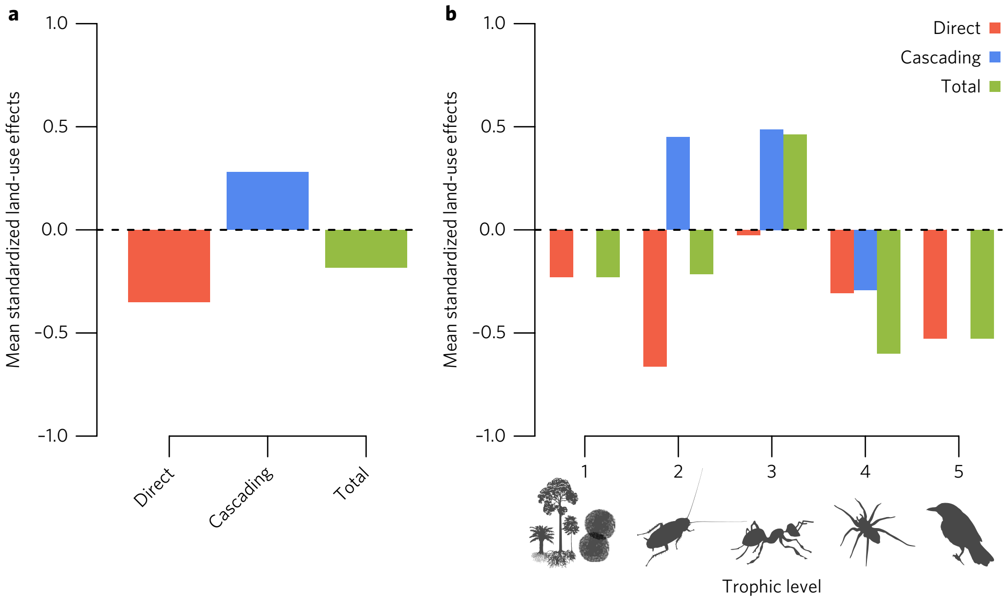

Fig. 3 | Summary of land-use effects on diversity and biomass of interacting taxa. a,b, Mean standardized effect sizes of direct, cascading and total land-use effects across all taxa and trophic levels (**a**), and for individual trophic levels (**b**) are shown. Cascading effects were estimated by multiplying coefficients along pathways of interacting taxa in the path model, whereas total effects were estimated by summing the direct and cascading effect sizes of land-use change on each trophic level. Generalized trophic levels were separated into (1) plants and soil microorganisms, (2) litter invertebrate detritivores and herbivores, (3) litter invertebrate omnivores and arboreal ants, (4) litter invertebrate predators, and (5) bird predators and omnivores, as shown in Table 1.

are also newly colonizing species that are adapted to such disturbed habitat[28]. However, the shift towards lower species richness in the litter invertebrate omnivores was found to have negative cascading impacts on the higher-trophic-level litter invertebrate predators (Fig. 2), further indicating that although omnivore groups may not clearly respond negatively to land-use change, these changes in omnivore communities might still yield negative impacts at other trophic levels when considering biotic interactions over time.

Despite considerable support for the cascading effects hypothesis in the belowground taxonomic groups (soil microorganisms and litter invertebrate communities), in the aboveground taxa there seemed to be far more direct effects of land use, such as the positive effects on arboreal ant communities and the negative direct effects on bird communities (Fig. 2). There are various potential explanations for why land-use impacts seem to be more direct on these taxa. In the case of arboreal ants, this could be a result of their ability to shift among resources according to availability, as well as their eusocial behaviour allowing them to acquire resources far more efficiently than solitary organisms[29], somewhat reducing their reliance on the variability of lower trophic levels. The detection of only direct effects in birds could be due to the scale on which these organisms operate, as birds are more likely to be influenced by landscape-level variation in resource availability[30]. Thus, local changes in invertebrate and plant communities are likely to have much less influence on birds than direct land-use impacts such as differences in habitat structure and disturbance of habitats by humans (for example, disturbance of nesting sites or harvesting of species for the bird trade). Investigating the scale dependence (both spatial and temporal) of cascading effects across taxa would be important to better understand how different taxonomic groups are likely to be impacted by land-use change. However, such conclusions need to be made with caution, as the detection of cascading effects is also partly contingent on the inclusion of all interacting trophic groups; that is, a direct land-use effect on bird biomass could in fact be cascading, but the detection of such a cascade could be missed if an intermediate trophic group was not sampled. For example, in the ecosystems sampled here, such missing groups could include invertebrates dwelling in the canopy, or those flying through the sampled habitats but that are not resident (such as from adjacent aquatic systems). Furthermore, in our analyses we focus on two major characteristics of ecological communities: total biomass and species richness. As mentioned above, we do not consider more complex measures of community composition, such as the relative abundances of species or functional diversity, although such measures are also important for capturing community responses to land-use change[26,31] and could also yield ecological cascades, in addition to the biomass and species richness of trophic groups, alone. These factors (that is, scale dependence of cascading effects, non-sampled trophic groups and other measures of community responses) could also explain the surprising lack of land-use effects (direct or cascading) on the herbivorous birds. Nevertheless, our results provide strong support for where cascading effects do occur across trophically broad communities, and provide crucial insight into how these effects act in concert with direct land-use impacts.

Drawing on more general patterns of land-use effects on broad-scale assemblages of interacting taxa, we found strongly negative direct compared with generally positive cascading land-use effects. This occurred because certain taxa that responded positively to land-use change in turn had positive effects on their consumers, even if the direct effects of land use on those consumers were negative. For example, we found a direct negative response of litter invertebrate detritivores to land use that was partially counterbalanced by indirect positive effects via microbial species richness, which responded positively to land-use change. Despite such contradictory trends in the paths of direct and indirect effects, the overall net land-use change effects still yielded negative responses across the entire multi-taxon dataset (Fig. 3). This is probably owing to a dissipation of effect strength with an increasing degree of separation from the external forcing mechanism (in this case land-use change), rendering direct effects stronger than the indirect effects. By breaking down these effects into generalized trophic levels, we found positive cascading effects at the lower trophic levels (invertebrate detritivores and omnivores) but negative cascading effects at the invertebrate predator trophic level (Fig. 3). This could be

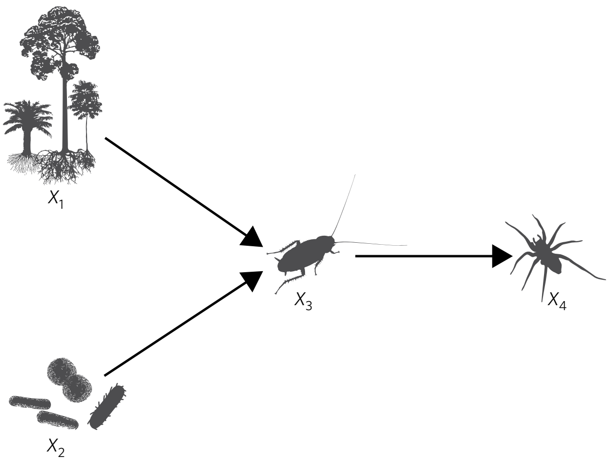

Fig. 4 | Example of the d-sep procedure used to construct the multilevel path models. Here we present a hypothetical causal diagram that can be expressed as a set of independence claims B_U. The B_U set consists of each independent pair of variables (X_i, X_j) and their conditioning set {Z}, which consists of all other variables that directly affect either X_i or X_j. In this example, we have three independence claims in the B_U set: (X_1, X_2) | {∅}; (X_1, X_4) | {X_3}; and (X_2, X_4) | {X_3}, which together infer indirect causal dependence of X_4 on X_1 and X_2.

explained by increased microbial species richness with land-use change that indirectly enhanced detritivore species richness and omnivore biomass, contrasted with decreasing invertebrate detritivore and omnivore species richness, which indirectly reduced the species richness of reliant invertebrate predators[32]. Thus, our study demonstrates that the reliance of predator communities on the stability of the communities of their resources, combined with the direct impacts of land-use change, may together be responsible for increased sensitivity of higher trophic levels to land-use change. Indeed, we found that with increasing trophic level, the magnitude of negative total species richness and biomass responses to land-use change increased considerably (Fig. 3), lending support to the notion that higher trophic level species are the most sensitive to anthropogenic disturbances[26].

In summary, we demonstrate that tropical land-use change drives large-scale ecological shifts across trophic levels via direct and cascading land-use effects. Our findings shed light on the relative impact of direct effects and those that cascade upward through multiple trophic levels, and how biotic interactions can mediate land-use impacts in complex, diverse ecological communities. By accounting for shifting drivers of ecological change across the trophic spectrum, we can better understand which factors determine taxon-specific responses to anthropogenic disturbances, such as the ongoing conversion of tropical rainforests to plantation agriculture[33].

Methods

Study and sampling design. The study was carried out in Jambi Province, Sumatra, Indonesia—a tropical lowland region that has experienced massive recent land-use change. The study design comprised two landscapes with four land-use systems common to the region: primary degraded forest (as described in ref. [34]); jungle rubber (a smallholder agroforest system where rubber trees are planted into previously logged rainforests); and smallholder monoculture plantations of rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*). The two landscapes were classified by their corresponding protected forest areas—Bukit Duabelas National Park and Harapan Rainforest—which contained the secondary forest plots (see Supplementary Fig. 3). Plots were selected in 2012 using a range of biophysical and socio-economic criteria. All plots had to be on well-drained, heavily weathered soils ('acrisols' using World Reference Base (WRB) classification[35], 'ultisols', using US Department of Agriculture (USDA) classification[36]) with slopes not exceeding 10%. In the Harapan landscape, soil texture was a mixture of sand, silt and clay (loam acrisols), while in the Bukit Duabelas landscape soils had higher clay content (clay acrisols)[19,37]. We selected rainforest plots from forests that had never been used for any other land use but showed signs of selective logging and extraction of non-timber forest products such as rattan[34]. All agricultural land-use plots were selected only if they were owned and managed by smallholders, were regularly harvested and were large enough to establish a 50 × 50 m (0.25 ha) plot. Plots in jungle rubber were estimated to be at least 20 yr old, based on rubber tree size. For the rubber and oil palm monoculture plots, important additional selection criteria were that they had to be well established with a closed canopy, were in the most productive phase of their lifecycle and could be expected to be productive for at least ten more years. We selected rubber plantations that varied in age between 7 and 16 yr, and oil palm plantations that varied in age between 8 and 15 yr (all determined in 2012, at the time of site selection). Management practices in the smallholder agricultural systems are described in refs [19,37]. In summary, during our study period (2013), oil palm plantation management practices included fertilization (varying between 48 and 138 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$, 21 and 38 $\mathrm{kg\,P\,ha^{-1}\,yr^{-1}}$, and 40 and 157 $\mathrm{kg\,K\,ha^{-1}\,yr^{-1}}$ with NPK complete and KCl fertilizers), liming (200 kg dolomite ($\mathrm{CaMg(CO_3)_2}$) $\mathrm{ha^{-1}\,yr^{-1}}$) and weeding (manual and herbicides). Prior to our study year, kieserite ($\mathrm{MgSO_4{\cdot}H_2O}$) and borate ($\mathrm{Na_2B_4O_7{\cdot}5H_2O}$) fertilizers were also used in several of the oil palm plantations. Rubber plantation management practices included weeding (manual and herbicides), but no soil amendments during 2013.

In each landscape, four 50 × 50 m replicate plots (0.25 ha) per land-use system were selected (a typical minimum plot size for tropical lowland forest plant surveys[38]) with a minimum distance of 117 m between plots ($n = 32$) and five randomly selected 5 × 5 m subplots were established in each plot (see Supplementary Fig. 3). Subplot placement was carried out by first using a 10 × 10 m grid to randomly assign five locations in each plot, followed by a second randomized selection of the corner for which the 5 × 5 m subplot should be placed, which was then fixed for all 32 plots. Detailed information concerning the study region, study design and land-use systems is provided in ref. [39].

Soil characteristics. Soil sampling was conducted in all 32 plots between June and December 2013. Within each 0.25 ha plot, a 10 × 10 m grid was established and ten grid points that were at least 5 m distance from the plot's border were selected (including within the five randomly selected subplots associated with the project) and fixed within each plot as subplots for point soil sampling. Soil samples were taken from the top 0–0.1 m depth interval at each grid point. The ten subplots were averaged to represent each plot ($n = 32$). Soil biochemical analysis for pH, soil organic carbon ($\mathrm{kg\,C\,m^{-2}}$), total nitrogen ($\mathrm{g\,N\,m^{-2}}$), effective cation exchange capacity ($\mathrm{mmol_c\,kg^{-1}}$), base saturation (%), extractable phosphorus ($\mathrm{g\,P\,m^{-2}}$) and ^{15}N natural abundance signatures (δ^{15}N; ‰) was completed on air-dried and sieved (2 mm) soil samples at the Soil Science of Tropical and Subtropical Ecosystems laboratory at Georg-August Universität Goettingen, Germany. A full description of the sampling protocol and biochemical analysis can be found in ref. [19].

Soil texture (% sand, % silt and % clay) was measured using the pipette method[40] from soil samples taken in the top 0.1 m depth at three of the four plots per land-use system ($n = 24$). The core method[41] was used to measure soil bulk density ($\mathrm{g\,cm^{-3}}$) from soil cores taken in the top 5 cm soil depth at two randomly selected subplots per plot. Volumetric moisture content of the soil (%) was measured using moisture sensors (IMKO Trime-PICO, Ettlingen, Germany) and recorded every hour with a data logger (see 'Microclimatic variability').

Microclimatic variability. Weather stations were installed in the centre of each of the 32 plots. They were equipped with thermohygrometers (Galltec Mella, Bondorf, Germany) placed at a height of 2 m to record air temperature (°C) and humidity (%) inside the canopy, and soil sensors (IMKO Trime-PICO, Ettlingen, Germany) at 0.3 m depth, to monitor soil temperature (°C) and moisture (%). Both sensors were connected to a data logger (LogTrans16-GPRS, UIT, Dresden, Germany) and measurements were recorded every hour. From the period of June 2013 to October 2014, the 5th and 95th percentiles of air and soil temperature, and atmospheric humidity were used to calculate ranges for each variable.

Above- and belowground plant biomass and species richness. Within each 0.25 ha plot, the diameter and height of all trees, palms and lianas with a diameter at breast height (DBH) ≥10 cm (DBH at 1.3 m) were measured. Wood density values (dry mass per fresh volume in $\mathrm{kg\,m^{-3}}$) were measured for extracted cores of 204 trees. The interpolated wood density values were applied on the remaining trees based on a calibration equation with pin penetration depth measured using a Pilodyn 6 J wood tester (PROCEQ SA, Zürich, Switzerland). Additionally, forest understorey trees with a diameter of 2–9.9 cm were inventoried as described above, within two subplots in each plot. To convert the recorded tree structural data into aboveground plant biomass ($\mathrm{Mg\,ha^{-1}}$), the allometric equations developed by ref. [42] for all forest trees, ref. [43] for rubber trees, ref. [44] for oil palms and ref. [45] for lianas were applied.

To calculate coarse root and root-stock biomass ($\mathrm{Mg\,ha^{-1}}$), we used the allometric equations developed by ref. [46] for forest trees, ref. [43] for rubber trees and ref. [47] for oil palms. We added our measurements of small-diameter (≤2 mm) root biomass to the calculated total biomass. Fine root biomass was measured using ten vertical soil cores (3.5 cm in diameter) down to 0.5 m soil depth, including the organic layer, in each plot. All fine root segments longer than 1 cm were extracted by washing over a 200 µm sieve and separated under a stereomicroscope into live (biomass) and dead fractions (necromass).

Woody coarse debris was analysed within all forest and jungle rubber plots where snags (DBH ≥ 10 cm) and logs (mid-point diameter ≥ 10 cm, length ≥ 1 m) were recorded. This was not measured in monoculture rubber and oil palm plantations because woody coarse debris is cleared regularly due to plantation management. Three decay stages based on ref. [48] were used to characterize the woody debris. Biomass of the debris was calculated using the equations by ref. [49] and by applying the allometric equation by ref. [42] for calculating aboveground biomass of non-degraded trees.

In each 0.25 ha plot, all individual trees with DBH ≥ 10 cm were identified and measured (spatial position within the plot, height, DBH, crown structure). Additionally, all vascular plant individuals with DBH < 10 cm growing within the five subplots were identified and measured (height). Whenever possible, herbarium specimens were prepared from three individuals per species for identification and were later archived at several Indonesian herbaria (Herbarium Bogoriense, BIOTROP Herbarium, UNJA Herbarium, Harapan Rainforest Herbarium). All individuals measured on the plots were identified to taxonomic species. However, this was not always possible for certain individuals such as young seedlings, in which cases these specimens were assigned a morphospecies name based on consistent morphological characteristics. Plant species richness was calculated as the total number of sampled species within each plot.

Microbial biomass and species richness. Microbial biomass carbon (mg C kg^{-1}) was measured from soil cores (top 5 cm) sampled in two subplots at each plot. The $CHCl_3$ fumigation–extraction method was followed[50,51]. A subsample of soil from a core was extracted immediately with 0.5 mol l^{-1} K_2SO_4 (unfumigated) and another subsample was fumigated with $CHCl_3$ for six days and then extracted (fumigated). Organic carbon in the extracts was analysed by UV-enhanced persulfate oxidation using a Total Organic Carbon Analyser (TOC-Vwp, Shimadzu Europa GmbH, Duisburg, Germany) with an infrared detector. Microbial biomass carbon was calculated as the difference in extractable organic carbon between the fumigated and unfumigated soils divided by $k_C = 0.45$ for a six-day fumigation period[50].

Sampling of soils for microbial species richness (top 5–7 cm) was carried out in three subplots in each plot. Samples were placed in a cool box containing ice packs in the field, and were transported directly from the field to the lab (<4 hr). All samples were stored at −80 °C until further use. DNA was isolated by employing the PowerSoil DNA isolation kit as recommended by the manufacturer (Dianova, Hamburg, Germany). Subsequently, 16 S rRNA gene amplicons of bacteria and archaea were generated from the isolated DNA as described by ref. [52]. The resulting 16 S rRNA gene datasets were processed and analysed by employing QIIME 1.8[53]. Initially, sequences shorter than 300 base pairs (bp), containing unresolved nucleotides, exhibiting an average quality score lower than 25, harbouring mismatches longer than 3 bp in the forward primer, or possessing homopolymers longer than 8 bp and primer sequences were removed. Sequencing noise and potential chimeric sequences were resolved by using Acacia[54] and UCHIME[55] with RDP[56] as reference datasets (trainset10_082014_rmdup.fasta). Operational taxonomic unit (OTU) determination was performed at a genetic divergence of 3% by using 'pick_open_reference_otus.py' of the QIIME 1.8 package using the Silva NR SSU 119 database version as a reference[53,57]. Taxonomic classification was performed with 'parallel_assign_taxonomy_blast.py' against the same database. Unclassified OTUs and OTUs occurring as singletons (sequences observed fewer than two times), chloroplasts, and extrinsic domains were removed. OTU tables were subsampled and comparisons were performed at the same surveying effort (bacteria 6.800 and archaea 2.000 sequences per subplot). Diversity estimates were generated employing 'alpha_rarefaction.py'. The 16 S rRNA gene sequences were deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under study accession number SRP056374.

Litter macroinvertebrate biomass and species richness. In each of the plots, three subplots were sampled by sieving 1 m^2 leaf litter through a coarse 2 cm mesh-width sieve. A total of 7,472 macroinvertebrates were hand-collected from the sieving samples and stored in 65% ethanol. Specimens were identified to morphospecies and, based on morphology and literature, assigned to one of four feeding guilds: omnivores, detritivores, predators and herbivores. To assess sampling completeness, observed species richness was compared with both extrapolated and rarefied richness, which revealed that the mean estimated sampling coverage for each land-use system was 56% and was highly consistent among the four different land-use systems (for details, see ref. [8]). For each animal, individual body length was measured and then converted to fresh body mass using allometric length–mass regressions from the literature[8]. Community biomass (fresh mass in mg m^{-2}) was then calculated for each of the 32 sampled communities by summing together all individual body masses that were derived from the individually measured body lengths.

Arboreal ant biomass and species richness. Surveys were conducted in each plot four times between November 2012 and February 2014, between 9:00 and 11:00. No sampling was conducted during or immediately after rain due to a reduction in ant activity in wet conditions. Plastic observation plates with two baits of 2 cm^3 of tuna in oil and two sponges saturated with 70% sucrose solution attached were used to sample arboreal ant species[58]. One plate was tied at breast height on two trees within five subplots in each plot. If there were not two trees in a subplot (often the case in oil palm plantations), the closest trees to the subplot were chosen. Sixty minutes after placing the plates on the trees, the abundance of ants on the plate was recorded and a number of specimens were collected for further identification. Ant abundance was defined as the mean of all recorded abundances within a plot. All collected ants (Hymenoptera: Formicidae) were identified to genus using published keys[59]. We identified specimens to species level where possible and assigned the remainder to morphospecies. Ant species richness was quantified as the total observed species richness per plot. Body length was measured on up to five individuals from each species at each plot and, using a length–mass regression specific to ants[60], an average fresh body mass was calculated for each species. Ant community biomass (mg per bait station hr^{-1}) for each plot was calculated by summing the total biomass of each species (abundance × average species body mass).

Bird biomass and species richness. Birds were sampled using point counts located in the centre of the plots. All birds detected visually and aurally within the plot were recorded for 20 min between 6:00 and 10:00 in June to July 2013. The timing of bird data collection alternated between early and late morning, and all plots were visited three times. Individuals flying above the canopy were excluded and unfamiliar birdcalls were recorded using a directional microphone (Sennheiser ME66). The recordings were compared with an available online birdcall database (www.xeno-canto.org) for confirmation. Additionally, birds were sampled with passive acoustic monitoring stations that were attached at ca. 2 m height to a centrally located tree within each plot. We recorded sound at 44,100 Hz on two channels using song meters (SM2+ recorder with two SMX-II microphones, Wildlife Acoustics). Sampling of all 32 plots took place from 10 May to 7 June 2013. The first 20 min after sunrise were uploaded to http://soundefforts.uni-goettingen.de/, where two independent ornithologists identified all birdcalls within an estimated 35 m radius. Bird detections were reviewed by a third ornithologist and the species lists from sound recordings and point counts were subsequently merged. Body mass and feeding guilds for each bird species were retrieved from ref. [61]. Bird species were divided into three main feeding guilds: herbivores (eating plant material); predators (eating invertebrates); and omnivores (eating both invertebrates and plant material). Total biomass for each plot was calculated by summing together species-specific body masses for all detected individuals.

Principal component analysis. To reduce the number of parameters in our models and avoid issues of multicollinearity while maintaining as much variability in our predictors as possible, composite variables were calculated using principal component analysis (PCA; 'princomp' function in R 3.0.1[62]) of soil, microclimatic and plant community parameters. Soil components were created using a combination of soil biochemical and physical properties[63], and plant community components were created using above- and belowground biomass as well as species richness (see Supplementary Methods).

Multilevel path modelling. We employed generalized multilevel path analysis (a form of structural equation modelling, also more recently referred to as 'piecewise SEM')[18,64] to account for the hierarchical layout of our sampling design, whereby plots were split between two different landscapes. Specifically, we incorporated landscape as a random effect to account for our blocked sampling design, which would not be possible with the more commonly used SEM approach based on covariances among variables. This method of path modelling also allows for constructing and testing highly complex causal models with comparatively low sample sizes[64], making it ideal to test for cascading effects in complex communities in observational studies. To construct such a model, we identified the basis set B_U of independence claims implied by a hypothetical causal model. B_U expresses the full set of independence claims, which describe the p_i probability that variable pairs (X_i, X_j) are independent, conditional on the variable set Z, which is a direct cause of either X_i or X_j. This directional separation (d-sep) test procedure is explained diagrammatically in Fig. 4. The probabilities p_i for each of the k independence claims in B_U were identified using linear mixed-effects models with the 'nlme' package in R 3.0.1[62]. The combined p_i of the full model was then calculated as

$$C = -2\sum_{i=1}^{k}\ln(p_i)$$

and the C value was then compared to a chi-squared (χ^2) distribution with $2k$ degrees of freedom[18]. The resulting probability, P, indicates whether the data depart significantly from what would be expected under the specified causal model. A model is rejected if the resulting P value is smaller than the specified α-level (in this case $\alpha = 0.05$). Thus, if $P > 0.05$, the causal model cannot be rejected and is considered an appropriate fit to the data[18].

We constructed hypothetical models to allow for direct and interactive effects between land use and abiotic variables on biotic response variables for ecologically meaningful relationships (see Supplementary Fig. 2). Land-use change was modelled as a four-level categorical variable comprising forest, jungle rubber, rubber monoculture and oil palm monoculture. In all cases where the effects of land use were significant, these effect sizes were interpreted by taking the coefficient of the non-forest level (that is, from jungle rubber, rubber monoculture, or oil palm monoculture) that had the largest difference from the coefficient of the forest level (specified in each model as the intercept). We permitted only likely bottom-up trophic effects among biotic variables (see Supplementary Fig. 2 for all possible direct and cascading effects). Although top-down effects also play a role in structuring multi-trophic communities, here we assume the prevalence of bottom-up effects because we expected the direct impacts of land-use change to be most severe on plant and microbial communities[65]. To further investigate the likelihood of top-down processes dominating in our dataset, we constructed another path model where only top-down effects were assumed (Supplementary Fig. 4), allowing us to qualitatively determine the ecological validity of such a model compared with the bottom-up model.

Subplot-level data were aggregated to the plot level by averaging values for biomass and taking the accumulative total of species richness across subplots. Variables were mean-centred and linear mixed-effects models with random intercepts were fitted, with 'landscape' (that is, Bukit Duabelas and Harapan locations) specified as a random effect. Normality of the data and homoscedasticity of variance were tested by inspecting frequency distributions of each variable and the variance structure of each model. Where necessary, variables were then log-transformed to satisfy assumptions of normality and achieve homoscedasticity of variance. For each model, we additionally tested for spatial autocorrelation by conducting a Moran's I test on the model's residuals. For all models, results from the Moran's I test provided no support for the influence of spatial autocorrelation on the component linear mixed-effects models within each path model (all Moran's I test results yielded $P > 0.3$). Individual model fits were assessed using the procedure for calculating R^2 values for generalized linear mixed-effects models as outlined by ref. [66]. This indicates the proportion of total variation of endogenous variables explained by all significant predictors and their conditioning variables (that is, those included in the variable set Z). Standardized coefficients were calculated to assess relative effect sizes of each predictor on endogenous variables by rescaling predictor variables between 0 and 1. In this way, standardized effects can be directly compared and thus indicate the relative importance of each path. Furthermore, this allowed us to calculate effect sizes of whole paths that represent cascading land-use effects by multiplicative path tracing[17,67].

We constructed two different path models to quantify direct and cascading effects resulting from land-use conversion to rubber and oil palm systems. The first model included all possible significant effects that could be retained while yielding an overall P value > 0.05, but we found critical issues with model specification due to multicollinearity between predictor variables, as indicated by a high variance inflation factor (VIF > 4)[68], leading to erratic estimation of path coefficients (that is, <-1 and >1; see Supplementary Table 3). As such erratic coefficient estimation can indicate a misspecification of model structure[69], we compiled a second path model where we removed variables from component models (indicated in Supplementary Table 3) that exhibited a VIF value >3, yielding a final correct model structure. Furthermore, we analysed an alternative model where only top-down processes were assumed. However, in all but one case of biotic interactions where a top-down effect was tested, we found only positive effects of consumers on their prey/resources (see Supplementary Fig. 5), leading us to believe that the assumption of top-down land-use cascades in this system would be incorrect and further supporting the assumption of prevailing bottom-up effects. To quantify the strength of cascading effects in the multi-trophic communities, these indirect effects were estimated by multiplying coefficients along pathways of interacting taxa in the path model. We then estimated total effects by summing the direct and cascading effect sizes of land-use change on each trophic level.

Data availability. The data that support the findings of this study are available from the corresponding author upon request.

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Author contributions

K.A., A.D.B. and U.B. designed the study; K.A., A.D.B., M.J., K.D., L.H.D., M.M.K., S.K., A.M., K.R., W.E.P. and D.S. collected the data; K.A. and A.D.B. analysed the data; all authors contributed to the writing of the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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