Land use imperils plant and animal community stability through changes in asynchrony rather than diversity

Nico Bluethgen, Nadja K. Simons, Kirsten Jung, Daniel Prati, Swen C. Renner, Steffen Boch, Markus Fischer, Norbert Hözel, Valentin H. Klaus, Till Kleinebecker, Marco Tschapka, Wolfgang W. Weisser & Martin M. Gossner

Human land use may detrimentally affect biodiversity, yet long-term stability of species communities is vital for maintaining ecosystem functioning. Community stability can be achieved by higher species diversity (portfolio effect), higher asynchrony across species (insurance hypothesis) and higher abundance of populations. However, the relative importance of these stabilizing pathways and whether they interact with land use in real-world ecosystems is unknown. We monitored inter-annual fluctuations of 2,671 plant, arthropod, bird and bat species in 300 sites from three regions. Arthropods show 2.0-fold and birds 3.7-fold higher community fluctuations in grasslands than in forests, suggesting a negative impact of forest conversion. Land-use intensity in forests has a negative net impact on stability of bats and in grasslands on birds. Our findings demonstrate that asynchrony across species—much more than species diversity alone—is the main driver of variation in stability across sites and requires more attention in sustainable management.
The long-term functional stability of ecosystems is driven by the stability of species’ populations and communities that contribute to ecosystem functions. Community stability thus represents a main goal for biodiversity conservation and sustainable management of natural resources. Populations of single species tend to fluctuate over time, an instability that is commonly quantified by the coefficient of variation in abundance across years: $CV = \sigma / \mu$, where $\sigma$ is the s.d. of the species’ abundance over time and $\mu$ its temporal mean. Stability is the inverse of the coefficient of variation ($CV^{-1}$).

Unless species abundances are perfectly synchronous, the total community $CV_{\text{tot}}$ must be smaller than the average species’ $CV_{\text{sp}}$. The reduction in $CV_{\text{tot}}$ relative to $CV_{\text{sp}}$ increases with the number of species as well as with their asynchrony. This stabilization is known as portfolio effect and insurance hypothesis, respectively, in analogy to financial market theory and is comparable to risk minimization in financial investments. The portfolio metaphor emphasizes the statistical averaging effect of multiple species, while the insurance hypothesis explicitly describes the species’ asynchrony in environmental responses and their dynamics. Asynchrony has been recognized as a key driver behind a positive diversity–stability relationship. In principle, asynchrony and its positive contribution to stability can mirror interspecific competition, heterogeneity in species responses to environmental conditions (response diversity) or simply demographic stochasticity. Total abundance may additionally influence stability in several ways either indirectly via changes in the variance ($\sigma$) or directly as its mean. The denominator in the ratio ($\sigma / \mu$) that defines $CV_{\text{tot}}$ (refs 8,14).

Empirical support for the diversity–stability relationship and its underlying drivers in terrestrial ecosystems mainly comes from primary producers, such as plants in experimentally or naturally assembled grasslands and trees in mixed forests. A few studies examined the effect of fertilization on inter-annual asynchrony and stability of grassland plant communities, with conflicting results. It remains unknown whether findings on grassland plants can be generalized for other taxa and trophic levels, for other ecosystems such as forests or for other land-use impacts. Given that land-use change is a main driver of biodiversity loss, conversions between habitat types and intensification of land use within habitat types should also affect community stability.

Our study evaluates the changes in stability of plant and animal communities across 4–6 years in naturally assembled forests and grasslands under characteristic land-use regimes in three regions in Germany (50 forests and 50 grasslands per region). Analyses were performed for four taxonomic groups, encompassing a total of 562 plant, 1,982 arthropod, 114 bird and 13 bat species. We chose sampling methods that adequately represent the whole community within a taxon.

We hypothesized that changes in land-use type and increasing land-use intensity have negative net effects on community stability via reduced diversity, asynchrony and abundance. Habitat conversion from (managed) forest to cultivated grassland and arable land has been the main change in land uses in vast parts of the Central European cultural landscape for many centuries, although this trend is now partly reversed. Therefore, we first tested whether forests have more stable communities than grasslands, reflecting the historical deforestation and conversion. Secondly, we evaluated whether gradual increases in land-use intensity within forests and grasslands additionally destabilize communities. Finally, we modelled the indirect effects of land-use intensity on stability via changes in diversity, asynchrony and total abundance using structural equation modelling. Our study revealed that arthropod and bird communities were more stable in forests than in grasslands. Land-use intensity had negative impacts on the stability of bats in forests and birds in grasslands. In contrast, plant communities were not destabilized through increased land-use intensity, despite strong diversity declines in highly fertilized and frequently mown grasslands. Overall, stability was most strongly driven by asynchrony, followed by diversity and abundance, confirming a key role of the insurance effect in real-world ecosystems.

### Results and Discussion

#### Variation in community stability

Inter-annual variability of the total abundance of all species in a community ($CV_{\text{tot}}$) was much lower than the mean species-level variability ($CV_{\text{sp}}$) in both forests and grasslands (Fig. 1). This stabilizing effect ranged from a 27% lower $CV_{\text{tot}}$ of forest bats to a 70% lower $CV_{\text{tot}}$ in resident forest birds and even a 72% lower $CV_{\text{tot}}$ in cover of grassland plants compared with the respective mean $CV_{\text{sp}}$ (arrows in Fig. 1). Community stability ($CV_{\text{tot}}^{-1}$) was significantly reduced in grasslands compared with forests, but the effect differed across taxa (Supplementary Tables 1 and 2). For arthropods and birds, we found a 2.0- and 3.7-fold decrease, respectively, in community stability from forests to grasslands, whereas no differences were observed in bats. This destabilization was associated with lower asynchrony and higher level of $CV_{\text{sp}}$ in grassland arthropods and birds (Supplementary Table 2). Plants had the most stable communities and showed the opposite trend, that is, grassland communities and populations were more stable and asynchronous than the forest understory vegetation. Note, however, that we excluded the tree and shrub layers, hence the most stable vegetation layers, from the analysis in forests.

Land-use intensity gradients within forests and within grasslands showed relatively weak effects on community stability, which were only significant for grassland birds and forest bats (Fig. 2). Land-use impacts on animal community stability were thus stronger for conversion of forests into open grassland than for gradual intensity variation, partly corresponding to a study on...
tropical birds\textsuperscript{22}. Moreover, results for grassland plants—the taxon that has received most attention so far—may not fully represent the potential land-use responses of other organisms. Stability of arthropods, birds and bats negatively responded to conversion and/or intensity, whereas plants did not, supporting the idea that higher trophic levels can show increased sensitivity to land use and accelerate the losses of plant diversity\textsuperscript{23,24}. Stability theories for consumers often focused on the roles of food-web structure, species mobility or body size\textsuperscript{25,26}. While such food-web approaches often developed separately from merely plant-centred studies, we show that food-web processes such as parasitism, predation, herbivory, decomposition or pollination\textsuperscript{28}. Hence, we also analysed herbivorous and carnivorous arthropods separately and found marked differences in how land-use intensity affects their stability. Forest land-use intensity reduced the stability of carnivores via asynchrony (Supplementary Fig. 4). Although grassland

**Drivers of stability.** Generally, high instability ($\text{CV}_\text{tot} = \sigma/\mu$) may arise from high standard deviation ($\sigma$) or from a low mean of the total abundance ($\mu$), suggesting that either the community density or fluctuations are critical. In all communities in our study, $\sigma$ was consistently more variable across sites than $\mu$ (Supplementary Table 2), suggesting an important role of variance-driven instability. The negative land-use intensity effect on stability for forest bats (Fig. 2) was driven by a significant decline in $\mu$, which was not compensated by a decline in $\sigma$. The negative land-use effects on stability for grassland birds were, however, neither accompanied by significant changes in $\mu$ nor in $\sigma$ (Supplementary Figs 5 and 6).

Gradual increases in land-use intensity indirectly affected stability through changes in asynchrony, diversity and abundance (Fig. 3). Despite differences in the strength and significance of the three stabilizing pathways between taxa, land-use intensity generally decreased at least one of them (Fig. 3 and Supplementary Figs 2 and 3). The strongest effects occurred via asynchrony and abundance for all taxa in forests, with an additional strong effect via diversity for forest bats. In grasslands, the strongest effects of land-use intensity on stability also occurred via asynchrony for all taxa, and additional effects via diversity were also consistent across all taxa. Land-use effects on animal community stability most likely also translate into changes in their ecosystem functions, for example, consumption-related processes such as parasitism, predation, herbivory, decomposition and/or pollination\textsuperscript{28}. Hence, we also analysed herbivorous and carnivorous arthropods separately and found marked differences in how land-use intensity affects their stability. Forest land-use intensity reduced the stability of carnivores via asynchrony and abundance, whereas herbivore stability was affected via diversity (Supplementary Fig. 4). Although grassland

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**Figure 2 | Effect of land-use intensity on community stability within forests and grasslands.** Changes in community stability (calculated as the inverse of community variability, $\text{CV}_\text{tot}^{-1}$) with the combined land-use intensity in forests (top row) and grasslands (bottom row) are shown for each of the four taxa. Significance values are derived from linear models.

**Figure 3 | Indirect effects of land-use intensity on community stability.** Results from structural equation models are summarized over all taxa for forests (a) and grasslands (b). Community stability (the inverse of variability) is affected via different stabilizing and destabilizing paths. Green arrows show positive, blue negative directional effects. Taxon symbols next to arrows indicate significant effects ($P < 0.05$) for the respective taxon.
herbivore communities might become more unstable when fewer plant species are available, as shown in experimental grasslands, the negative effects of land-use intensity on plant diversity did not translate into reduced stability of herbivorous arthropods in our study.

Diversity decline in response to land use was not prevalent in all taxa, corresponding to earlier findings in the same sites and elsewhere. Hence, species diversity alone does not sufficiently capture critical changes in communities and ecosystems. In addition, different components of land use can have variable or even contrasting effects (Supplementary Figs 2 and 3). In forests, harvesting of trees had the strongest negative impact on birds and bats, whereas non-natural tree species affected plants and arthropods most strongly. The proportion of non-natural trees also contributed to reduced bird abundance but increased plant and arthropod diversity. In contrast, the amount of dead wood with saw cuts was positively related to bird asynchrony. In grasslands, increases in bat abundance were driven by grazing intensity. Increased mowing and fertilization intensity as well as grazing intensity were associated with a lower diversity of plants, whereas mowing and fertilization increased the plants’ asynchrony and abundance. Land-use intensity thus showed a negative impact on diversity, but this was compensated by asynchrony and abundance; thus, no net effect on stability was found. This finding corresponds to a study conducted in a grassland site in Michigan, where fertilization increased the asynchrony of plant communities and compensated for destabilizing diversity losses. In contrast, in a Mongolian semiarid grassland plant community, the addition of nitrogen and phosphorus was found to be destabilizing for the plant community, whereas mowing had a stabilizing effect. In a global meta-analysis, Hautier et al. also showed that plant communities were destabilized when grasslands were fertilized, partly via a decreased asynchrony.

Asynchrony significantly increased stability in all taxa and had by far the strongest impact on community stability in all taxa, except in forest bats where diversity had an equally strong influence. The primary importance of asynchrony was unaffected when an unweighted asynchrony index was used (see Supplementary Tables 3 and 4). Diversity also contributed to stability in all grassland communities. Abundance had a stabilizing effect for birds, bats and plants in forests and for bats and arthropods in grasslands, but was destabilizing for forest arthropods (Fig. 3). Asynchrony, diversity and abundance were often correlated (Supplementary Figs 2 and 3). Diversity was positively correlated with asynchrony in forest bats and grassland arthropods, suggesting that common mechanisms may jointly affect both, or that compensatory dynamics increase with diversity. In contrast, plants, birds and bats in grasslands showed negative correlations between diversity and asynchrony. Different, complementary conservation and management actions in grasslands may thus be required when aiming to stabilize communities via both diversity and asynchrony. Interestingly, the decrease in asynchrony with higher diversity of grassland plants contrasts with the opposite trend reported along plant richness gradients in experimental and naturally assembled grasslands.

**Outlook.** Several studies found that the composition of species and their functional traits, functional performances or interactions can show marked changes with land use even when diversity remains unchanged. Some of these functional traits can be relevant for stability, for example, thermal niches or phenotypic plasticity. Our results strongly support the view that other measures such as traits or inter-annual variability should complement diversity surveys to evaluate potential impacts of global change. We show that, despite the unequivocal positive diversity–stability relationship, diversity alone, without knowledge of the level of asynchrony, may be a poor indicator of community stability. Stabilization of communities and, of their functional performance, involves an established goal for sustainable ecosystem management. However, so far, conservation assessments evaluating land-use impacts or the impact of land sharing versus land sparing between natural habitats and agriculture are almost exclusively based on short-term diversity surveys. We suggest that future sustainable management concepts should also target and monitor processes and spatial habitat requirements that facilitate compensatory dynamics to promote inter-annual asynchrony as a key factor driving long-term stability.

**Methods**

**Study system and definition of land-use intensity.** Our study was conducted within the framework of the Biodiversity Exploratories program, which includes grasslands and forests within three regions in Germany: (1) Schwäbische Alb in South-west Germany (48°34' to 48°53’N, 9°18' to 9°60'E), (2) Hainich-Dün in central Germany (50°94' to 51°38’N, 10°17' to 10°78'E) and (3) Schorfheide-Chorin in North-east Germany (52°47' to 53°13’N, 13°23' to 14°09’E). Within each study region, seven experimental plots were chosen, each with a 50 m x 50 m size on managed grasslands. The plots were selected to represent the regional range of management intensity for both forests and grasslands.

The forest plots cover different management strategies (unmanaged beech forests, even-aged age-class forests or uneven-aged selection-cutting forests), different age classes (European Beech (Fagus sylvatica), Norway spruce (Picea abies), Scots pine (Pinus sylvestris)) and different developmental stages within managed age-class forests (for example, thicket stage, pole wood, young timber and old timber). Unmanaged beech forests were set aside from management 20–70 years ago, but have been managed before. No pristine forest exists in Central Europe. Our land-use intensity measure for forests is based on inventory data of the living stand, stumps and dead wood, and includes the following three components: (1) the proportion of harvested tree volume (Iharv), (2) the proportion of trees provided by species that are not part of the natural forest community (Inonat) and (3) the proportion of dead wood showing signs of saw cuts (Idwcut). The single components were used in structural equation models while the compound index (ForMI) was used for main regressions. The compound ForMI index for each plot i is the sum of its three components, that is, ForMIi = Iharv + Inonat + Idwcut, ranging from zero (unmanaged forest) to three (intensively managed forest).

In grasslands, land-use intensity includes the three components fertilization, mowing and grazing, often applied in combination (meadows, pastures and mown pastures). Land use was assessed for each plot yearly from 2006 to 2012 through standardized questionnaires with the land owners. Fertilization intensity Fi was defined as the amount of nitrogen applied (kg nitrogen per ha per year), mowing frequency of cuts per year on each site i and intensity was calculated as the amount of nitrogen applied (kg nitrogen per ha per year). Each land-use component was standardized against its mean across regions (FMn, FMm, Gnm) as

\[ F_{i} = \frac{F_{m} - F_{m}}{F_{m} - F_{m}} \]

where FM and Fm are the average fertilization intensity across the study areas, and Fm is the mean fertilization intensity across all plots. For regressions, a compound index of land-use intensity was used as follows:

\[ LUI_i = M_{i} + G_{i} \]

where M and G are the amount of mowed and grazed land, respectively, and LUI is calculated for each year. For forests, species diversity and mowing were used to calculate diversity and mowing, whereas in grasslands, species diversity and mowing were used to calculate diversity and mowing. For forests, species diversity and mowing were used to calculate diversity and mowing, whereas in grasslands, species diversity and mowing were used to calculate diversity and mowing.

There was a significantly negative association with fertilization (\( r = 0.65, P < 10^{-12} \)) and mowing (\( r = 0.39, P = 0.001 \)) that is, these treatments were more commonly applied alone in combination (Supplementary Table 5). Moreover, fertilization intensity and mowing frequency were highly positively correlated, whereas grazing intensity was negatively related to these two treatments. The correlation between (sqrt-transformed) fertilization and (sqrt-transformed) mowing was highly significantly positive (\( r = 0.65, P < 10^{-12} \)) whereas grazing (\( G_{i} \)) was negatively related to \( F_{m} \) (\( r = 0.30, P < 0.001 \)) and to \( M_{i} \) (\( r = 0.70, P < 10^{-15} \)) in all (\( n = 150 \) sites). The non-independence of fertilization and mowing reflects the decision of the farmer to utilize the site for hay or silage yield, whereas the use as pasture represents an alternative target based on livestock.

**Sampling methods.** Plants, birds and grassland arthropods were sampled yearly from 2008 to 2013, bats and forest arthropods from 2008 to 2012 and forest plants from 2009 to 2012. The average of plant species was estimated in quadrats, arthropods
were collected by standardized sweep-netting in grasslands and flight-interception traps in forests, bird abundance was determined by audio–visual counts of males, and bats by their flight activity.

**Plants.** Grassland vegetation was surveyed yearly from 2008 to 2013 from mid-May to mid-June simultaneously in all regions. The cover of all vascular plant species was estimated on 4 m × 4 m permanent plots in the grasslands. In forests, plant cover was estimated in spring and late summer from 2009 to 2012 in an area of 20 m × 20 m per plot. We used different plot sizes for the two types of vegetation following general recommendations for assessing vegetation for grassland and forest understorey. Only understorey plants including shrubs and tree seedlings were analysed; species of the tree and shrub layers are not expected to show noteworthy variation in abundance over the sampling period. Counts of plant species are conservative as they include aggregates that are counted as a single species.

**Arthropods.** Grassland arthropods were sampled yearly from 2008 to 2013 in each of the three regions. Counts of plant species were estimated on 4 m × 4 m grassland plots where samples were taken in both months; for 124 grassland plots we included all 6 species.

For grassland and forest communities, a separate analysis for herbivores and remaining trophic levels (mainly predators) was performed. The assignment to trophic levels was based on the main larval and adult feeding source following Gossner et al. for grassland and Böhme for forest communities.

**Birds.** At each of the 300 sites we surveyed birds by standardized audio–visual point counts for 5 min point count locality and time period and recorded all birds displaying territories. We used 50–m–fixed radius point counts and noted all birds of each species during the 5-min interval. Each site was visited five times between March 15 and June 15 in 2008 to 2013. A minimum of 5 and a maximum of 15 sites were surveyed per day by one observer from sunrise to 1 AM. The number in which sites were visited was randomized. Each song or call heard on a site was interpreted as one male territory display behaviour. The maximum number of birds displaying per site per year (that is, the maximum number of individuals per species observed in any of the five surveys) was used as a measure of the abundance of each bird species. Aerial species were excluded from analysis as they are not detectable by their activity by the two methods used for the analysis of ground activity and of community stability itself. Despite the different approaches, synchrony indices were highly correlated with each other and with 

**Structural equation modelling of land-use intensity effects.** We used structural equation modelling based on a maximum likelihood method to estimate the indirect effect of land-use intensity on stability via changes in asynchrony (\( r_{ij} \)) and diversity (\( D^2 \)) and total abundance (mean \( A, A_{ij} \)) per year. Path coefficients were estimated separately for forests and grasslands, and for arthropods, birds, bats and plants. We model the effects of land-use intensity as a composite variable. Models were performed using the R package `lavaan` version 0.5–18 (ref. 52).

For grasslands and forests only differed in the definition of the combined land-use intensity and its components (forests: \( \text{Iharv}, \text{Inonnat}, \text{Idwcut} \); grasslands: fertilization, mowing and grazing, see above). Following Grace and Bollen, the combined land-use intensity could be defined either as a latent variable or as a composite variable. We decided to use a composite variable, assuming that the component biodiversity (the combined change in species composition and community structure) is more relevant. In lavaan, correlations between the components of composite variables are not considered. As a composite variable is a representation of the collective effects of its components, it is assumed that it has no further error variance. Therefore, the error variance was fixed to zero in the model, and the scale of the measurement for the composite was defined by setting the path coefficient from Ilavar or grazing, respectively, to the composite to 1. The path coefficients and their associated P values were estimated with the maximum likelihood method, and the overall model fit was estimated from a \( \chi^2 \)-test between the modelled and observed covariance matrix. It is important to notice that this \( \chi^2 \)-test shows significant P values (\( P < 0.05 \) if there is significant difference between the modelled and the composite model). Before the calculation of the e.s.m. s, all variables (except the land-use components) were visibly inspected for normality and transformed where necessary. When composite variables with more than one outward-pointing pathway (here diversity, abundance and synchrony) are used in a model, it is assumed that the effects of the indicator variables on the measured variables are proportional to each other. If this assumption is not met, the parameter values are likely biased. This is often reflected by very high error variances associated with the measured variables. To test whether we correctly assumed proportional effects, we calculated an additional basic model that did not include any composite variables but direct pathways between the three indicator variables (the land-use components) and the three measured variables. Smaller error variances in this basic model compared with the original model would indicate that the measured variables are not proportional to the three measured variables. As we fixed the path coefficient between Ilavar or grazing and the composite in the original model, it was not significant, which indicates that our assumption is valid.
possible to estimate its statistical significance in the original model. We evaluated the statistical significance of these path coefficients using the basic model as well.

The original structural equation models showed nonsignificant overall P values for most of the taxa, indicating that the models represent the covariance structure in the data adequately. In cases for which the overall P value showed a significant difference between the model and the data, we first calculated a reduced model in which three composite variables were included (one composite for each of the three measured variables diversity, abundance and asynchrony). If the overall P value was also significant with the reduced model, we used the basic model for this group. We found very high error variances (>0.75) for asynchrony, diversity and abundance and in all models, indicating that effects of the land-use components are not proportional between these three variables. Basic models without a composite variable, however, reduced the error variances only for some groups (grassland arthropods as well as forest birds). Within the basic model for grassland arthropods, none of the components significantly affected diversity; however, mowing and fertilization showed significant effects on asynchrony and abundance. Basic models for forest birds showed no significant effect on diversity, but did show significant effects of Idav and Imor on abundance as well as Idav and Iwot on asynchrony.

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Author contributions
N.B. conceived the idea for the manuscript and wrote the first manuscript draft. N.B., N.K.S., M.M.G., K.J., D.P. and S.C.R. defined the final analysis and outline of the manuscript. N.K.S. analysed the data. N.B., N.K.S. and M.M.G. finalized the manuscript. K.J., D.P., S.C.R., S.B., M.F., N.H., V.H.K., T.K., M.T. and W.W.W. contributed data and contributed to writing.

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