

Supporting Information

Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems?

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Appendix S1: Details of study design and plot characteristics

Table S1-1. Characteristics of the environment, spatial arrangement, stand size and stand structure of plots for even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forest management systems. Values are means and standard deviations. Environmental conditions (i.e. elevation, slope, soil properties and climate) of plots are comparable between forest management systems, with UNM located at slightly lower elevation. The spatial arrangement of plots is comparable for EA and UEA, while UNM are located in closer distance within the National park. Size of management units in which plots were located is about double in UEA and UNM compared to EA. The reason for this is that management operation in UEA are only cost efficient at larger areas due to lower intensity of interventions. In case of UNM we report the size of management units before abandonment, while with time, differences between management units vanished.

Variability of stand microclimate differentiates EA from UEA and UNM. In EA daily temperature range and maximum temperature during the vegetation period are elevated and more variable between plots, which is due to varied canopy height and cover of developmental phases. The highest values were observed in thickets (daily range: 10.0 ± 1.1 °C, daily maximum: 19.0 ± 0.9 °C). For the mature timber phase of EA (daily range: 7.0 ± 0.3 °C, daily maximum: 17.5 ± 0.3 °C) temperature amplitude was not different from UEA and UNM. The stand structure represents the characteristics of the different forest management systems: (i) low average basal area/timber volume and high variation of basal area, timber volume and stand density in EA due to forest developmental phases, (ii) high diameter variation within plots, medium stocking density and presence of large trees in UEA, and (iii) high basal area, high timber volume, high diameter variation within plots, and largest trees in UNM. In UNM the higher tree species richness and lower dominance of European beech are legacies of former forest management (coppice with standards). Dead wood volume of EA was on average higher than in UEA and UNM and more variable compared to UEA. Especially thickets (36.4 ± 13.8 m³ ha⁻¹), pole woods (32.4 ± 15.9 m³ ha⁻¹) and thickets with shelterwood (35.1 ± 13.3 m³ ha⁻¹) contributed to the quantity and variability of dead wood in EA. In these developmental phases dead wood volume is driven by final harvest and density related natural tree mortality.

	Forest management system		
	Even-aged	Uneven-aged	Unmanaged
Number of plots	17	13	13
Environment			
Elevation (meters a.s.l.)	429.6 \pm 50.8	425.0 \pm 55.6	373.4 \pm 42.4
Slope (°)	3.1 \pm 1.8	3.8 \pm 1.8	3.5 \pm 1.1
Soil type	Luvisol: 13 Stagnosol: 4	Luvisol: 10 Stagnosol: 3	Luvisol: 9 Stagnosol: 4
Soil pH (0 to 10 cm depth)	4.7 \pm 0.8	4.5 \pm 0.9	4.6 \pm 0.4
Mean air temperature (°C)*	7.3 \pm 0.3	7.3 \pm 0.3	7.4 \pm 0.3
Max. air temperature (°C)†	17.7 \pm 0.8	17.5 \pm 0.5	17.5 \pm 0.3
Air temperature range (°C)‡	7.6 \pm 1.3	6.9 \pm 0.3	6.6 \pm 0.3
Total area (hectare)	6600	5000	3900
Spatial arrangement			
Mean distance (km)	13.9 \pm 9.4	13.9 \pm 12.4	2.7 \pm 1.7
Distance range (km)	0.3 to 33.6	0.3 to 27.7	0.3 to 7.3
Management units (= stands)[#]			
Size (hectare)	11.6 \pm 2.6	26.9 \pm 6.5	24.1 \pm 5.8
Size range (hectare)	8.4 to 18.2	19.3 to 42.2	18.4 to 36.8
Stand structure[¶]			
Basal area (m ² ha ⁻¹)	22.6 \pm 12.2	26.9 \pm 3.3	33.5 \pm 3.5
Timber volume (m ³ ha ⁻¹)	350.8 \pm 215.7	436.2 \pm 82.2	507.4 \pm 96.2

Basal area share of European beech (%)	83.4 ±19.2	95.5 ±2.7	80.9 ±10.8
Stand density (trees ha ⁻¹)	407.1 ±427.5	273.9 ±68.4	396 ±113.8
Stand density of large trees, dbh > 65 cm (trees ha ⁻¹)	4.5 ±6.3	17.9 ±9.8	20.2 ±9.2
Maximum diameter (cm)	71.6 ±13.9	84.5 ±8.2	92.3 ±11.4
Standard deviation of diameter within plots (cm)	11.6 ±5.0	19.5 ±2.4	18.1 ±3.0
Tree species richness (⁰ D)	4.5 ±2.0	4.2 ±1.5	5.6 ±1.4
Tree species diversity (¹ D)	1.8 ± 0.9	1.3 ± 0.2	2.1 ± 0.7
Dead wood			
Dead wood volume (m ³ ha ⁻¹) [§]	27.8 ±12.1	17.7 ±8.2	21.6 ±13.5

* Annual mean temperature of the period 2009 to 2011 recorded in the shade 2 m above ground.

† Mean daily maximum air temperature during the growing season (May to September) of the period 2009 to 2011 recorded in the shade 2 m above ground.

‡ Mean daily air temperature range (max - min) during the growing season (May to September) of the period 2009 to 2011 recorded in the shade 2 m above ground.

Based on governmental forest planning maps of 2006, which we verified using aerial photographs.

¶ Species identity and diameter at breast height (dbh) of all trees (with dbh ≥7 cm) growing at the plots (1 ha in size) were recorded in winter 2008/09.

§ Dead wood was surveyed in summer 2012 considering standing and downed dead wood of large diameter (> 25 cm), downed dead wood of small diameter (> 7 cm and < 25 cm) and stumps (> 7 cm).

Table S1-2. Tree species composition of plots for even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forest management systems. Values are means and standard deviations based on basal area percentages. European beech dominates in all forest management systems, with UEA showing higher share than EA and UNM. The dominance of beech is in line with composition of natural beech forests on nutrient-rich soils, which also comprise only minor contributions of other tree species (ash, maple, hornbeam, lime and elm trees) in mid and late successional phases (Ellenberg 1988). Based on basal area, most abundant hardwood species other than beech (87.3 %) and oak (1.2 %) were common ash (*Fraxinus excelsior*, 5.2 %), sycamore maple (*Acer pseudoplatanus*, 3.1 %), hornbeam (*Carpinus betulus*, 1.4 %), lime trees (*Tilia spec.*, 1.1%), Norway maple (*Acer platanoides*, 0.4 %). Most abundant broadleaf softwood was *Betula pendula* (0.07%). In UNM the lower abundance of European beech and the increased abundance of oak and broadleaf hardwoods are legacies of the former coppice with standards forest management. Under this silvicultural management beech was systematically prevented entering the standards layer, in order to favour more versatile usable tree species. The frequent cutting of the coppice layer additionally decreased beech abundance due to poor resprouting capability. Since those days beech regained dominance and today UNM forests develop towards the less diverse species composition of natural beech forests. In EA abundance of hardwoods other than beech decreased with stand age. While ash, maple, oak, hornbeam and lime (which are less shade tolerant than beech) profit from the high light availability in early developmental phases (Ellenberg 1988), beech successively outcompetes admixed trees later on (Schall et al. 2018).

	Beech	Oak	Other hardwoods	Broadleaf softwoods	Spruce	Other conifers
Unmanaged	80.9 ±10.8	1.8 ±3.0	17.2 ±9.7			0.03 ±0.1
Uneven-aged	95.5 ±2.7	0.1 ±0.3	4.3 ±2.6	0.1 ±0.3		
Even-aged	83.4 ±19.2	2.0 ±3.4	14.1 ±18.4	0.3 ±0.6	0.1 ±0.3	0.1 ±0.3
· Thicket	69.1 ±29.2	3.1 ±5.4	27.6 ±29.6	0.1 ±0.2		
· Pole wood	63.1 ±21.1	4.5 ±4.2	31.2 ±22.5	0.9 ±1.2	0.3 ±0.6	
· Immature timber	88.7 ±8.5		10.6 ±9.0	0.3 ±0.7	0.3 ±0.4	
· Mature timber	94.2 ±5.1	2.0 ±4.1	3.5 ±2.5	0.1 ±0.2		0.2 ±0.4
· Thicket with shelterwood	96.7 ±2.8	0.9 ±1.6	1.9 ±1.7			0.4 ±0.7

Ellenberg, H. (1988) *Vegetation ecology of Central Europe*, 4th edn. Cambridge Univ. Press, Cambridge.

Schall, P., Schulze, E.-D., Fischer, M., Ayasse, M. & Ammer, C. (2018b) Relations between forest management, stand structure and productivity across different types of Central European forests. *Basic and Applied Ecology*, 39–52.

Boundary conditions of plot selection

Forest management systems cover large contiguous areas.

- Study area size between 1600 ha (Westerwald) and 3900 ha (unmanaged Hainich).

➤ FMS are independent from one another. That is, the measurements were neither affected by landscape configuration nor conditional to a specific landscape configuration.

Plots are located within large homogeneous stands.

- Stands size is larger than 8 ha. Mean size is 20 ha.
- Plots represent distinct forest types and developmental phases.
- Minor interference by adjacent stands/neighborhood.

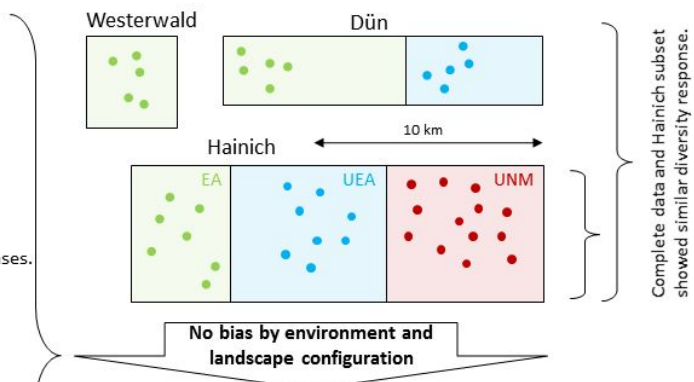
Plots are located with spacing.

- 300 m minimum distance.
- Plots in FMS are independent from one another.

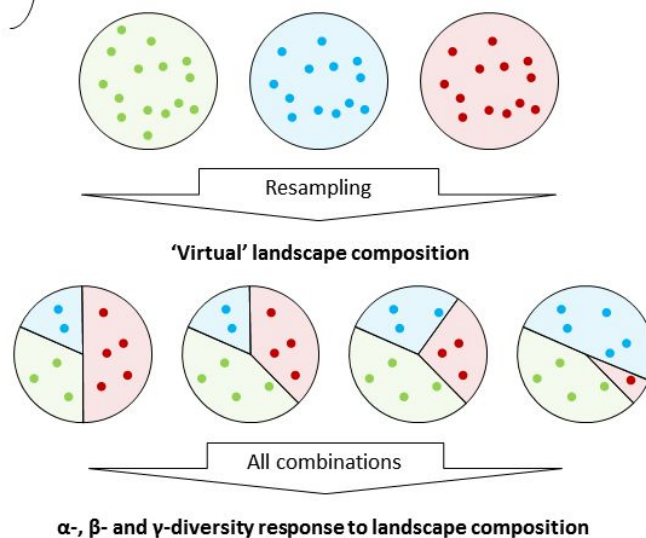
FMS comprise similar environmental gradients.

- Edaphic and altitudinal gradients are comparable.
- Data is not biased by differences in environment

Real world landscape composition and configuration



Conceptual data structure



α -, β - and γ -diversity response to landscape composition

Figure S1-1. Study design with boundary conditions to ensure an unbiased data structure for resampling of 'virtual' landscapes.

(Top) Sketch of the forested hill chains of Hainich, Westerwald, and Dün with the available number of plots. The area of the hill chains and forest management systems is drawn to scale, but the spatial arrangement of the hill chains is simplified. Criteria for the selection of plots were: (i) forest management systems cover large contiguous areas to eliminate effects of forest configuration on measurements, (ii) location of plots within stands that are sufficiently large to provide habitat for the species under study, (iii) spacing between plots to ensure independence of measurements, and (iv) similar environmental gradients between forest management systems to factor out environmental bias.

(Mid) As criteria for selection of plots ensured that landscape configuration did not affect measurements and environmental gradients were balanced between management systems, we consider each forest management system to be represented by independent observations.

(Bottom) In order to quantify the effect of landscape composition on biodiversity 10 plots were randomly drawn from the EA, UEA and UNM plot pools, systematically varying the shares of the EA, UEA and UNM. We described the entire compositional gradient in steps of 10% arriving at 66 compositionally distinct 'virtual' forest landscapes. Each of this 'virtual' forest landscape was resampled 1000 times with α -, β - and γ -diversity being quantified.

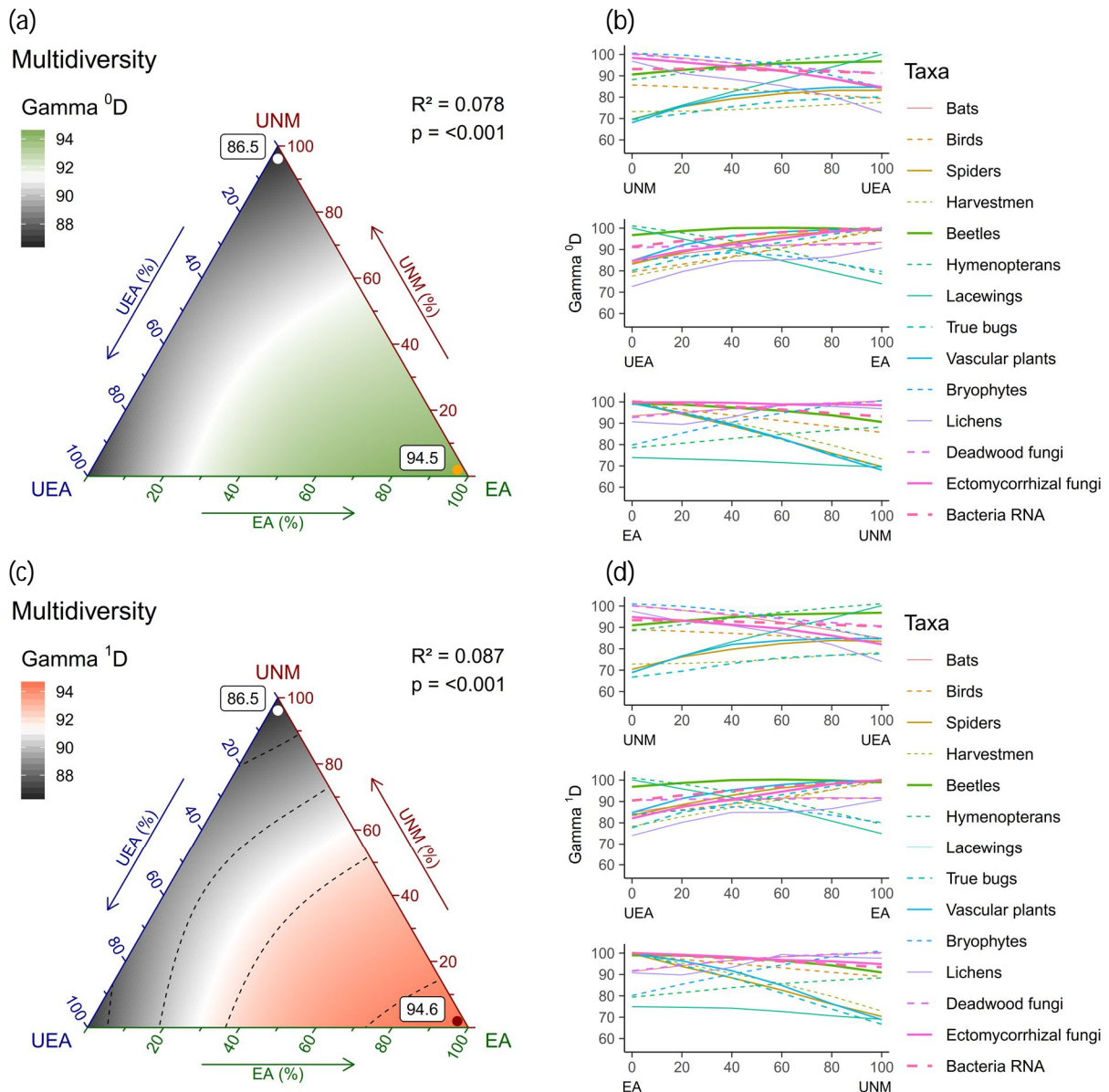


Figure S1-2. Effect of spatial arrangement of forest management systems on findings: Gamma-multidiversity and relative gamma diversity for Hill-numbers 0 (a, b) and 1 (c, d) of 14 taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests of the Hainich ridge. The composition of forest landscapes was varied in steps of 20% using 100 resamplings of 5 plots per step (21 unique landscape compositions). Gamma-multidiversity (a) quantifies the mean relative gamma-diversity of organismic groups accounting for the absolute diversity within groups (log weighting of diversity). The diversity response to forest landscape composition across organismic groups was analysed using spline regression (GAM) and characterised by R² and p-value. Labelled dots mark the maximum (orange/red dot) and minimum (white dot). Relative gamma-diversity along bivariate gradients of forest composition (b, d) show how organismic groups drive gamma-multidiversity (line thickness resembles weighting of organismic groups).

Climatic and edaphic gradients of plots are comparable between the three management systems. While the managed forests are equally scattered across the study area (mean \pm SE distance between plots: 13.9 \pm 2.3 km for EA and 13.9 \pm 3.4 km for UEA), the UNM forests are aggregated in the southern part of the Hainich ridge (mean distance between plots 2.7 \pm 0.5 km). To explore if the aggregated occurrence of UNM affected our results, we generated a subset of plots in which EA and UEA were restricted to the area of the Hainich ridge. The subset contains all UNM, 8 UEA and 5 EA plots in similar spatial configuration within management systems (mean distance between plots: 3.2 \pm 0.6 km for EA, 1.2 \pm 0.2 km for UEA and 2.7 \pm 0.5 km for UNM) arranged in blocks from south to north. Due to their low number, EA plots do not fully represent the rotation cycle (1 thicket, 1 pole wood, 1 immature timber, 2 mature timber, but no thicket with shelterwood) and the shares of

developmental phases on the rotation period. Despite these constraints, we observed a similar regional multidiversity response for this subset of the Hainich ridge (see Figure S1-1) as for the complete set of plots. We thus suppose that findings based on the complete set of plots were not driven by the spatial configuration of UNM.

Appendix S2: Details on results

Table S2-1. Explained variance R^2 of alpha diversity, beta turnover and beta nestedness response to forest landscape composition and landscape composition comprising maximum and minimum diversity of 14 taxonomic groups. Biodiversity minimising and maximising landscape compositions were only given for significant differences (bold printing of either EA, UEA or UNM means pure forest landscapes of that type; for mixed landscapes the dominating forest management system was printed bold). Results are based on 66 compositionally distinct forest landscapes characterised by resamplings ($N = 64572$). * $p < 0.05$ significant difference between the minimum and maximum diversity. For the respective ternary diagrams, see Figures S2-7 to S2-9.

Taxon	Alpha			Beta					
	Min	R^2	Max	Turnover			Nestedness		
				Min	R^2	Max	Min	R^2	Max
Bats	UEA	0.251*	UNM	UNM	0.31*	EA	EA	0.281*	UNM-UEA
Birds	EA	0.670*	UNM	UEA	0.66*	EA		0.187	
Spiders	UNM	0.742*	EA	UEA	0.491*	EA	EA	0.413*	UNM
Harvestmen	UNM	0.703*	EA		0.028		EA	0.140*	UNM-EA
Beetles	UNM	0.559*	EA	UEA	0.244*	UNM-EA		0.183	
Hymenopterans		0.091		UEA	0.204*	EA		0.050	
Lacewings	UNM	0.334*	UEA		0.015			0.013	
True bugs	UNM	0.332*	EA		0.177			0.052	
Vascular plants	UNM	0.527*	EA	UEA	0.426*	EA-UNM		0.135	
Bryophytes		0.099			0.102			0.164	
Lichens	UEA	0.304*	UNM	UEA	0.181*	EA		0.081	
Deadwood fungi	UEA	0.597*	UNM	UNM	0.264*	UEA	UEA	0.186*	EA
Ectomycorrhizal fungi	EA-UEA	0.399*	UNM	UNM	0.268*	EA-UEA	UNM	0.339*	EA
Bacteria	UNM	0.054	UEA		0.145		UNM	0.352*	UEA

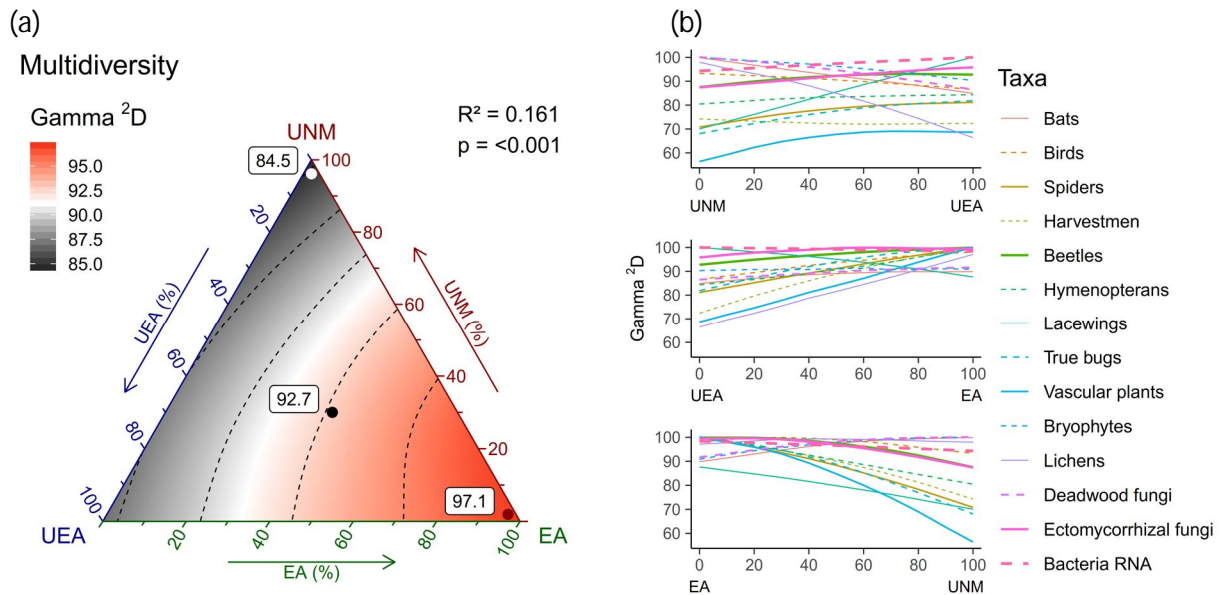


Figure S2-1. Gamma-multidiversity and relative gamma-diversity for Hill-number 2 of 14 organismic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step (66 unique landscape compositions). Gamma-multidiversity (a) quantifies the mean relative gamma-diversity of organismic groups accounting for the absolute diversity within groups (log weighting of diversity). The diversity response to forest landscape composition across organismic groups was analysed using spline regression (GAM) and characterised by R^2 and p-value. Labelled dots mark the multidiversity of the actual landscape composition (black dot; 40% EA, 30% UEA and 30% UNM) and the maximum (red dot) and minimum (white dot). Relative gamma-diversity along bivariate gradients of forest composition (b) show how organismic groups drive gamma-multidiversity (line thickness resembles weighting of organismic groups). For ternary gradients of forest composition, see Figure S2-6.

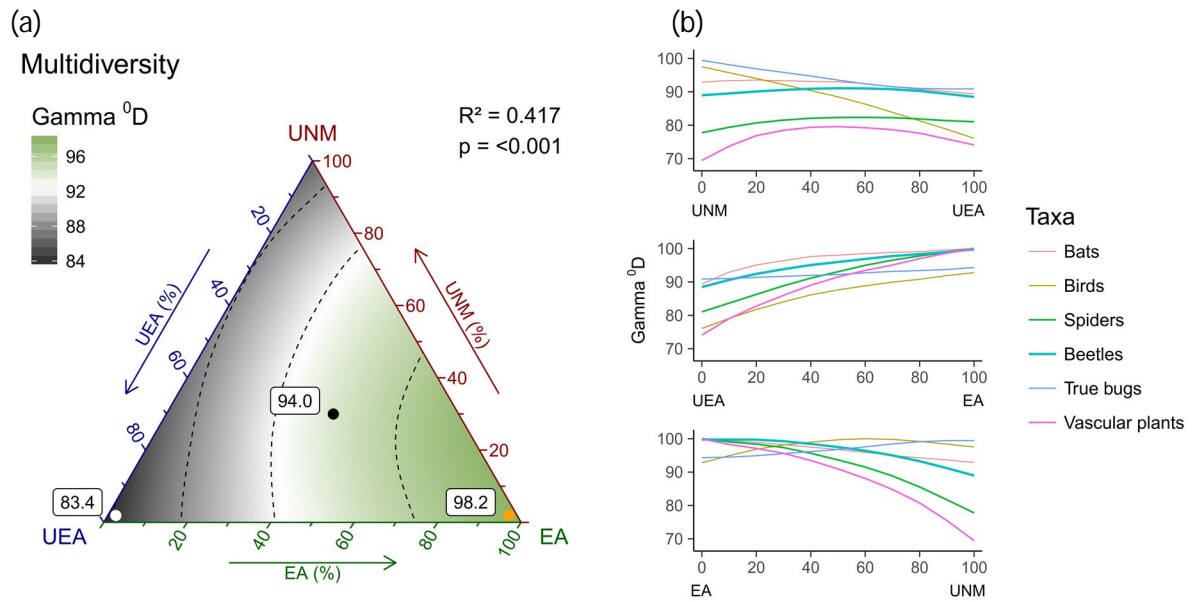


Figure S2-2. Gamma-multidiversity (a) and relative γ -diversity (b) of forest specialists for Hill-number 0 along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. Labelled dots mark the multidiversity of the actual landscape composition (black dot, 40% EA, 30% UEA and 30% UNM) and the maximum (orange dot) and minimum (white dot).

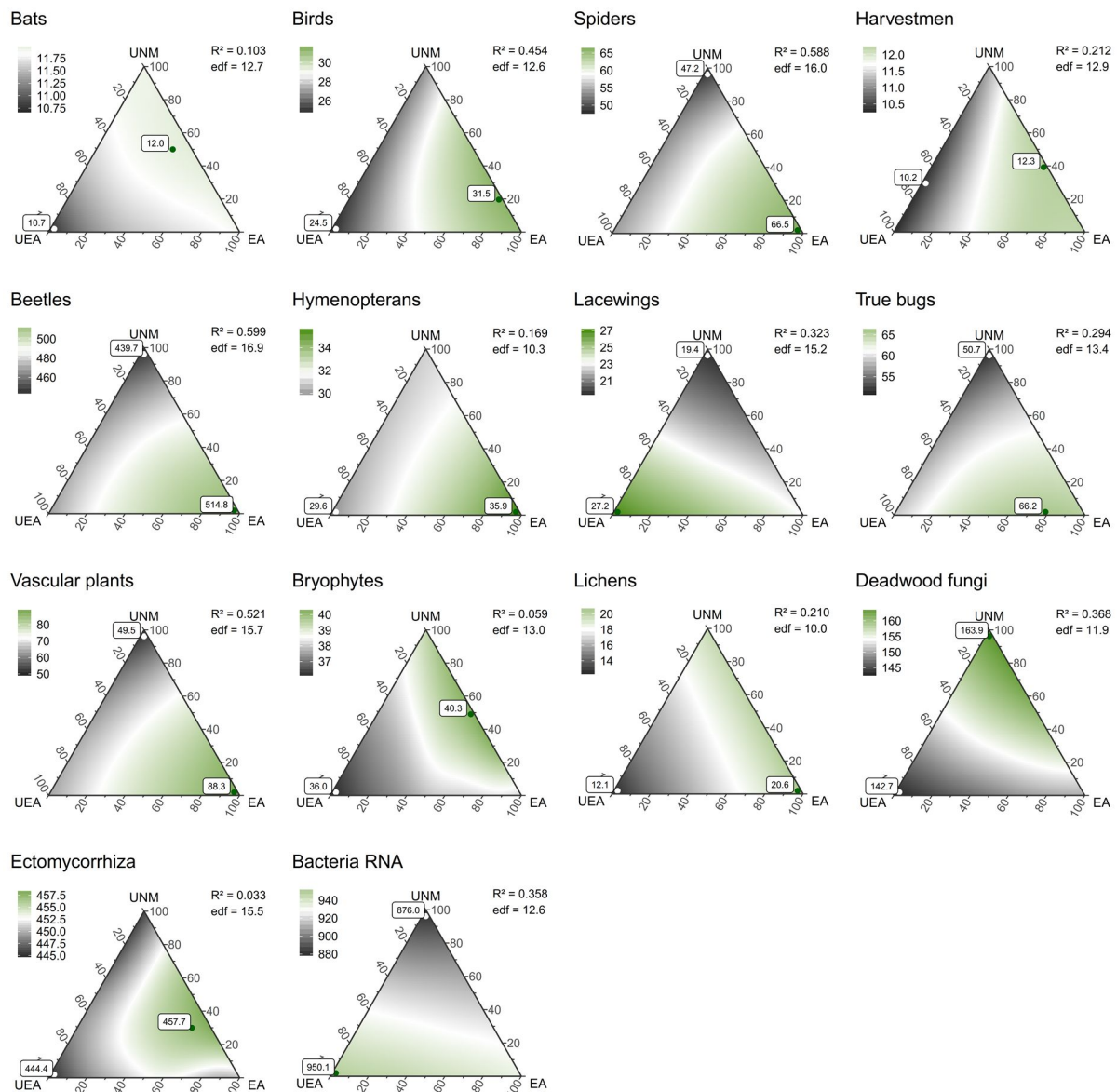


Figure S2-4. Gamma diversity 0D of taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step ($N = 66$). Based on resamplings the shape of the diversity response surface was analysed using spline regression (GAM), and characterised by R^2 and estimated degrees of freedom (edf). With higher edf the shape of the diversity response surface becomes more complex. Originating from median diversity (white) the colouring of the response surface becomes more saturated with decreasing (grey) and increasing (green) diversity. Labelled dots mark the maximum (green dot) and minimum (white dot).

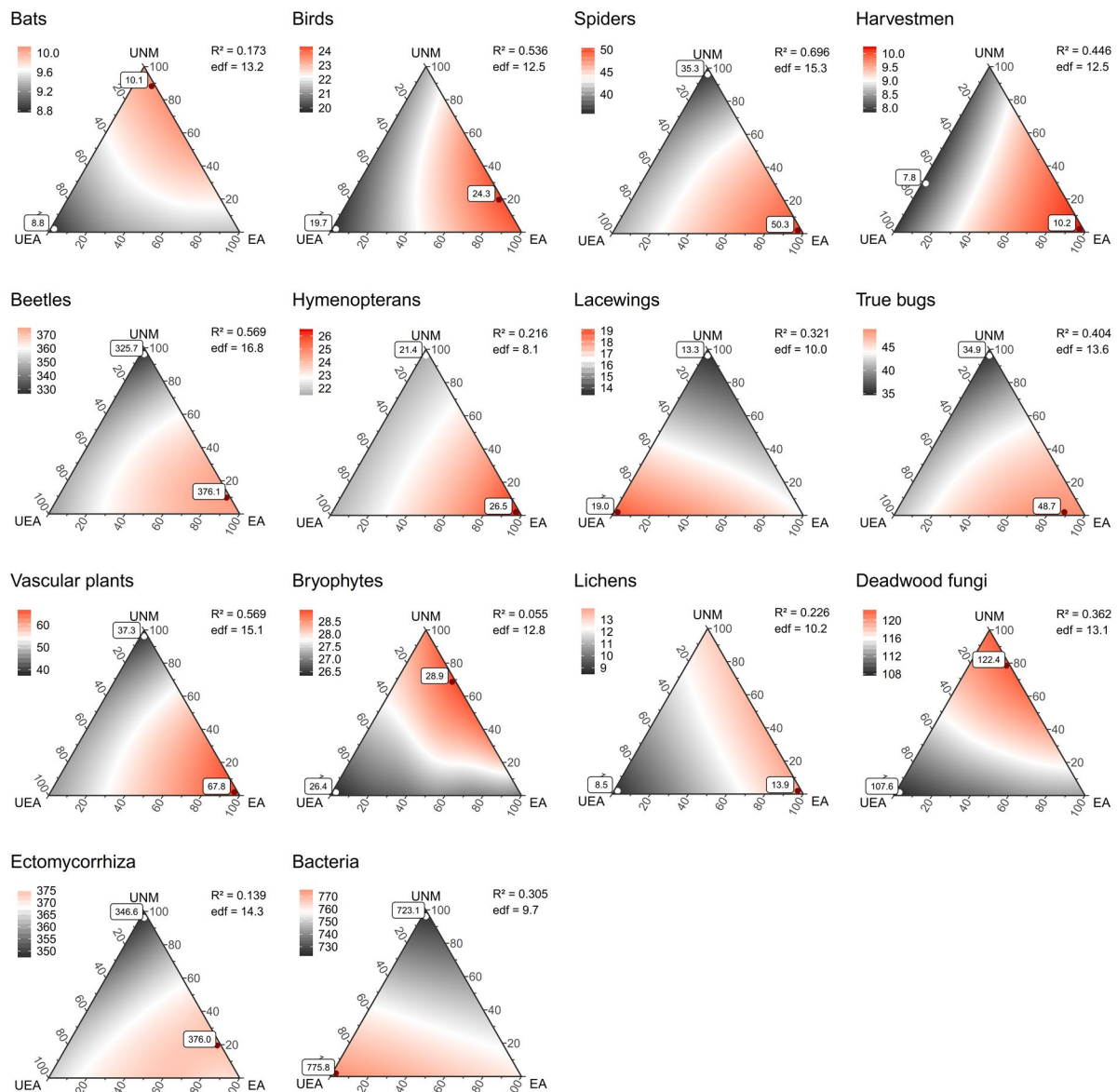


Figure S2-5. Gamma diversity 1D of taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step ($N = 66$). Based on resamplings the shape of the diversity response surface was analysed using spline regression (GAM), and characterised by R^2 and estimated degrees of freedom (edf). With higher edf the shape of the diversity response surface becomes more complex. Originating from median diversity (white) the colouring of the response surface becomes more saturated with decreasing (grey) and increasing (red) diversity. Labelled dots mark the maximum (red dot) and minimum (white dot).

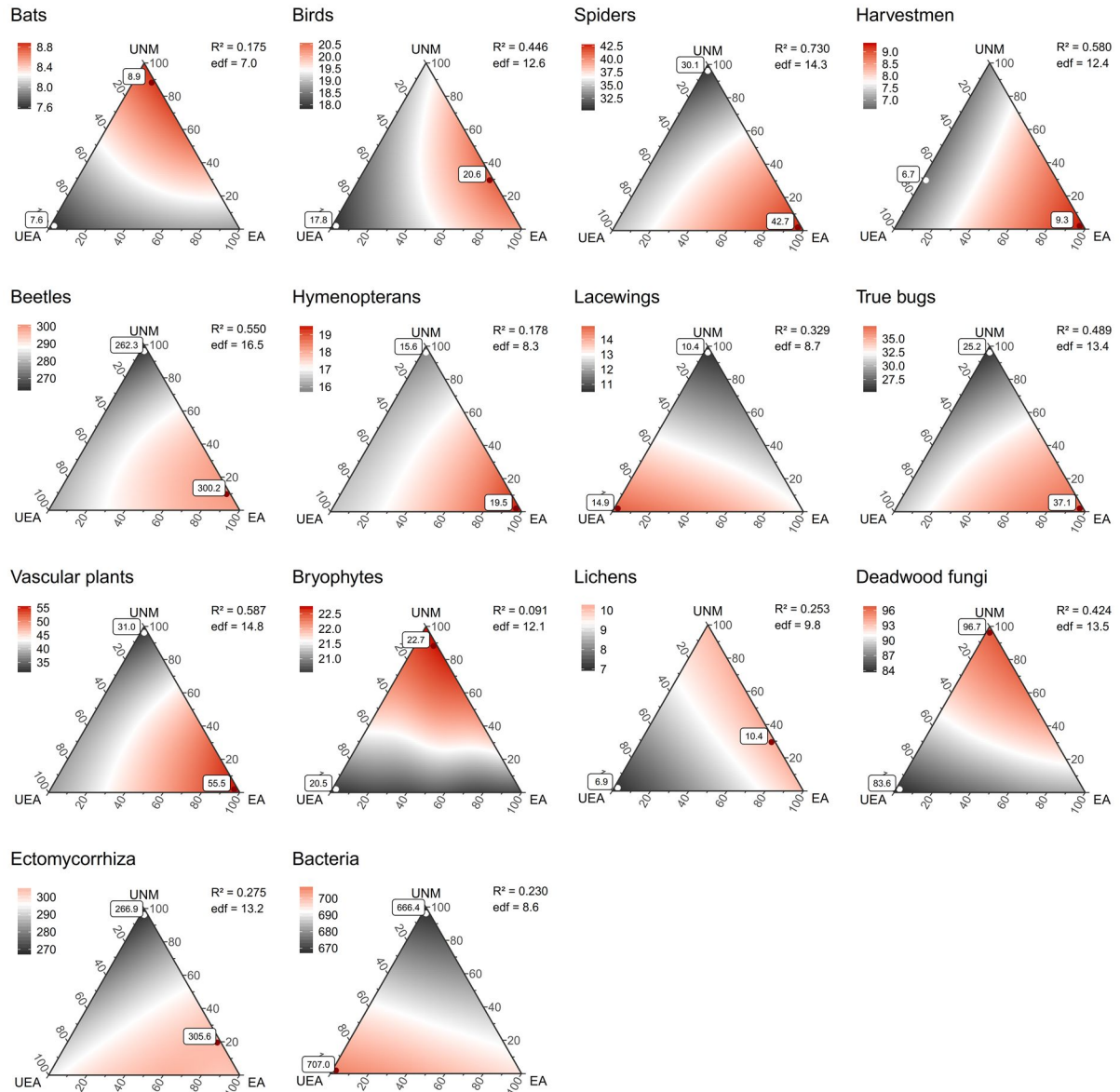


Figure S2-6. Gamma diversity ²D of taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step (N = 66). Based on resamplings the shape of the diversity response surface was analysed using spline regression (GAM), and characterised by R² and estimated degrees of freedom (edf). With higher edf the shape of the diversity response surface becomes more complex. Originating from median diversity (white) the colouring of the response surface becomes more saturated with decreasing (grey) and increasing (red) diversity. Labelled dots mark the maximum (red dot) and minimum (white dot).

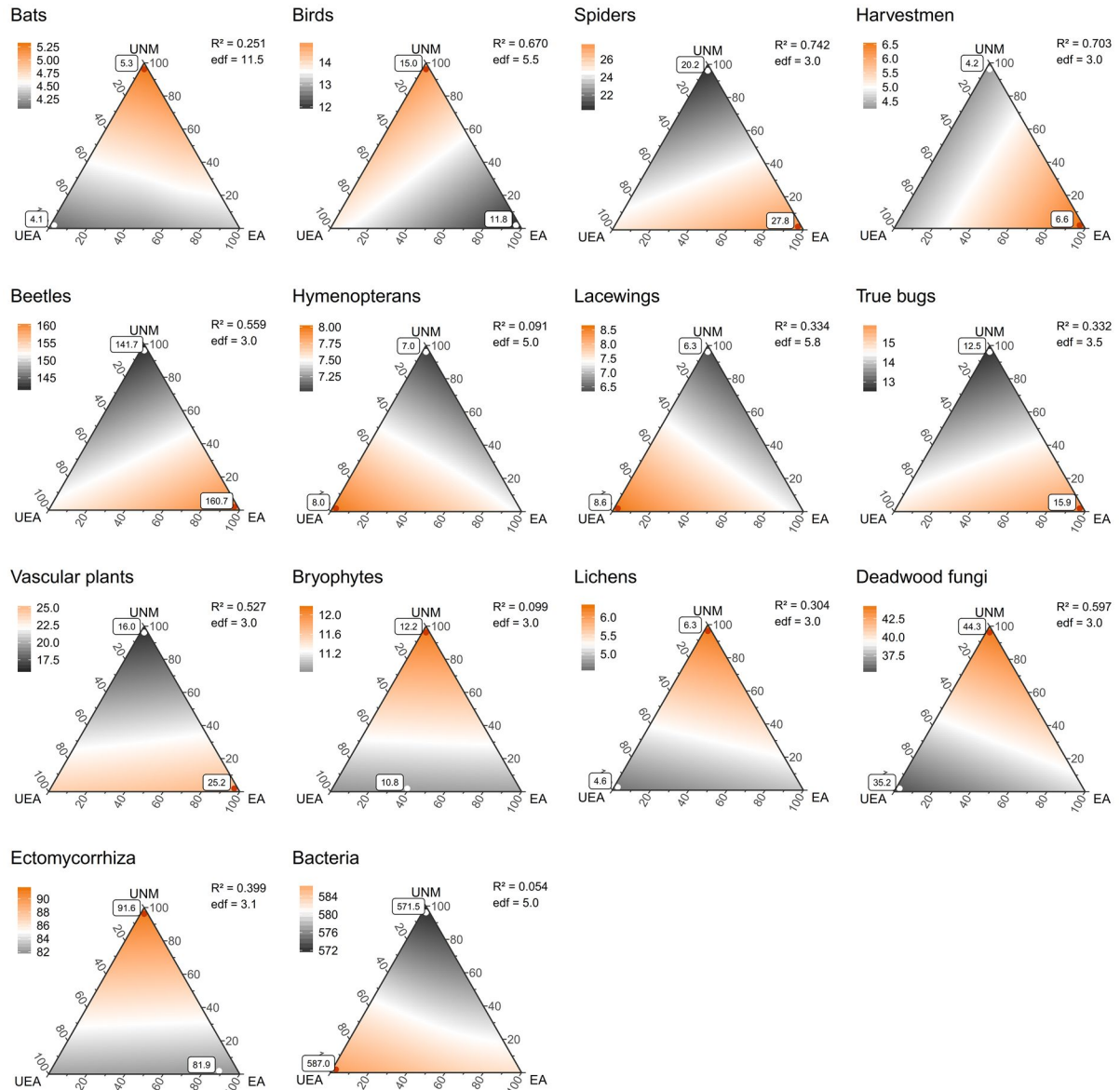


Figure S2-7. Alpha diversity D of taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step ($N = 66$). Based on resamplings the shape of the diversity response surface was analysed using spline regression (GAM), and characterised by R^2 and estimated degrees of freedom (edf). With higher edf the shape of the diversity response surface becomes more complex. Originating from median diversity (white) the colouring of the response surface becomes more saturated with decreasing (grey) and increasing (orange) diversity. Labelled dots mark the maximum (red dot) and minimum (white dot).

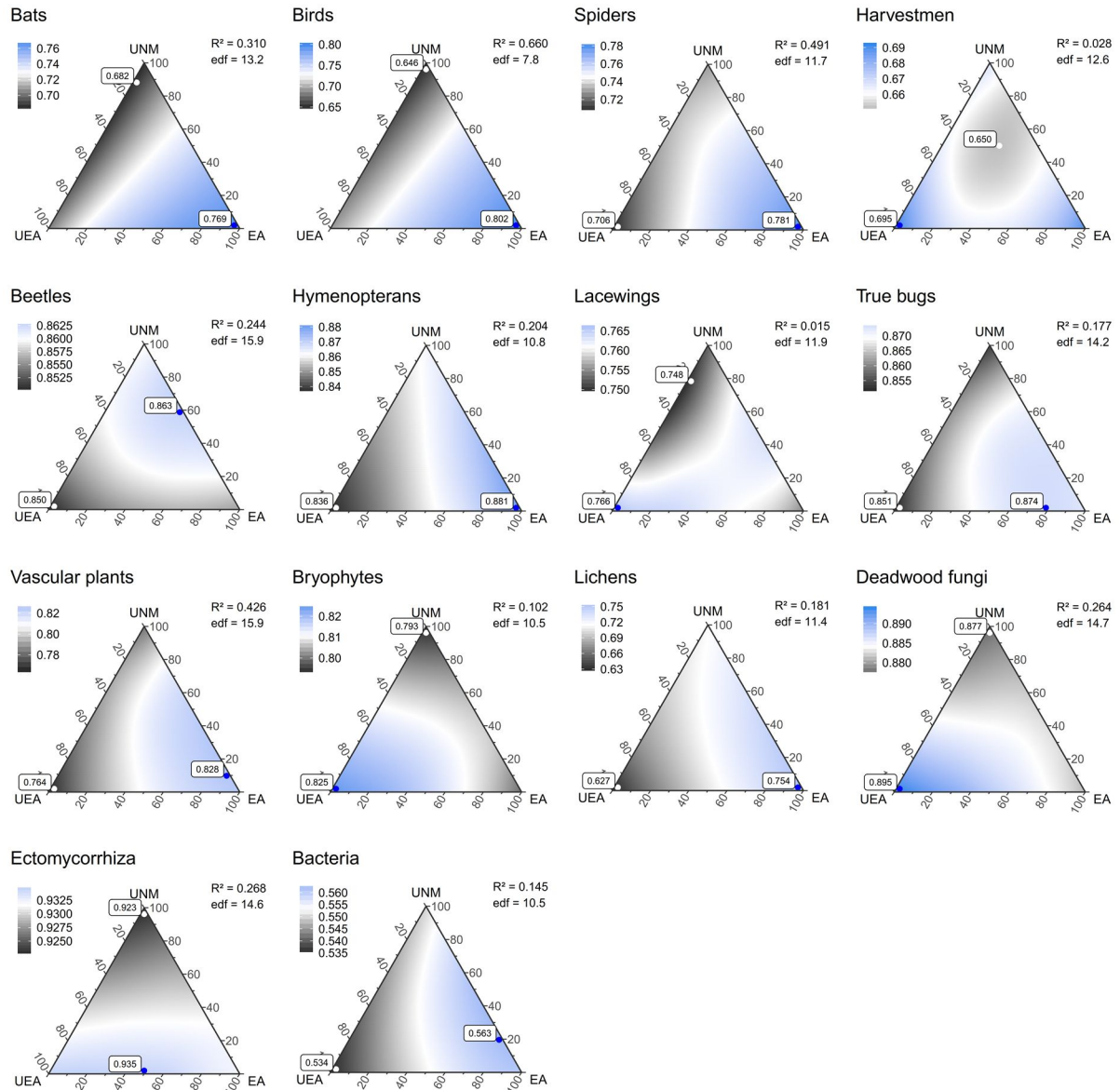


Figure S2-8. Turnover component of multiple-site Jaccard dissimilarity diversity of taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step ($N = 66$). Based on resamplings the shape of the diversity response surface was analysed using spline regression (GAM), and characterised by R^2 and estimated degrees of freedom (edf). With higher edf the shape of the diversity response surface becomes more complex. Originating from median diversity (white) the colouring of the response surface becomes more saturated with decreasing (grey) and increasing (blue) diversity. Labelled dots mark the maximum (blue dot) and minimum (white dot).

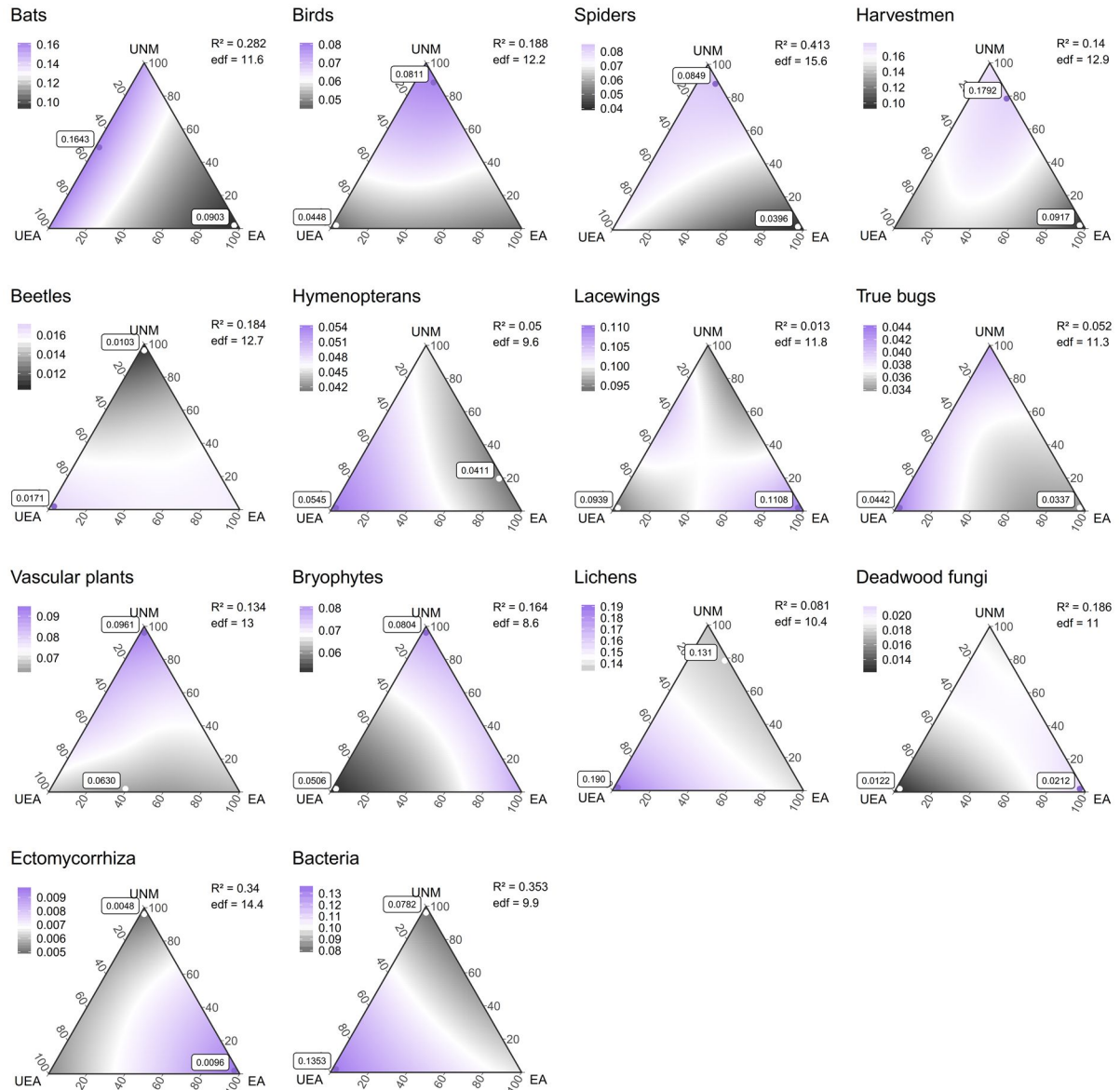


Figure S2-9. Nestedness component of multiple-site Jaccard dissimilarity diversity of taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1000 resamplings of 10 plots per step ($N = 66$). Based on resamplings the shape of the diversity response surface was analysed using spline regression (GAM), and characterised by R^2 and estimated degrees of freedom (edf). With higher edf the shape of the diversity response surface becomes more complex. Originating from median diversity (white) the colouring of the response surface becomes more saturated with decreasing (grey) and increasing (purple) diversity. Labelled dots mark the maximum (purple dot) and minimum (white dot).

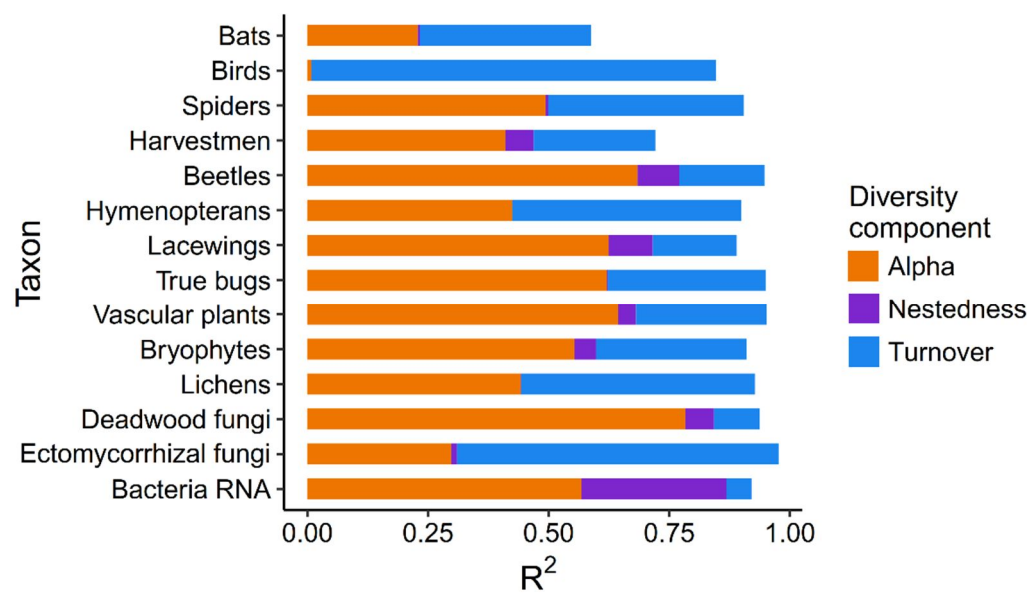


Figure S2-10. Control of γ -diversity by α -diversity and turnover and nestedness components of multisite β -diversity. The result of variable importance analysis using CAR scores is based on linear additive models with α -diversity, β -turnover and β -nestedness predicting γ -diversity ⁰D.

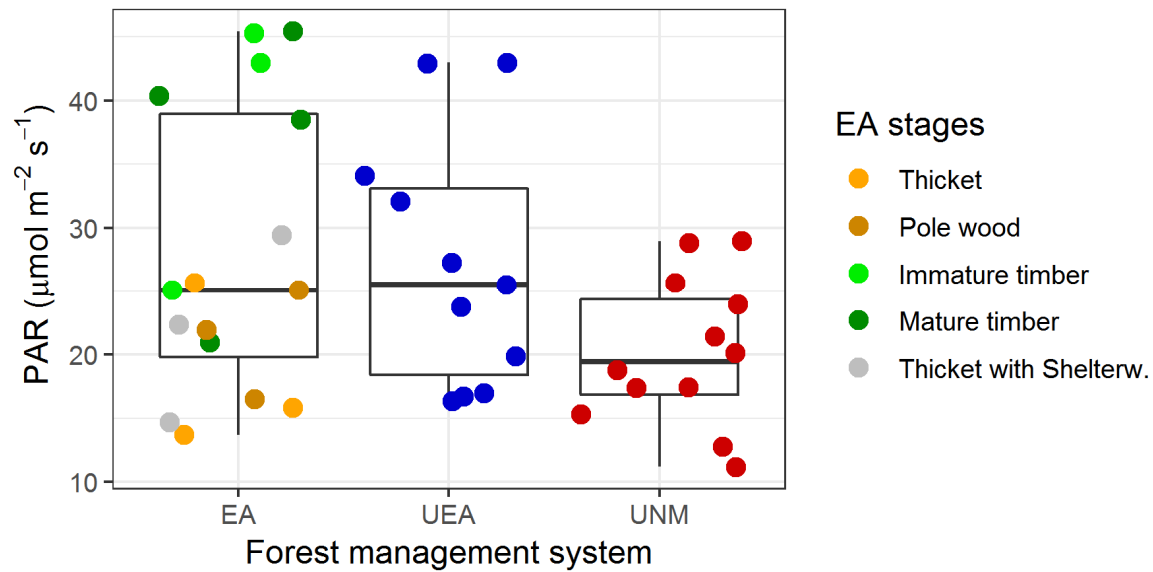


Figure S2-11. Light availability at shrub layer level (2 m above ground) for forest management systems. Values are means for daytime hours 7 am to 11 am and 14 pm to 18 pm (Central European Summer Time) of 13th to 16th July 2018.

As PAR was measured with one spatially fixed sensor per plot, we excluded daytimes with high position of the sun that are known to comprise effects of light flecks. The variation in light availability was highest in EA and lowest in UNM. Within EA, timber stages showed the highest light availability, most likely due to thinning from above silvicultural operations, which opened the canopy. Thickets and thickets with shelterwood showed lowest PAR values within EA. However, taking into account the rapid growth of thickets this observation does not truly reflect the conditions in 2008. Values rather demonstrate that early developmental phases develop high LAI when not thinned. This is also true for pole woods, which also remain un-thinned under traditional shelterwood system.

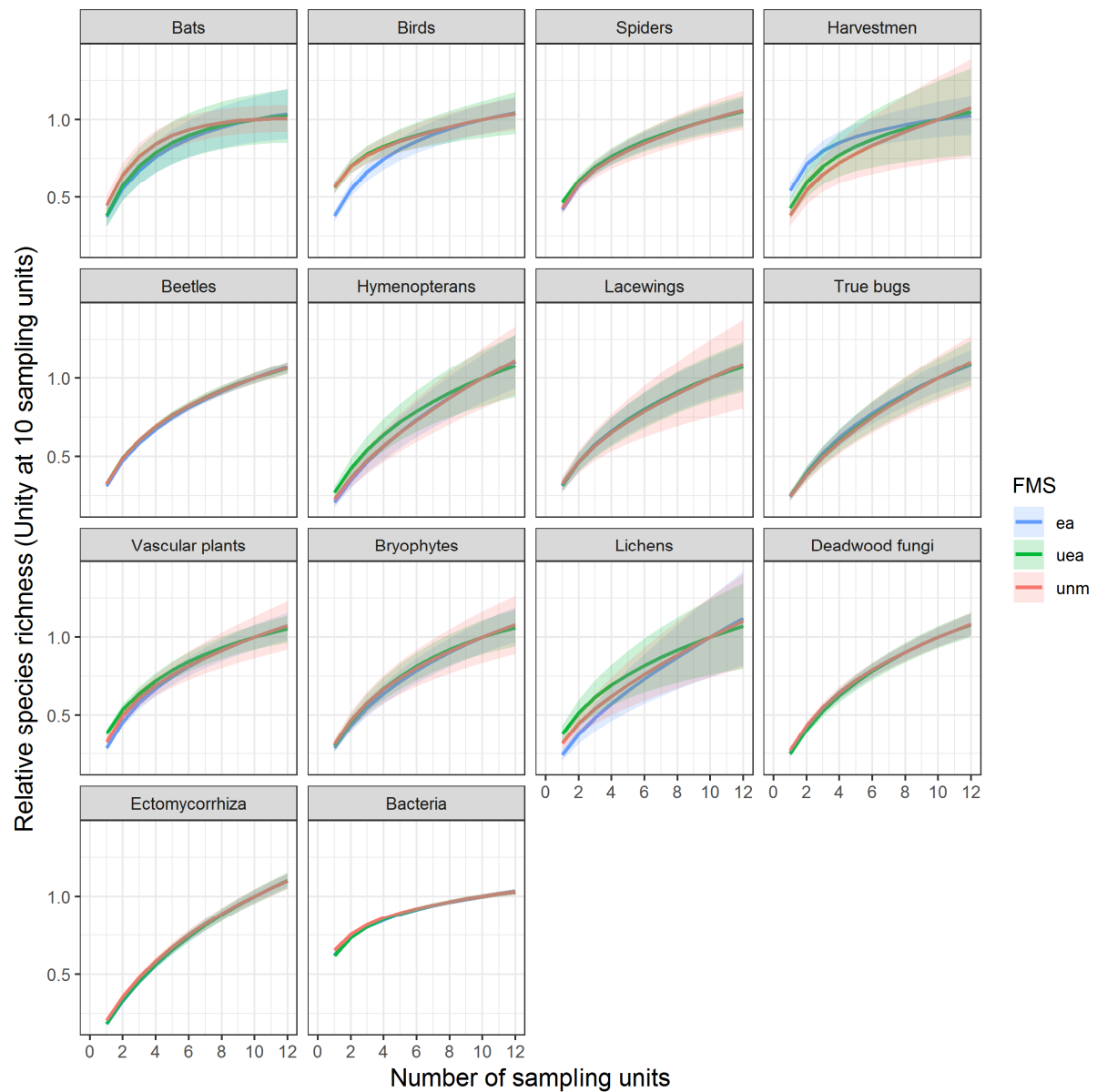


Figure S2-12. Relative species accumulation curves 0D . Rarefaction of 0D γ -diversity of 14 taxonomic groups for even-aged ($N = 17$, blue), uneven-aged ($N = 13$, green) and unmanaged ($N = 12$, red) forests. Sample-size based rarefaction up to 12 samples was scaled to the diversity at 10 samples. Scaling was conducted to compare the shape of SACs by factoring out different levels of diversity between forest management systems. All curves include 95% confidence intervals obtained by bootstrapping based on 200 replications. Curves for all taxonomic groups are overlapping, except for birds. This means that a reduction of habitat area reduces the taxonomic group diversity irrespective of the management system. For birds, β -diversity among forest developmental phases drives γ -diversity in the EA system (see Figures 3b, S2-8, S2-10). Thus, a reduction in sampling units affects γ -diversity more strongly in EA compared to UEA or UNM as the five forest developmental phases increasingly become underrepresented.

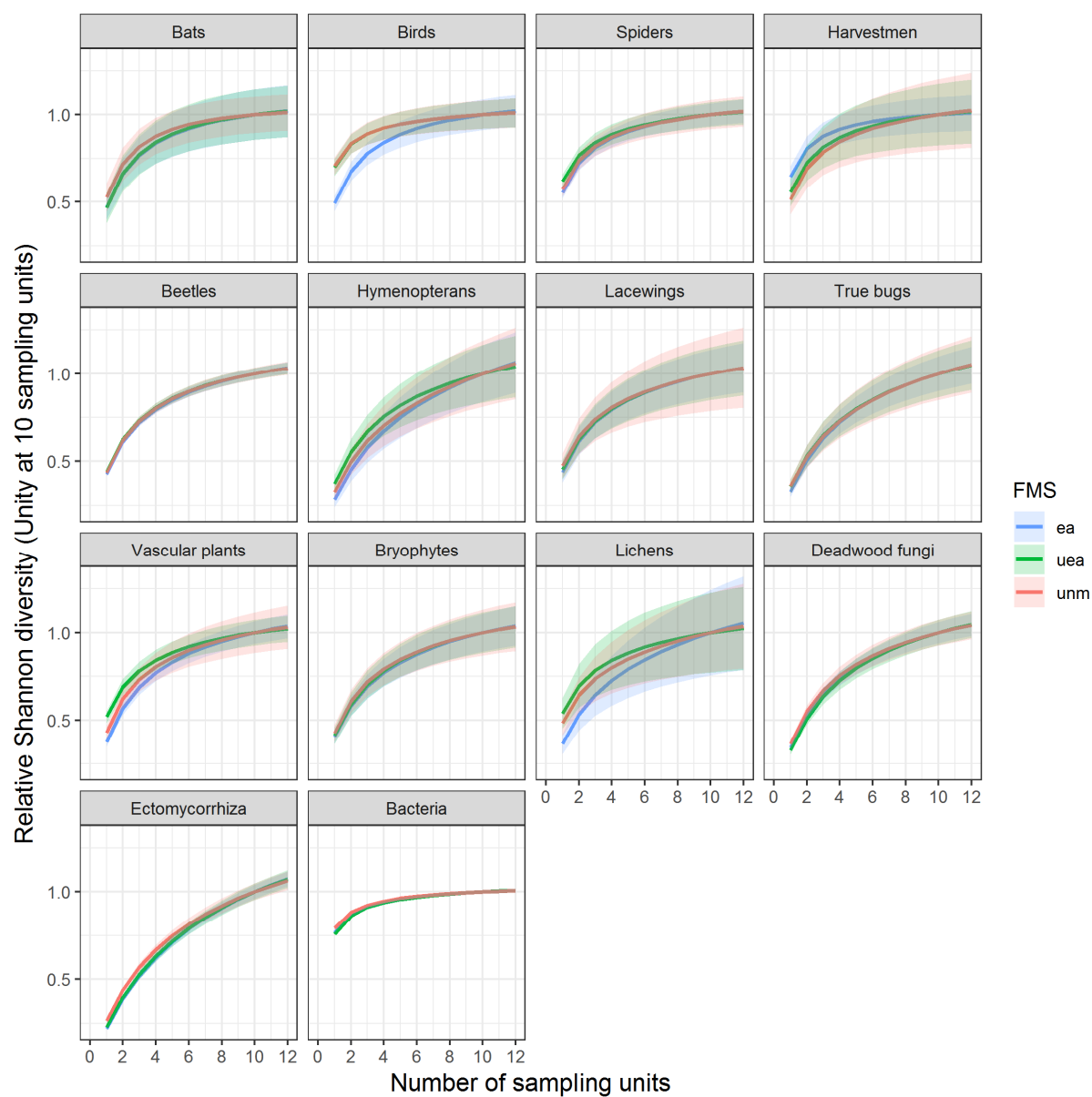


Figure S2-13. Relative species accumulation curves ¹D. Rarefaction of ¹D γ -diversity of 14 taxonomic groups for even-aged (N = 17, blue), uneven-aged (N = 13, green) and unmanaged (N = 12, red) forests. For details see Figure S2-12.