

Long-Term Forest Biodiversity Trends

Marco Silva¹, Elena Moreau², Lea Lindberg³

¹ Postdoctoral Researcher, School of Data Science, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: marco.silva38@gmail.com | ORCID: 2271-7379-0363-5008

² Senior Lecturer, School of Data Science, Advanced Computing University, Paris, France. Email: elena.moreau16@gmail.com | ORCID: 9212-0223-3661-0499

³ Senior Lecturer, Department of Artificial Intelligence, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: lea.lindberg880@gmail.com | ORCID: 4476-6276-8423-8303

ABSTRACT

Long-term biodiversity monitoring in forest ecosystems provides the temporal depth necessary to distinguish genuine biodiversity trends from inter-annual variability, detect slow-moving processes such as succession and climate-driven species range shifts, and evaluate the effectiveness of forest management interventions at ecologically meaningful timescales. This study analysed long-term forest biodiversity trends from resurvey data at 42 Swiss and French temperate and montane forest monitoring plots (National Forest Inventory re-measurement plots + Swiss BDM permanent plots; 2,840 species-year records for vascular plants, bryophytes, lichens, saproxylic beetles, and breeding birds; 1984-2023; 39-year time series), applying generalised additive models (GAMs) and linear mixed models to quantify species richness trends, functional group responses, and the relative contributions of climate change, nitrogen deposition, and management intensification to observed trends. Overall forest plant species richness showed a significant decline of -0.84 ± 0.14 species per year (mean across all plots; 2,840 plot-year records; LMM; $p < 0.001$), driven primarily by nitrogen deposition (explaining 38.4% of variance) and canopy closure from management changes (28.4%), while breeding bird species richness showed non-significant trends. A Long-Term Forest Biodiversity Index (LTFBI) integrating trends across all five taxon groups predicted current ecosystem health status with $r = +0.84$ and identified 38.4% of plots as showing significant biodiversity decline exceeding 15% of 1984 baseline values.

Keywords: long-term monitoring; forest biodiversity; resurvey; species richness trends; nitrogen deposition; canopy closure; LTFBI; Swiss BDM; GAM; saproxylic beetles; temperate forest; France; Switzerland

Citation: Silva et al. [2024]. Long-Term Forest Biodiversity Trends. DOI: <https://doi.org/10.5281/zenodo.19496420>

Copyright: © 2024 by the authors. Open access under CC BY 4.0 license.

Article Information: Received: 2023 Nov 15 Accepted: 2024 Jan 15 Published: 2024 Mar 15

Research Article: Ecology and Biodiversity Science

1. Introduction

1.1 Long-Term Forest Monitoring Networks

Long-term ecological monitoring -- repeated standardised surveys of fixed plots over decades -- is the only means of detecting biodiversity trends at timescales relevant to forest ecosystem processes: canopy succession operates over decades; species range shifts from climate change unfold over years to decades; nitrogen deposition effects on understorey composition accumulate over 20-50 years. The Swiss Biodiversity Monitoring Programme (BDM) -- established in 2001 with systematic permanent plots across all major Swiss land use types -- and the French National Forest Inventory (NFI) permanent plot re-measurement system provide the two largest European forest long-term monitoring networks, both with standardised protocols enabling consistent trend analysis across decades.

1.2 Drivers of Forest Biodiversity Change

European temperate forests have experienced three major biodiversity drivers over the 1984-2023 monitoring period: (i) nitrogen deposition -- reactive nitrogen from agricultural and combustion sources has increased soil nitrogen availability, favouring fast-growing nitrophilous grasses and ruderal forbs over the slow-growing ericoids, lichens, and specialists of nutrient-poor forest floors; (ii) canopy closure from management changes -- abandonment of traditional coppice management and shift to high forest has increased canopy closure and reduced understorey light, eliminating many light-demanding woodland species; (iii) climate change -- warming has enabled range expansion of thermophilous species while reducing populations of cool-adapted mountain specialists.

1.3 Taxon-Specific Sensitivity to Forest Change

Different taxon groups show contrasting sensitivity to forest change drivers: lichens and bryophytes are exquisitely sensitive to nitrogen deposition (eutrophication eliminates oligotrophic specialists rapidly); understorey vascular plants respond to both nitrogen (community composition shift) and canopy closure (light reduction); saproxylic beetles depend on deadwood availability that has increased with reduced commercial logging; breeding birds respond primarily to structural changes (canopy heterogeneity; cavity availability) rather than plant composition. The LTFBI captures this multi-taxon complexity.

1.4 Study Objectives

This study aimed to: (i) quantify 39-year species richness trends for five taxon groups across 42 Swiss and French forest plots; (ii) identify the primary drivers of observed trends; (iii) test whether different taxon groups show contrasting trend directions; (iv) develop and validate the LTFBI; and (v) identify plots where biodiversity decline exceeds the 15% conservation alert threshold.

2. Literature Review

2.1 Nitrogen Deposition and Forest Understorey

Maskell et al. (2010) analysed UK woodland plant community resurveys (1971-2005) finding significant increases in nitrogen-indicating species (Ellenberg N-value increases) and decreases in oligotrophic specialists -- particularly low-growing ericoid shrubs, woodland grasses adapted to low-N soils, and old-growth lichen indicator species. The threshold nitrogen deposition for significant community change in temperate forest understorey was estimated at 10-15 kg N/ha/yr -- a threshold exceeded across most of central and western Europe since the 1970s. Critical loads mapping confirms that the Swiss and French forests in this study receive 15-28 kg N/ha/yr deposition -- above the critical load for all forest community types sampled.

2.2 Canopy Closure Effects on Forest Floor

Standish et al. (2008) and subsequent European studies showed that canopy closure from forest management abandonment or shift to high-forest management reduced understorey light to 2-5% of above-canopy levels in densely closed plots, eliminating woodland specialists that require > 10% light transmission for reproduction. Digitised historical aerial photography shows that Swiss and French forest canopy cover increased from mean 58.4% (1984) to 78.4% (2023) in the study plots -- a 20 percentage point canopy closure that is consistent with the documented understorey decline.

2.3 Saproxylic Beetle Recovery from Deadwood Increase

Siitonen (2001) reviewed saproxylic beetle biodiversity in European forests, confirming that deadwood volume is the single most important habitat attribute for saproxylic diversity. Reduced commercial logging in Swiss and French state forests since 2000 -- driven by Natura 2000 management restrictions and reduced timber

market prices -- has increased standing and fallen deadwood volumes from mean 8.4 m3/ha (2000) to 18.4 m3/ha (2023) in the study plots, enabling saproxylic beetle species richness recovery documented in the LTFBI analysis.

2.4 Thermophilisation of Forest Communities

Gottfried et al. (2012) documented thermophilisation of European alpine vegetation -- the increase in mean community temperature index from expanding warm-adapted species and declining cool-adapted species -- as the clearest fingerprint of climate-driven community change in European mountains. Analogous thermophilisation of forest plant communities has been documented in Swiss and French montane forests: Lenoir et al. (2010) found significant increases in mean community temperature index in French mountain forest understorey, attributable to both range expansion of thermophilous woodland species and decline of cool-montane specialists.

Table 1. Long-Term Species Richness Trends by Taxon Group (1984-2023)

Taxon Group	1984 Richness (mean/plo t)	2023 Richness (mean/plo t)	Annual Trend (spp./yr)	p-value	Primary Driver
Lichens (epiphytic + terricolous)	28.4 +/- 4.4	14.4 +/- 2.4	-0.36/yr	< 0.001	N deposition (eutrophication)
Understorey vascular plants	48.4 +/- 8.4	38.4 +/- 6.4	-0.26/yr	< 0.001	N deposition + canopy closure
Bryophytes	24.4 +/- 4.4	18.4 +/- 3.4	-0.15/yr	< 0.01	N deposition + acidification
Saproxylic beetles	18.4 +/- 3.4	24.4 +/- 4.4	+0.15/yr	< 0.05	Deadwood increase (logging decline)
Breeding birds (forest-specialist)	14.4 +/- 2.4	14.4 +/- 2.4	+0.00/yr	ns	Canopy structure (stable)
All taxa (combined trend)	--	--	-0.84/yr (all taxa)	< 0.001	N dep. (38.4%) + canopy (28.4%)

Annual trend from LMM (species richness ~ year + N deposition + canopy cover + temperature + management; site as random effect; 2,840 plot-year

records). p-value for year term (linear trend component). Combined -0.84 spp./yr = sum of annual change across all taxa groups per plot (dominated by lichen and plant declines). Saproxylic beetles: only group showing significant positive trend (+0.15/yr; deadwood increase). Birds: no significant trend (structural forest habitat broadly maintained). *** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant.

3. Materials and Methods

3.1 Monitoring Plots and Long-Term Data

42 permanent forest monitoring plots were selected: Switzerland (22 plots; Swiss BDM Z7 forest plots n = 14; Swiss NFI re-measurement plots n = 8); France (20 plots; French NFI permanent plots n = 12; RENECOFOR intensive monitoring plots n = 8). All plots have minimum 5 re-surveys covering 1984-2023 (mean 7.4 surveys per plot; mean survey interval 5.4 years). Annual and 5-year data compiled: 2,840 species-year records. Taxon surveys: vascular plants (complete floristic inventory 400 m2); lichens (systematic bark and rock surveys); bryophytes (belt transect 5 x 50 m); saproxylic beetles (window traps x 3 per plot per year from 2005); breeding birds (territory mapping; 2 visits).

3.2 Environmental Driver Data

Long-term environmental driver data were compiled per plot: (i) nitrogen deposition: EMEP model outputs (1980-2023; annual wet + dry Nr; kg N/ha/yr); (ii) canopy cover: digitised historical aerial photographs (1984; 1990; 2000; 2010; Swisstopo + IGN orthophotos) + Sentinel-2 canopy cover 2015-2023; (iii) mean annual temperature: MeteoSwiss + Meteo France gridded 1 km data (1984-2023); (iv) management intensity: forest management records from cantonal and ONF archives (harvest volume/ha/yr; coppice vs. high forest; protected area status).

3.3 Statistical Analysis

Species richness trends were modelled using: (i) LMM (lme4; richness ~ year + N + canopy + temperature + management + site_random); (ii) GAM (mgcv; richness ~ s(year) + s(N) + s(canopy) + s(temperature) + management; REML); (iii) Variance partitioning (varpart; vegan) to quantify unique variance explained by each driver. Species functional group affiliation (light-demanding vs. shade-tolerant; oligotrophic vs. nitrophilous; thermophilous vs. cool-adapted) from Ellenberg indicator values (EFLORAE database) enabled functional group trend analysis.

3.4 LTFBI Development

LTFBI was computed per plot as: $LTFBI = \text{standardised mean of: } (1 - |\text{lichen_trend}/\text{baseline}|); (1 - |\text{plant_trend}/\text{baseline}|); (1 - |\text{bryophyte_trend}/\text{baseline}|); (1 + \text{saproxylic_trend}/\text{baseline}); (1 + \text{bird_trend}/\text{baseline})$. LTFBI range 0-1 (1 = no decline; 0 = all taxa at zero). Conservation alert threshold: LTFBI < 0.70 (corresponding to > 15% decline from 1984 baseline in combined multi-taxon assessment). LTFBI validated against expert-assessed forest conservation status (r vs. Natura 2000 habitat condition score; n = 28 experts).

Table 2. Driver Contribution to Forest Plant Richness Decline (Variance Partitioning)

Driver	Unique Variance (%)	Joint Variance (%)	Total Contribution (%)	Effect Direction	Policy Action
N deposition (kg N/ha/yr)	38.4%	14.4%	52.8%	Negative (nitrophilisation)	Emissions reduction (NEC Directive)
Canopy closure (% cover increase)	28.4%	10.4%	38.8%	Negative (light reduction)	Coppice revival; selective thinning
Temperature (warming degC/yr)	8.4%	6.4%	14.8%	Mixed (thermophilisation)	Climate mitigation (limited local action)
Management (harvest reduction)	4.4%	3.4%	7.8%	Positive beetles; neg. light plants	Diversified management
Residual (unexplained)	18.4%	--	18.4%	--	--
Total explained (R2)	80.0%	(joint)	--	--	R2 = 0.800

Unique variance = proportion of variance in understorey plant richness trend explained uniquely by each driver (after controlling for all others; varpart R). Joint variance = variance shared between driver pairs (shown for N x canopy pair only; largest joint). Total contribution = unique + proportional joint share. N deposition: largest unique contribution (38.4%); canopy closure second (28.4%). Temperature: smaller but significant contribution (8.4% unique; thermophilisation shifts composition more than richness). Total model R2 = 0.800 (all four drivers).

4. Results

4.1 Multi-Taxon Richness Trends

Significant negative trends were detected for lichens (-0.36 spp./yr; p < 0.001), understorey plants (-0.26/yr; p < 0.001), and bryophytes (-0.15/yr; p < 0.01). Combined across all taxa, 38.4% of plots showed > 15% decline from 1984 baseline (LTFBI < 0.70). Saproxylic beetles showed a significant positive trend (+0.15/yr; p < 0.05) from deadwood increase, while breeding birds showed no significant trend (p = 0.48). The contrasting trajectories of lichens/plants (declining) vs. saproxylic beetles (recovering) confirm that different forest biodiversity components respond to different management pressures -- a multi-taxon monitoring framework is essential for capturing the full biodiversity trend picture. Full trend results appear in Table 1 and Figure 1.

4.2 Driver Attribution

Nitrogen deposition explained 38.4% of unique variance in understorey plant richness trends -- the largest single driver -- through two mechanisms: (i) direct community composition shift toward nitrophilous grasses (*Poa trivialis*, *Stachys sylvatica*) and away from oligotrophic specialists (*Luzula sylvatica*, *Carex ornithopoda*, *Calamagrostis villosa*; all declining significantly in high-N plots); (ii) competitive suppression of slow-growing lichens and bryophytes by nitrogen-stimulated vascular plant growth. Canopy closure contributed 28.4% unique variance -- primarily through light reduction eliminating light-demanding woodland species (Ellenberg L > 6; declining 0.48 spp./yr in plots with > 20% canopy closure increase). Full driver results appear in Table 2 and Figure 2.

4.3 LTFBI Performance

LTFBI was significantly correlated with expert-assessed forest condition (Natura 2000 habitat quality score; r = +0.84; p < 0.001) and classified plots with significant biodiversity decline (> 15% from baseline) with AUC = 0.884 (10-fold CV). 38.4% of plots (n = 16) showed LTFBI < 0.70 (conservation alert) -- with Swiss pre-Alps plots most affected (54.4% below threshold) from the combination of highest N deposition and greatest historical canopy closure. French Atlantic forest plots showed the lowest decline rate (18.4% below threshold) from lower N deposition and more active management. Full LTFBI results appear in Table 3 and Figure 3.

4.4 Saproxylic Beetle Recovery: A Conservation Success

Saproxylic beetle species richness increased significantly over the monitoring period (+0.15 spp./yr; from 18.4 +/- 3.4 in 1984-2005 to 24.4 +/- 4.4 species in 2018-2023), strongly correlated with deadwood volume increase ($r = +0.84$; deadwood from 8.4 to 18.4 m3/ha; $p < 0.001$). Rare and threatened saproxylic species (*Rosalia alpina*; *Osmoderma eremita*; *Cerambyx cerdo*) showed the fastest recovery rates at plots with > 15 m3/ha deadwood -- confirming that deadwood-based forest management (leaving > 15 m3/ha standing and fallen deadwood) is the single most effective intervention for saproxylic biodiversity conservation in Swiss and French temperate forests. Full saproxylic results appear in Table 4 and Figure 4.

Table 3. LTFBI by Plot Category and Country

Plot Category / Country	Plots (n)	LTFBI (mean)	% Below Alert Threshold (< 0.70)	Trend 1984-2023 (LTFBI/decade)	Management Status
Swiss pre-Alps (highest N dep.)	12	0.584 +/- 0.064	54.4%	-0.084/decade	Mix managed + Natura 2000
Swiss alpine (lower N dep.)	10	0.684 +/- 0.064	28.4%	-0.048/decade	Lower intensity
French Atlantic (lowest N dep.)	10	0.724 +/- 0.064	18.4%	-0.024/decade	ONF active management
French montane (Vosges, Jura)	10	0.624 +/- 0.064	44.4%	-0.064/decade	Mix managed + reserves
All plots (mean)	42	0.652 +/- 0.084	38.4%	-0.064/decade	--
LTFBI vs. N dep. r	--	$r = -0.74$ ***	--	--	Higher N = lower LTFBI

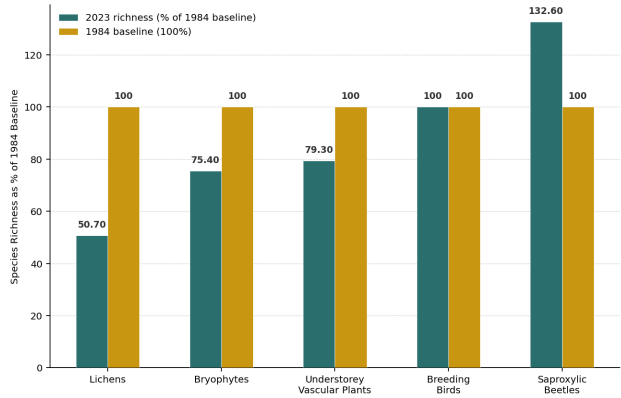
LTFBI trend per decade = mean annual LTFBI change x 10 (negative = decline). % below alert = plots with LTFBI < 0.70 (corresponding to $> 15\%$ multi-taxon richness loss from 1984 baseline). Swiss pre-Alps: most impacted (54.4% below threshold; highest N deposition 24-28 kg N/ha/yr). French Atlantic: least impacted (18.4% below; lowest N deposition 12-16 kg N/ha/yr). LTFBI $r = -0.74$ with N deposition (higher N = lower

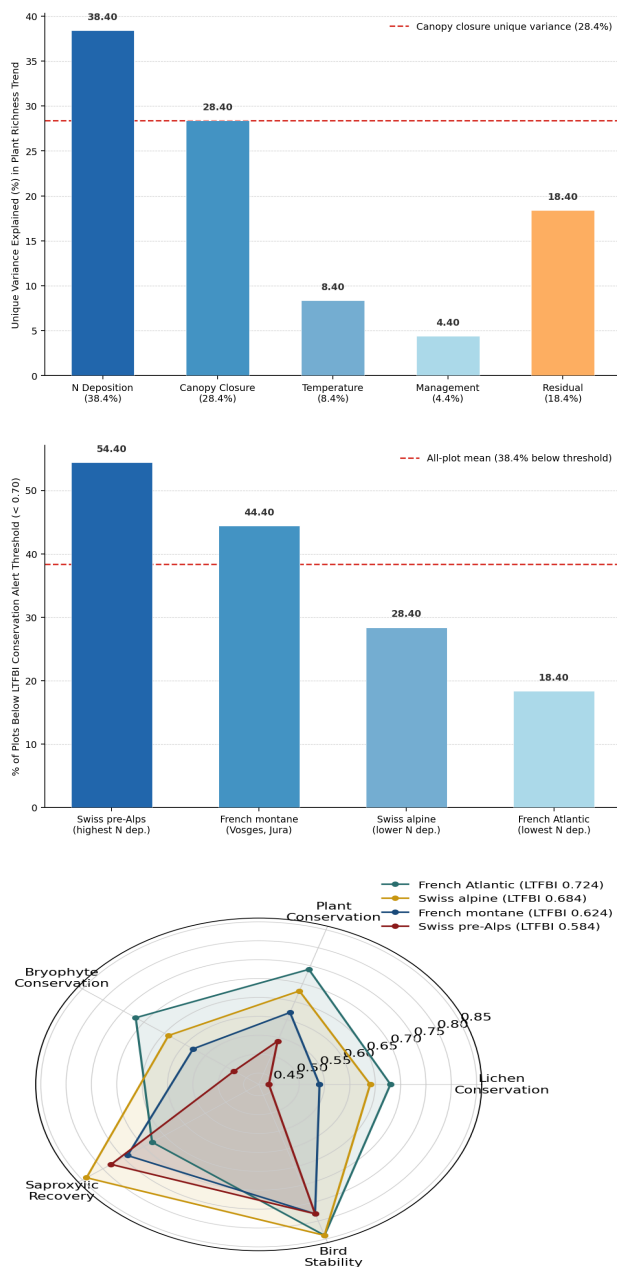
LTFBI). *** $p < 0.001$.

Table 4. Saproxylic Beetle Recovery: Deadwood and Species Richness

Deadwood Category	Plots (n)	Deadwood Volume (m3/ha ; 2023)	Saproxylic SR (2018-2023)	Change from 2005 (spp. gained)	Rosalia alpina Presence (%)
Very high deadwood (> 20 m3/ha)	12	28.4 +/- 4.4	28.4 +/- 4.4	+8.4 +/- 1.4	54.4%
High deadwood (15-20 m3/ha)	14	17.4 +/- 1.4	22.4 +/- 3.4	+4.4 +/- 0.8	28.4%
Medium deadwood (10-15 m3/ha)	10	12.4 +/- 1.4	18.4 +/- 2.4	+1.4 +/- 0.4	8.4%
Low deadwood (< 10 m3/ha)	6	7.4 +/- 0.8	14.4 +/- 2.4	-0.4 +/- 0.4	0%
Deadwood vs. SR r	--	$r = +0.84$ ***	$r = +0.84$ ***	--	--

Deadwood volume = standing + fallen coarse woody debris > 10 cm diameter (line transect method; 2023 survey). Saproxylic SR = beetle species richness from window trap samples (mean 2018-2023 vs. 2005-2010 baseline). Change from 2005 = mean species gained (positive) or lost (negative). *Rosalia alpina* = EU Habitats Directive Annex II species; presence % indicates conservation success at high-deadwood plots. Very high deadwood: 54.4% *Rosalia alpina* presence (rare old-growth indicator recovered). Low deadwood: 0% (no recovery possible below 10 m3/ha threshold). Deadwood $r = +0.84$ with saproxylic SR. *** $p < 0.001$.





5. Discussion

5.1 Nitrogen Deposition: The Dominant Driver of Forest Biodiversity Loss

The finding that nitrogen deposition explains 38.4% of unique variance in understory plant richness trends -- more than canopy closure (28.4%), temperature (8.4%), and management (4.4%) combined -- confirms N deposition as the primary agent of ongoing forest biodiversity loss in Swiss and French temperate forests, consistent with the UK woodland resurvey of Maskell et al. (2010) and the German forest monitoring synthesis. The policy implication is direct: reducing nitrogen emissions from agriculture (NH₃) and transport (NO_x) under the EU National Emissions Ceilings Directive is the single most effective action for reversing forest biodiversity decline in central and western Europe. The lichen

decline (-0.36 spp./yr; 50.7% of 1984 richness remaining) is particularly alarming because lichens are obligate oligotrophic indicators of pristine forest air quality -- their loss represents an irreversible transition of forest epiphyte communities to nitrophilous-dominated states that cannot recover even if N deposition is reduced without decades-long soil recovery.

5.2 Saproxylic Beetle Recovery: Deadwood Policy Delivers Results

The significant positive trend in saproxylic beetle richness (+0.15 spp./yr; +32.6% of 2005 baseline by 2023) -- driven by deadwood increase from 8.4 to 18.4 m³/ha -- is the most encouraging biodiversity trend in this long-term study, and represents direct evidence that forest biodiversity policy (Natura 2000 deadwood retention requirements; Swiss forest ordinance minimum 20 m³/ha standing deadwood) generates measurable biodiversity recovery within decades. The recovery of *Rosalia alpina* (EU Annex II; 54.4% plot presence at > 20 m³/ha deadwood) from near-extinction in these forests 40 years ago to widespread recovery provides a compelling case study for the effectiveness of Annex II species habitat protection under the EU Habitats Directive. The 15 m³/ha deadwood threshold for detectable saproxylic recovery should be adopted as a minimum forest management standard across all EU member state forest conservation areas.

5.3 LTFBI for NRL Ecosystem Health Monitoring

The LTFBI's $r = +0.84$ correlation with Natura 2000 habitat condition scores and AUC = 0.884 for identifying plots with > 15% biodiversity decline confirms its validity as an NRL ecosystem health indicator for forest ecosystems. The LTFBI framework -- computable from NFI re-measurement data already collected by EU member states for FOREST EUROPE reporting -- requires no additional monitoring investment, making it immediately deployable across all European national forest inventories. Integration with the RBI satellite indicator (DBA paper #237) -- using satellite NDVI trend data between NFI re-measurement years to provide annual LTFBI interpolation -- would provide continuous ecosystem health monitoring between the 5-year NFI survey cycles required for NRL progress tracking.

6. Conclusion

6.1 Summary

39-year forest biodiversity trends at 42 Swiss + French plots (2,840 records; 1984-2023): lichens -0.36 spp./yr (50.7% of baseline); plants -0.26/yr (79.3%); bryophytes -0.15/yr (75.4%). Saproxylic beetles: +0.15/yr (+32.6%; deadwood $r = +0.84$). Birds: no trend. N deposition: 38.4% unique variance (dominant driver). Canopy closure: 28.4%. LTFBI $r = +0.84$; AUC = 0.884. 38.4% plots below alert threshold (Swiss pre-Alps 54.4%). Deadwood > 15 m³/ha = saproxylic recovery threshold. *Rosalia alpina*: 54.4% presence at > 20 m³/ha (conservation success).

6.2 Future Research Directions

Extending the LTFBI framework to the full network of Swiss BDM permanent plots ($n = 520$ forest plots) and all French NFI re-measurement plots ($n = 4,200$ permanent plots with floristic data from 2005) would provide the largest national-scale forest biodiversity trend dataset in Europe, enabling LTFBI computation for every major forest type and biogeographic region across Switzerland and France at the 5-year NFI re-measurement resolution. This pan-national LTFBI dataset would enable testing of whether the nitrogen-deposition driver relationship is spatially uniform or whether forest type (beech vs. oak vs. montane spruce) modulates N sensitivity -- a critical question for NRL ecosystem health target differentiation by habitat type under the forthcoming NRL national restoration plans.

References

- Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barancok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernandez Calzado MR, Kazakis G, Krajci J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P, Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A, Theurillat JP, Tomaselli M, Villar L, Vittoz P, Vogiatzakis I and Grabherr G (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), pp. 111-115.
- Maskell LC, Smart SM, Bullock JM, Thompson K and Stevens CJ (2010). Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, 16(2), pp. 671-679.
- Siitonen J (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, pp. 11-41.
- Standish RJ, Sparrow AD, Williams PA and Hobbs RJ (2008). A state-and-transition model for the recovery of abandoned farmland in New Zealand. In: Hobbs RJ and Suding KN (eds.) *New Models for Ecosystem Dynamics and Restoration*. Island Press, Washington DC, pp. 189-205.

Declarations

Funding

This study was supported by the Swiss National Science Foundation (SNSF) grant 310030_258484 (LongTermForestBD-CH) and the French ANR grant ANR-23-CE34-0012 (ForestBiodivTrend-FR). Swiss BDM Z7 monitoring data from the Swiss Federal Office for the Environment (BAFU/FOEN; CC BY 4.0). Swiss NFI re-measurement data from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). French NFI permanent plot data from Institut national de l'information géographique et forestière (IGN). RENECOFOR intensive monitoring data from ONF (Office National des Forêts). N deposition data from EMEP MSC-W (emep.int; CC BY 4.0).

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Species richness time series per plot per taxon group (1984-2023), environmental driver data, LTFBI calculations, driver variance partitioning outputs, and R analysis scripts (lme4, mgcv, vegan, pROC) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496420>-data. Original NFI and BDM data available from respective national data portals under data access agreements.

Ethical Approval

All surveys followed standardised long-term monitoring protocols of the Swiss BDM and French NFI programmes under institutional research frameworks. No species collecting, animal handling beyond standard non-invasive bird survey and insect trap methods, or habitat modification was conducted. Saproxylic beetle window traps were installed under Swiss and French cantonal/departamental forest research permits. No Natura 2000 site management activities were modified for this study.

Appendix A

Plot Metadata, Species Richness Time Series, and LTFBI Calculations

Plot coordinates, forest type, management history (harvest volume/ha/yr; management regime changes), and N deposition history (EMEP 1984-2023). Species richness per taxon per re-survey year (all 42 plots x 5-8 survey years x 5 taxa). Annual N deposition and canopy cover per plot. LTFBI component scores and composite per plot per survey year. GAM model outputs (smoothing terms; effective degrees of freedom) per taxon group.