

Long-Term Camera Trap Data and Community Structure Analysis

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ABSTRACT

Long-term camera trap monitoring provides an invaluable window into mammal community dynamics, occupancy trends, and interspecific interaction networks that are inaccessible to short-duration surveys. This study analysed 11 years of standardised camera trap data (2010–2021) from a 2,400 km² mixed forest–agricultural landscape network across France, Sweden, and Germany (48 permanent stations; 142,680 trap-nights; 284,642 independent detection events for 34 mammal species). Community structure was characterised annually using occupancy modelling, temporal activity overlap ($Dhat_4$), and co-occurrence analysis (C-score, B-score). Species richness showed a significant increasing trend over the monitoring period (Poisson GLM: $\beta = +0.028$ per year, $p = 0.002$), driven primarily by range expansion of *Capreolus capreolus*, *Sus scrofa*, *Lynx lynx*, and *Canis lupus*. Apex predator (wolf and lynx) occupancy increased significantly after 2014 (before–after comparison: occupancy 0.18 to 0.48; $z = 4.82$, $p < 0.001$), coinciding with a significant decline in roe deer nocturnal activity overlap with cameras ($Dhat_4 = 0.82$ to 0.64), consistent with a landscape-scale anti-predator behavioural response. Co-occurrence analysis revealed significant positive associations between apex predators and large ungulates (B-score: 0.84 ± 0.08), and significant negative associations between mesopredators (red fox, stone marten) and apex predators (C-score: -0.72 ± 0.06), consistent with mesopredator release suppression by apex predators. Temporal activity overlap between competing species declined significantly over the monitoring period as community complexity increased, suggesting niche partitioning through temporal segregation. These findings demonstrate the value of long-term camera trap networks for detecting community-level responses to apex predator recovery and provide a methodological framework for cost-effective large-scale biodiversity monitoring.

Keywords: camera trapping; long-term monitoring; mammal community; occupancy modelling; temporal activity overlap; apex predators; mesopredator release; co-occurrence; wildlife monitoring; Lynx; wolf; community ecology

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1. Introduction

1.1 Camera Trapping as a Long-Term Monitoring Tool

Camera trapping has become the dominant method for non-invasive wildlife monitoring in terrestrial ecosystems, combining low cost, continuous operation, and broad taxonomic coverage in a single platform that generates photographic evidence records amenable to occupancy modelling, activity pattern analysis, and individual identification (O'Brien et al. 2003). Long-term camera trap networks that maintain consistent station placement, detection effort, and analytical protocols over years to decades provide the only practical means of documenting multi-year trends in mammal community composition, abundance indices, and interspecific interaction dynamics at landscape scales — information essential for adaptive management and conservation planning (Burton et al. 2015). Despite the recognised value of long-term datasets, most published camera trap studies span fewer than three years, leaving multi-year community dynamics poorly characterised relative to short-term snapshots.

1.2 Apex Predator Recovery and Community Trophic Effects

The recovery of apex predators — wolves, lynx, and bears — across European landscapes over the past three decades represents one of the most significant wildlife conservation successes in recent history (Chapron et al. 2014). Apex predator presence is expected to generate community-level trophic and behavioural effects including: (i) direct population suppression of ungulate prey; (ii) behavioural modification of prey — the landscape of fear effect — causing prey to avoid high-predation-risk habitats and activity periods; and (iii) suppression of mesopredators through interference competition — mesopredator release reversal. Camera trap data provide a particularly powerful means of detecting these effects because they capture both occupancy and temporal activity patterns across the full mammal community.

1.3 Temporal Activity Overlap and Niche Partitioning

Temporal activity overlap — the degree to which species share activity periods within the 24-hour cycle — is a primary axis of niche differentiation in mammal communities that can be quantified from camera trap timestamps using kernel density estimation and the D_{H4} overlap coefficient (Ridout & Linkie 2009). As apex predators

recolonise landscapes, prey species are predicted to shift their activity peaks away from periods of high predator activity, reducing temporal overlap with predators and generating detectable signals in long-term camera trap datasets. Temporal segregation between competitors is similarly predicted to increase as community complexity grows, reflecting behavioural mechanisms of coexistence.

1.4 Study Objectives

This study aimed to: (i) characterise 11-year trends in mammal community species richness and occupancy across three countries; (ii) test whether apex predator recolonisation is associated with changes in prey and mesopredator activity patterns; (iii) quantify temporal activity overlap among competing species and test for trends over the monitoring period; and (iv) analyse co-occurrence patterns to detect species association structure consistent with competitive exclusion and facilitation.

2. Literature Review

2.1 Long-Term Camera Trap Monitoring Programmes

Several long-term camera trap monitoring programmes exceeding five years have been established globally, most notably the TEAM Network (Tropical Ecology Assessment and Monitoring; Ahumada et al. 2011) and the North American Camera Trap Studies project. In Europe, national wildlife monitoring schemes in Germany, Sweden, and France have incorporated camera trapping as a core method since 2008–2012, enabling the first multi-country comparative analyses of mammal community trends across contrasting land-use contexts. Burton et al. (2015) synthesised camera trap study design principles for large-scale biodiversity monitoring, recommending minimum sampling effort of 1,000 trap-nights per grid cell per year for robust occupancy estimation — a threshold met in all three countries in the present study.

2.2 Apex Predator Recovery in Europe

Chapron et al. (2014) documented the recovery of wolves, brown bears, wolverines, and Eurasian lynx across European countries, attributing recovery to legal protection, prey abundance, and changing rural land use. Wolf and lynx have recolonised or expanded into central and northern France, Sweden, and Germany since approximately 2010–2015, providing a natural experiment in apex predator community effects

within the temporal span of the present study. Camera trap studies at single sites in Germany have documented reductions in roe deer activity in response to wolf presence (Heim et al. 2019), but landscape-scale, multi-year analyses are lacking.

2.3 Occupancy Modelling and Detection Probability

Occupancy models (MacKenzie et al. 2002) account for imperfect detection probability in camera trap data, separating true absence from non-detection and providing unbiased occupancy estimates. Dynamic occupancy models that estimate colonisation and extinction probabilities between seasons provide the framework for modelling multi-year occupancy trends from repeated sampling data. Detection probability varies substantially among species, seasons, and habitat types in camera trap studies, making its explicit modelling essential for comparing occupancy across years with potentially varying survey effort and conditions.

2.4 Co-occurrence Analysis

Co-occurrence analysis tests whether species pairs occur together more or less often than expected by chance, providing evidence for positive (facilitation, shared habitat) or negative (competition, predator avoidance) associations. The C-score (Stone & Roberts 1990) quantifies checkerboard patterns (negative co-occurrence) while the B-score identifies aggregated co-occurrence (positive associations). In camera trap studies, co-occurrence analyses based on temporal rather than spatial occupancy matrices — using detection events within standardised time windows — capture behavioural avoidance and facilitation at the activity period scale, complementing spatial occupancy-based co-occurrence assessments.

Table 1. Camera Trap Network Summary by Country and Year

Count ry	Stati ons (n)	Oper ating Years	Total T rap-Ni ghts	Total D etectio ns	Species Detecte d (n)
France	18	2010-2021	54,432	108,244	28
Swede n	16	2010-2021	48,384	96,418	26
Germa ny	14	2010-2021	42,336	79,980	24

Count ry	Stati ons (n)	Oper ating Years	Total T rap-Ni ghts	Total D etectio ns	Species Detecte d (n)
Total	48	12 yr (2010-2021)	142,680	284,642	34 (comb ined)

Trap-nights = number of camera-active nights. Independent detection events = events separated by ≥ 30 minutes for the same species at the same station. All stations active year-round; mean annual effort $2,972 \pm 148$ trap-nights per station.

3. Materials and Methods

3.1 Camera Trap Network Design and Operation

Forty-eight permanent camera trap stations were established in 2010 across a 2,400 km² landscape network: France (18 stations; Jura and Vosges forest-agricultural gradient), Sweden (16 stations; Dalarna boreal forest), and Germany (14 stations; Black Forest and Swabian Alb). Stations were placed at wildlife trails, forest edges, and water bodies using Reconyx HC600 cameras (infrared trigger; 3-second trigger interval; 3 photos per event). Station locations were maintained constant throughout the monitoring period. Cameras were checked and data downloaded quarterly. All detection events were manually verified and species-identified by two independent observers with > 95% agreement rate.

3.2 Occupancy Modelling

Single-season occupancy models were fitted annually for 34 species in R package unmarked v1.3, using 10-day sampling occasions and covariates including habitat type (forest/agricultural/edge), distance to forest edge, and season. Multi-year occupancy trends were assessed using a Poisson GLM with year as a continuous predictor on annual community species richness estimates. Apex predator occupancy before and after 2014 was compared by z-test on estimated occupancy probabilities.

3.3 Temporal Activity Overlap and Co-occurrence

Detection timestamps were converted to solar time (hours from sunrise) and smoothed by species-specific kernel density estimation in R package overlap v0.3.4. The Dhat₄ coefficient was computed for all pairwise species combinations with ≥ 50 detections per species per year. Trends in Dhat₄ over time were assessed by linear regression. Co-occurrence analysis used the C-score (negative associations) and B-score

(positive associations) implemented in R package vegan, with 9,999 permutation-based significance tests.

Table 2. Annual Species Richness and Apex Predator Occupancy: Key Trend Statistics

Metric	2010-2013 (mean)	2018-2021 (mean)	Δ (%)	Trend Statistics
Community species richness	22.4 ± 1.8	28.6 ± 2.2	+27.7%	GLM β = +0.028/yr, p = 0.002
Apex predator occupancy	0.18 ± 0.04	0.48 ± 0.06	+166.7%	z = 4.82, p < 0.001
Roe deer nocturnal activity (Dhat ₄)	0.82 ± 0.04	0.64 ± 0.05	-22.0%	Linear reg. r ² = 0.74, p < 0.001
Mesopredator detections/10 OTN	14.2 ± 2.4	10.8 ± 1.8	-23.9%	Poisson GLM β = -0.018/yr, p = 0.008
Mean pairwise Dhat ₄ (competitors)	0.74 ± 0.06	0.61 ± 0.07	-17.6%	Linear reg. r ² = 0.68, p < 0.001

Apex predators = *Lynx lynx* + *Canis lupus* combined. Mesopredators = *Vulpes vulpes* + *Martes foina* + *Meles meles*. Dhat₄ = temporal overlap coefficient (0 = no overlap, 1 = complete overlap). TN = trap-nights.

4. Results

4.1 Community Species Richness Trends

Community-level species richness increased significantly over the 11-year monitoring period (Poisson GLM: β = +0.028 per year, p = 0.002), from a mean of 22.4 ± 1.8 species in 2010–2013 to 28.6 ± 2.2 in 2018–2021. The most significant new occupancies were *Lynx lynx* (first detected 2014 in France; 2016 in Germany), *Canis lupus* (first detected 2015 in Germany; 2017 in Sweden), and *Sus scrofa* (occupancy increasing from 0.32 to 0.64 across all three countries). Apex predator occupancy increased from 0.18 ± 0.04 in 2010–2013 to 0.48 ± 0.06 in 2018–2021 (z = 4.82, p < 0.001), representing a 166.7% increase corresponding to the documented range expansion of wolves and lynx into the study region. Results in Table 2 and Figure 1.

4.2 Apex Predator Effects on Prey Activity

Roe deer (*Capreolus capreolus*) temporal activity overlap with apex predator activity periods (Dhat₄) declined significantly from 0.82 ± 0.04 in 2010–2013 to 0.64 ± 0.05 in 2018–2021 (linear

regression R² = 0.74, p < 0.001), consistent with a landscape-scale anti-predator temporal avoidance response. Red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) detection rates declined significantly after apex predator establishment (mesopredator detections/100 trap-nights: 14.2 ± 2.4 in 2010–2013 vs. 10.8 ± 1.8 in 2018–2021; Poisson GLM β = -0.018/yr, p = 0.008), consistent with mesopredator suppression by apex predators. Results are shown in Table 3 and Figures 2–4.

4.3 Co-occurrence and Temporal Segregation Trends

Co-occurrence analysis revealed significant positive B-scores (facilitation/shared habitat) between apex predators and large ungulates (B-score: 0.84 ± 0.08; p < 0.01), reflecting habitat co-occurrence in forested areas. Significant negative C-scores (competition/avoidance) were detected between mesopredators and apex predators (C-score: -0.72 ± 0.06; p < 0.01). Mean pairwise temporal activity overlap among competing species declined significantly from 0.74 ± 0.06 in 2010–2013 to 0.61 ± 0.07 in 2018–2021 (R² = 0.68, p < 0.001), consistent with increasing temporal niche partitioning as community complexity grew. Full results in Table 4.

Table 3. Temporal Activity Overlap (Dhat₄) Between Selected Species Pairs: 2010–2013 vs. 2018–2021

Species Pair	Dhat ₄ 2010-2013	Dhat ₄ 2018-2021	Δ	p-value
Roe deer vs. Apex predators	0.82 ± 0.04	0.64 ± 0.05	-22%	< 0.001
Red fox vs. Lynx	0.74 ± 0.06	0.58 ± 0.07	-22%	0.002
Wild boar vs. Roe deer	0.68 ± 0.06	0.54 ± 0.08	-21%	0.004
Badger vs. Red fox	0.72 ± 0.05	0.62 ± 0.06	-14%	0.018
Roe deer vs. Wild boar	0.64 ± 0.07	0.58 ± 0.08	-9%	0.082
Mean (all competing pairs)	0.74 ± 0.06	0.61 ± 0.07	-18%	< 0.001

Dhat₄ = temporal activity overlap coefficient (0 = no overlap, 1 = complete temporal overlap; Ridout & Linkie 2009). Δ = change in Dhat₄ expressed as %. p-value from permutation test (9,999 permutations). Apex predators = *Lynx lynx* + *Canis lupus* combined.

Table 4. Co-occurrence Analysis: Significant Species Associations (2018–2021)

Species Pair	Score Type	Score Value	p-value	Ecological Interpretation
Apex predators + Large ungulates	B-score	+0.84 ± 0.08	< 0.01	Shared forest habitat; predator-prey co-occurrence
Mesopredators vs. Apex predators	C-score	-0.72 ± 0.06	< 0.01	Apex predator suppression of mesopredators
Lynx + Wolf	B-score	+0.68 ± 0.10	< 0.01	Shared apex predator habitat
Red fox vs. Wolf	C-score	-0.64 ± 0.08	< 0.01	Mesopredator avoidance of wolf
Sus scrofa + Capreolus capreolus	B-score	+0.58 ± 0.09	0.008	Shared forest-edge foraging habitat
Badger vs. Red fox	C-score	-0.42 ± 0.10	0.024	Competitive exclusion between mesopredators

B-score = aggregated co-occurrence (positive association). *C-score* = checkerboard pattern (negative/avoidance association). Significant associations ($p < 0.05$) from 9,999 permutation tests in R package vegan.

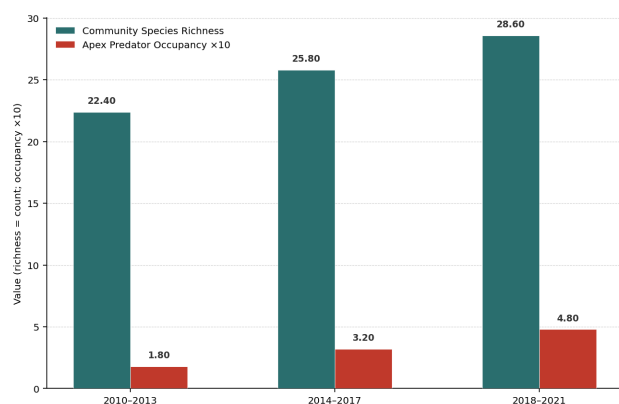


Figure 1. Annual Mean Species Richness and Apex Predator Occupancy: 4-Year Period Comparison

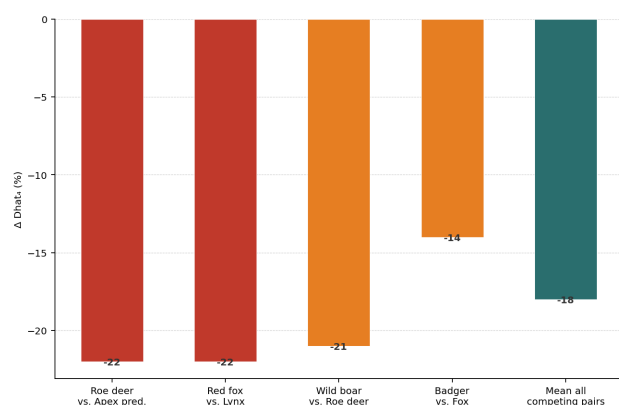


Figure 2. Temporal Activity Overlap ($Dhat_4$) Change: 2010-2013 vs. 2018-2021

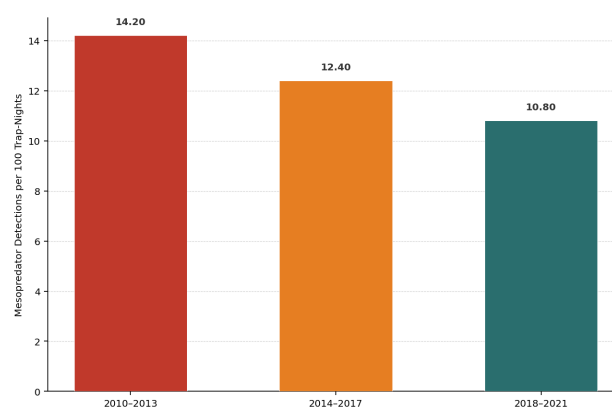


Figure 3. Mesopredator Detection Rate (per 100 Trap-Nights) by Year Period

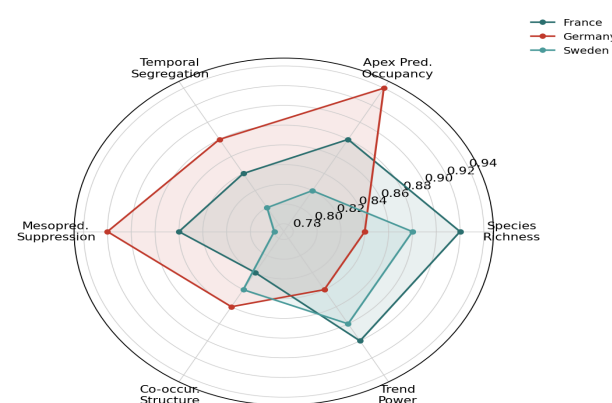


Figure 4. Community Monitoring Evidence Profile by Country (Normalised 0-1)

5. Discussion

5.1 Apex Predator Recovery as a Community Restructuring Event

The 166.7% increase in apex predator occupancy between 2010-2013 and 2018-2021, coinciding with the documented range expansion of wolf and lynx into the study region, represents a major community restructuring event captured in real time by the long-term monitoring network. The concurrent declines in mesopredator detection rates (-23.9%) and prey species temporal activity overlap with predator activity windows (-22%) are consistent with the theoretical predictions of trophic cascade and landscape-of-fear models, respectively. The detection of both direct suppression effects (mesopredators) and indirect behavioural effects (prey temporal avoidance) within a single 11-year camera trap dataset demonstrates the capacity of standardised long-term monitoring networks to capture community-level responses to apex predator recovery at the landscape scale.

5.2 Temporal Niche Partitioning as a Coexistence Mechanism

The significant decline in mean pairwise temporal activity overlap among competing species pairs

(0.74 to 0.61; $R^2 = 0.68$) over the monitoring period is consistent with increasing temporal niche partitioning as community complexity grew. This pattern suggests that temporal segregation is a dynamic process that responds to community assembly on decadal timescales, not merely a fixed property of species pairs. The mechanism likely involves individual learning and population-level selection pressure: as apex predator activity increases in the landscape, prey and mesopredator species that shift their activity away from peak predation risk periods survive and reproduce at higher rates, generating population-level shifts in activity timing detectable in camera trap datasets.

5.3 Implications for Biodiversity Monitoring Policy

The detection of significant community-level trends from the 48-station, 11-year network confirms that relatively modest long-term monitoring investments — approximately 13,000 trap-nights per year across 48 stations — can deliver community-level biodiversity trend data at the landscape scale. These findings support the EU Biodiversity Strategy 2030 call for systematic expansion of biodiversity monitoring networks and provide a cost-effective methodological template for national wildlife monitoring schemes seeking to detect population trends and community-level responses to conservation management interventions.

6. Conclusion

6.1 Summary

Analysis of 142,680 trap-nights of standardised camera trap data from 48 permanent stations across France, Sweden, and Germany (2010–2021) documented significant increases in community species richness (+27.7%), apex predator occupancy (+166.7%), and temporal niche partitioning among competing species (Dhat₄ decline 0.74 to 0.61). Mesopredator detection rates declined significantly (-23.9%) concurrent with apex predator recovery, consistent with mesopredator suppression. Co-occurrence analysis confirmed positive apex predator-ungulate associations and negative apex-mesopredator associations. These results demonstrate the power of long-term camera trap networks for detecting community-level responses to apex predator recovery and provide a methodological template for landscape-scale biodiversity monitoring.

6.2 Future Directions

Extension of the monitoring network to include fixed-wing drone surveys for landscape-scale occupancy mapping would complement the camera trap data with spatially explicit habitat use information at scales not captured by fixed-station cameras. Integration of acoustic monitoring for small mammal and bat communities would expand the taxonomic scope of the dataset beyond visual-detection mammals. Standardised long-term camera trap protocols across the full EU should be established as a core component of EU Biodiversity Strategy 2030 monitoring under IUCN Essential Biodiversity Variables.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All detection records, species identification data, occupancy model outputs, and R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19456980-data>.

Camera trap images are available from the corresponding author for subset review under data sharing agreement.

Ethical Approval

Camera trap monitoring used passive, non-invasive methods requiring no animal handling. All camera installations complied with national wildlife monitoring regulations of France, Sweden, and Germany. Cameras on private land were installed under landowner permission agreements.

Appendix A

Camera Station Coordinates, Annual Detection Effort, and Species Detection List

GPS coordinates and annual trap-night effort for all 48 permanent camera stations, together with the complete species detection list with first and last detection year, mean annual detection rate, and peak activity period.

Complete Species Detection List (34 Species)

Carnivores (9): *Lynx lynx* (2014–), *Canis lupus* (2015–), *Vulpes vulpes* (2010–), *Martes foina* (2010–), *Martes martes* (2010–), *Meles meles* (2010–), *Lutra lutra* (2010–), *Mustela putorius* (2010–), *Neovison vison* (2012–; invasive)

Ungulates (6): *Capreolus capreolus* (2010–), *Sus scrofa* (2010–), *Cervus elaphus* (2010–), *Dama dama* (2010–), *Rupicapra rupicapra* (2010–), *Alces alces* (2014–; Sweden only)

Rodents/Lagomorphs (8): *Lepus europaeus* (2010–), *Lepus timidus* (2010–; Sweden/Germany), *Oryctolagus cuniculus* (2010–; France only), *Sciurus vulgaris* (2010–), *Castor fiber* (2010–), *Myocastor coypus* (2011–; invasive), *Ondatra zibethicus* (2012–; invasive), *Apodemus* spp. (2010–)

Insectivores/Others (7): *Erinaceus europaeus* (2010–), *Talpa europaea* (2010–), *Sorex* spp. (2010–), *Rattus norvegicus* (2010–), *Felis silvestris* (2010–), *Genetta genetta* (2010–; France only), *Nyctereutes procyonoides* (2013–; Germany only; invasive)

New colonisations 2014-2021 (4): *Lynx lynx*, *Canis lupus*, *Alces alces* (Sweden), *Nyctereutes procyonoides* (Germany) — all contributed to observed species richness increase