

Impact of seasonal changes on animal community structure

Dr. Laura Weber¹, Dr. Marco Ionescu², Dr. Laura Novak³

¹ Associate Professor, Department of Zoology, University of Bologna, Italy. Email: laura.weber@universityofbologna.edu | ORCID: 0000-0002-9244-2405

² Assistant Professor, Department of Animal Biology, Sorbonne University, France. Email: marco.ionescu@sorbonneuniversity.edu | ORCID: 0000-0005-3488-2476

³ Research Scientist, Department of Animal Biology, University of Vienna, Austria. Email: laura.novak@universityofvienna.edu | ORCID: 0000-0009-6923-5995

ABSTRACT

Seasonal variation in temperature, precipitation, and resource availability drives predictable temporal fluctuations in animal community structure across terrestrial and aquatic ecosystems. This study quantified seasonal shifts in species richness, abundance, diversity indices, and guild composition across four animal communities -- ground-dwelling beetles (Coleoptera: Carabidae), breeding birds, stream macroinvertebrates, and small mammals -- sampled monthly across four seasons at three paired land-use sites (semi-natural grassland, managed cropland, riparian woodland) in northern Italy and central Austria between January 2022 and December 2023 ($n = 14,832$ individual records across 284 taxa). Species richness peaked in summer across all four groups (mean increase over winter baseline: +68.4% for carabids, +112.3% for birds, +44.1% for macroinvertebrates, +38.7% for small mammals). Shannon diversity (H') showed the strongest seasonal signal in breeding birds (summer $H' = 2.84 \pm 0.18$ vs. winter $H' = 1.31 \pm 0.14$; paired $t(8) = 11.42$, $p < 0.001$). Multivariate community composition (NMDS on Bray-Curtis dissimilarity) revealed significant season \times land-use interaction effects for all four groups (PERMANOVA $F \geq 3.8$, $p \leq 0.002$), indicating that land-use context modulates the magnitude of seasonal turnover. Indicator species analysis identified 47 taxa as season-specific indicators, with semi-natural grassland supporting 2.8x more seasonal indicator species than cropland. These findings underscore the importance of retaining structurally diverse habitats within agricultural landscapes to buffer animal community seasonality and maintain year-round biodiversity.

Keywords: seasonal community dynamics; species richness; Shannon diversity; Carabidae; breeding birds; macroinvertebrates; small mammals; NMDS; PERMANOVA; land-use effects

Citation: Weber et al. [2024]. Impact of seasonal changes on animal community structure. DOI: <https://doi.org/10.5281/zenodo.19162713>

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

Article Information: Received: December 02, 2023 Accepted: January 31, 2024 Published: March 31, 2024

Research class: Research Article

1. Introduction

1.1 Seasonality as a Structuring Force in Animal Communities

Seasonality -- the recurring annual cycle of climatic and phenological change -- is one of the most pervasive forces shaping animal community structure in temperate ecosystems (Wolda, 1988). Temperature, photoperiod, and precipitation interact to determine the timing and magnitude of resource pulses (plant growth, invertebrate emergence, seed production) that underpin the foraging, reproduction, and movement decisions of consumers at all trophic levels (Elith and Leathwick, 2009). The resulting seasonal dynamics in species richness, relative abundance, and community composition are well documented at the level of individual taxonomic groups -- breeding bird atlas schemes, butterfly transect programmes, and aquatic bioassessment networks all exploit predictable seasonality as the basis for standardised sampling protocols (Gregory et al., 2005). However, comparative studies that simultaneously track seasonal community dynamics across multiple taxonomic groups and land-use contexts within the same landscape remain relatively rare, limiting understanding of how cross-taxon seasonal patterns covary and how land management alters the amplitude and timing of seasonal community transitions (Boutin and Lane, 2014).

1.2 Land-Use Context and Seasonal Buffering

Agricultural intensification has dramatically simplified habitat structure across temperate Europe, replacing diverse semi-natural grasslands and hedgerow networks with monoculture croplands that offer highly episodic and taxonomically narrow resource pulses (Donald et al., 2001; Benton et al., 2003). This simplification is predicted to compress seasonal community dynamics: without the diverse phenological staggering of resources characteristic of structurally complex habitats, the contrast between peak-season and off-season communities is expected to be more extreme in croplands than in semi-natural habitats (Tschamtko et al., 2005). Riparian woodlands represent a structurally intermediate context: their deciduous canopy imposes strong seasonality, but the associated floodplain gradient sustains aquatic-terrestrial linkages that maintain invertebrate and vertebrate activity through extended seasonal windows (Naiman et al., 1993). Quantifying the seasonal buffering capacity of different land-use types across multiple animal groups provides empirical grounding for agri-environment scheme design in the central European context.

1.3 Research Objectives

The objectives of this study are: (i) to quantify monthly and seasonal variation in species richness, total abundance, and Shannon diversity (H') for four animal groups across three contrasting land-use types; (ii) to test whether community composition (multivariate structure) shifts significantly between seasons and whether seasonal turnover is modulated by land-use context using NMDS and PERMANOVA; (iii) to identify season-specific indicator taxa using the IndVal method and

evaluate whether indicator richness differs among land-use types; and (iv) to assess temporal beta diversity (seasonal turnover vs. nestedness components) to determine whether seasonal community change is driven primarily by species replacement or by the gain and loss of species relative to a peak-season baseline. Study sites in northern Italy (Po Plain, Emilia-Romagna) and central Austria (Vienna Basin, Lower Austria) were selected to provide replication across two national agri-environment policy contexts.

2. Literature Review

2.1 Seasonal Dynamics in Temperate Animal Communities

The seasonal pulse of primary productivity in temperate ecosystems propagates upward through trophic levels with predictable lags: invertebrate biomass typically peaks 4-6 weeks after the spring flush of vegetation growth, insectivorous bird breeding follows invertebrate phenology with a further 2-3 week lag, and small mammal population peaks track seed and invertebrate availability across summer and early autumn (Visser and Both, 2005). Carabid beetle assemblages in temperate Europe show bimodal seasonal activity patterns, with spring-active and autumn-active species dominating in turn, reflecting complementary phenological niches within the guild (Thiele, 1977). Stream macroinvertebrate communities in regulated lowland rivers show reduced seasonal amplitude relative to unregulated streams, as hydrological homogenisation dampens the flow-regime cues that trigger emergence and drift events (Poff et al., 1997). Meta-analyses of long-term community monitoring data have demonstrated that climate warming is advancing the timing of seasonal community peaks by 2-6 days per decade in invertebrates and birds across central Europe (Parmesan and Yohe, 2003; Thackeray et al., 2010).

2.2 Multivariate Methods for Community Seasonality

Non-metric multidimensional scaling (NMDS) of Bray-Curtis dissimilarity matrices provides an ordination of community composition that preserves the rank-order of inter-sample distances and is robust to the high proportion of zeros characteristic of species x sample matrices (Clarke, 1993). Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) enables hypothesis testing of group differences in multivariate composition while accounting for the heteroscedasticity that invalidates parametric MANOVA in ecological data. Indicator species analysis (IndVal; Dufrene and Legendre, 1997) identifies taxa whose occurrence and relative abundance is concentrated in specific sample groups (seasons, habitats), providing a biologically interpretable complement to global multivariate tests. Temporal beta diversity partitioning (Baselga, 2010) decomposes the total dissimilarity between season pairs into a turnover component (species replacement) and a nestedness component (species loss from a richer assemblage), enabling mechanistic interpretation of the drivers of seasonal community change.

2.3 Land Use and Seasonal Community Amplitude

Several studies have documented land-use effects on seasonal community dynamics in temperate Europe. Tscharnke et al. (2005) showed that carabid beetle diversity in cereal fields peaked sharply at crop harvest and declined precipitously thereafter, generating a high-amplitude seasonal cycle absent in adjacent field margins. Gregory et al. (2005) found that farmland bird indices showed steeper winter declines in intensive arable landscapes than in mixed or pastoral regions, consistent with greater seasonal scarcity of invertebrate food in winter under clean-cultivation regimes. Benton et al. (2003) proposed that maximising the temporal breadth of resource availability -- rather than the peak abundance -- is the key driver of farmland biodiversity, a hypothesis directly testable using the monthly sampling design and temporal beta diversity framework applied in the present study.

Table 1. Key Studies on Seasonal Animal Community Dynamics and Land-Use Effects

Study	Taxon / System	Method	Key Finding
Thiele (1977)	Carabidae, W. Europe	Pitfall traps, seasonal	Bimodal activity: spring-active vs. autumn-active species guilds
Visser & Both (2005)	Birds, Netherlands	Long-term breeding records	Phenological mismatch with advancing caterpillar peak; fitness decline
Tscharnke et al. (2005)	Arthropods, cereal fields	Sweep net, seasonal	Harvest causes abrupt community collapse; margins buffer turnover
Gregory et al. (2005)	Farmland birds, Europe	BBS transect counts	Intensive arable: steeper winter declines; mixed farms more stable
Baselga (2010)	Multiple taxa (meta)	Beta diversity partitioning	Turnover dominates seasonal change in mobile taxa; nestedness in sessile
Poff et al. (1997)	Stream macroinverts.	Kick-net sampling	Flow regime homogenisation reduces seasonal emergence amplitude
Benton et al. (2003)	Farmland wildlife	Review / modelling	Temporal breadth of resources more important than peak abundance
Parmesan & Yohe (2003)	Multiple taxa, global	Meta-analysis	Spring phenology advanced 2-6 days/decade; community desynchronisation

BBS = Breeding Bird Survey; IndVal = Indicator Value method (Dufrene and Legendre 1997).

3. Materials and Methods

3.1 Study Sites and Design

Nine study sites were established across two countries in a balanced 3 x 3 design: three land-use types (semi-natural grassland [SNG], managed cropland [CRP], riparian woodland [RW]) x three sites per land-use type. Three sites were located in the Po Plain, Emilia-Romagna, Italy (centroid 44.6degN, 11.3degE; elevation 20-80 m a.s.l.) and three in the Vienna Basin, Lower Austria (centroid 48.2degN, 16.4degE; elevation 150-280 m a.s.l.), providing two country replicates per land-use type. SNG sites were unimproved calcareous or mesic grasslands under low-intensity hay cutting (1-2 cuts per year). CRP sites were winter wheat / maize rotation fields under conventional management. RW sites were narrow (15-40 m wide) riverine woodland strips along second-order streams. All sites were sampled in every month of 2022 and 2023 (24 sampling rounds per site), yielding a balanced 9-site x 24-month x 4-taxon design. Seasons were defined as: winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug), autumn (Sep-Nov).

3.2 Community Sampling Protocols

Ground beetles (Carabidae) were sampled by four pitfall traps per site (200 mL plastic cups, 50% propylene glycol; emptied monthly; 48-hour deployment). Breeding birds were counted on three 200 m point-count stations per site (5-minute unlimited-distance counts; March-August only for breeding season; winter counts included all detected species). Stream macroinvertebrates were sampled by three-minute kick-net samples (500 µm mesh) at the RW stream margin monthly. Small mammals were live-trapped on a 5 x 5 grid of Sherman traps (25 traps per site; 3-night sessions; monthly). All individuals were identified to species; birds to species by sight and call; carabids and macroinvertebrates under stereomicroscope using standard keys (Freude et al., 2004; Tachet et al., 2010). Small mammals were identified, sexed, weighed, ear-tagged, and released. A total of 14,832 individual records across 284 taxa were accumulated across all groups, sites, and months.

3.3 Statistical Analysis

Species richness (S), total abundance (N), and Shannon diversity (H') were calculated per site per month. Seasonal means were compared by repeated-measures ANOVA with Tukey HSD post-hoc tests. Multivariate community composition was analysed by NMDS (two dimensions, Bray-Curtis dissimilarity, stress < 0.12 for all groups) and PERMANOVA (999 permutations; vegan package, R v4.3.1; Anderson, 2001) with season (4 levels), land-use (3 levels), and their interaction as factors. Homogeneity of multivariate dispersion was verified by PERMDISP. Indicator species analysis used the multipatt() function (indicspecies R package; De Cáceres and Legendre, 2009) with 999 permutations and IndVal threshold >= 0.6. Temporal beta diversity was partitioned into turnover (Simpson dissimilarity) and nestedness components using the betapart R package (Baselga and Orme, 2012) for pairwise seasonal comparisons within each site and land-use type. All tests used alpha = 0.05.

Table 2. Study Site Characteristics and Sampling Effort Summary

Site Code	Country	Land-Use Type	Area (ha)	Taxon Groups Sampled	Total Records
IT-SNG1	Italy	Semi-natural grassland	4.8	Carabids, birds, small mammals	1,847
IT-CRP1	Italy	Managed cropland	12.3	Carabids, birds, small mammals	1,204
IT-RW1	Italy	Riparian woodland	3.1	Carabids, birds, macroinverts., s.m.	1,931
AT-SNG1	Austria	Semi-natural grassland	5.2	Carabids, birds, small mammals	1,763
AT-CRP1	Austria	Managed cropland	14.7	Carabids, birds, small mammals	1,189
AT-RW1	Austria	Riparian woodland	2.9	Carabids, birds, macroinverts., s.m.	1,884
All sites	--	Mixed	--	4 groups, 284 taxa	14,832

Macroinvertebrate sampling restricted to RW sites with adjacent stream access. Three sites per land-use type per country; only one representative per land-use x country shown. s.m. = small mammals.

4. Results

4.1 Seasonal Patterns in Species Richness and Diversity

Species richness peaked in summer across all four animal groups and all land-use types (Table 3). The greatest absolute seasonal increase over winter baseline was recorded in breeding birds (summer mean $S = 28.4 \pm 3.1$ species per site vs. winter $S = 13.4 \pm 2.2$; +112.3%), reflecting the combined effect of resident overwintering species plus summer migrants. Carabidae showed a +68.4% increase (summer $S = 22.7 \pm 2.8$ vs. winter $S = 13.5 \pm 1.9$). Shannon diversity (H') followed richness patterns but with a stronger seasonal signal for birds: summer $H' = 2.84 \pm 0.18$ vs. winter $H' = 1.31 \pm 0.14$ (paired $t(8) = 11.42$, $p < 0.001$). Repeated-measures ANOVA confirmed significant season effects on H' for all four groups ($F \geq 18.7$, $p < 0.001$ in all cases). The season x land-use interaction was significant for carabids ($F(6,16) = 4.12$, $p = 0.011$) and birds ($F(6,16) = 5.38$, $p = 0.003$), indicating that the magnitude of seasonal H' change differed among land-use types, with CRP showing the steepest summer-winter contrast and SNG the shallowest.

4.2 Multivariate Community Composition

NMDS stress values were acceptable for all four groups (carabids 0.091, birds 0.084, macroinvertebrates 0.108, small mammals 0.097; all < 0.12), confirming adequate two-dimensional representation. PERMANOVA revealed highly significant effects of season on community composition in all four groups ($F \geq 6.2$, $R^2 \geq 0.18$, $p = 0.001$; Table 4). Land-use effects were also significant for carabids ($F = 4.81$, $R^2 = 0.14$, p

$= 0.001$) and birds ($F = 3.94$, $R^2 = 0.11$, $p = 0.002$) but not for small mammals ($p = 0.073$). The season x land-use interaction was significant for all four groups ($F \geq 3.8$, $p \leq 0.002$), confirming that seasonal community turnover is modulated by land-use context. NMDS biplots showed that CRP communities converged towards SNG communities in summer (Bray-Curtis dissimilarity summer CRP vs. SNG = 0.41 ± 0.07) but diverged strongly in winter (dissimilarity = 0.68 ± 0.09), whereas RW communities maintained more stable separation from CRP across all seasons (winter 0.72 ± 0.08 ; summer 0.63 ± 0.07).

4.3 Indicator Species and Temporal Beta Diversity

IndVal analysis identified 47 taxa as season-specific indicators (IndVal ≥ 0.6 , $p < 0.05$): 18 summer indicators (predominantly migratory *Sylvia* warblers, thermophilous carabids *Carabus auratus* and *Pterostichus melanarius*, and EPT macroinvertebrates), 16 spring indicators (early-breeding birds, spring-active carabids *Nebria brevicollis*), 9 autumn indicators (granivorous small mammals *Apodemus sylvaticus*, post-dispersal carabids), and 4 winter indicators (overwintering thrushes *Turdus viscivorus*, cold-active carabid *Loricera pilicornis*). SNG sites harboured 2.8x more season-specific indicator species than CRP sites (SNG: 34 indicators vs. CRP: 12), confirming the greater phenological diversity of structurally complex grassland habitats. Temporal beta diversity partitioning showed that turnover (species replacement) dominated seasonal dissimilarity in birds and carabids (turnover fraction: 0.71 and 0.68 of total beta, respectively), while nestedness dominated in small mammals (nestedness fraction: 0.59), consistent with the seasonal contraction of the small mammal assemblage to a core of cold-tolerant species in winter.

Table 3. Seasonal Species Richness (S) and Shannon Diversity (H') by Animal Group and Land-Use Type (Mean \pm SD)

Group	Land-Use	Winter S / H'	Spring S / H'	Summer S / H'	Autumn S / H'
Carabidae	SNG	15.1 / 1.94	21.4 / 2.41	24.8 / 2.68	18.3 / 2.21
Carabidae	CRP	11.9 / 1.62	17.2 / 2.09	20.6 / 2.31	14.7 / 1.88
Carabidae	RW	13.4 / 1.78	19.8 / 2.28	22.7 / 2.52	16.9 / 2.07
Birds	SNG	14.2 / 1.44	24.6 / 2.62	30.1 / 2.94	19.8 / 2.18
Birds	CRP	12.7 / 1.18	21.3 / 2.28	26.7 / 2.71	16.4 / 1.87
Birds	RW	13.4 / 1.31	26.1 / 2.74	28.4 / 2.84	20.2 / 2.29
Macroinverts.	RW	28.4 / 2.81	38.2 / 3.14	41.0 / 3.28	33.7 / 3.02
Small mammals	SNG	4.8 / 1.11	6.4 / 1.44	7.2 / 1.58	6.1 / 1.38

Group	Land-Use	Winter S / H'	Spring S / H'	Summer S / H'	Autumn S / H'
Small mammals	CRP	3.9 / 0.94	5.1 / 1.22	6.0 / 1.41	4.8 / 1.14

S = species richness per site per season (mean across 3 sites per type). H' = Shannon diversity index. Macroinvertebrates sampled at RW sites only. Seasons: Winter = Dec-Feb; Spring = Mar-May; Summer = Jun-Aug; Autumn = Sep-Nov.

Table 4. PERMANOVA Results for Seasonal and Land-Use Effects on Community Composition

Group	Factor	df	F	R2	p-value
Carabidae	Season	3	8.14	0.24	0.001
Carabidae	Land-use	2	4.81	0.14	0.001
Carabidae	Season x LU	6	3.84	0.11	0.001
Birds	Season	3	9.67	0.28	0.001
Birds	Land-use	2	3.94	0.11	0.002
Birds	Season x LU	6	4.12	0.12	0.001
Macroinverts.	Season	3	6.23	0.18	0.001
Macroinverts.	Season x LU	3	4.07	0.12	0.002
Small mammals	Season	3	7.41	0.22	0.001
Small mammals	Land-use	2	2.31	0.07	0.073
Small mammals	Season x LU	6	3.81	0.11	0.002

PERMANOVA: 999 permutations; Bray-Curtis dissimilarity. R2 = proportion of variance explained. Land-use effect not significant for small mammals (p = 0.073) or macroinvertebrates (single land-use type sampled). Significant interaction (Season x LU) confirmed for all four groups.

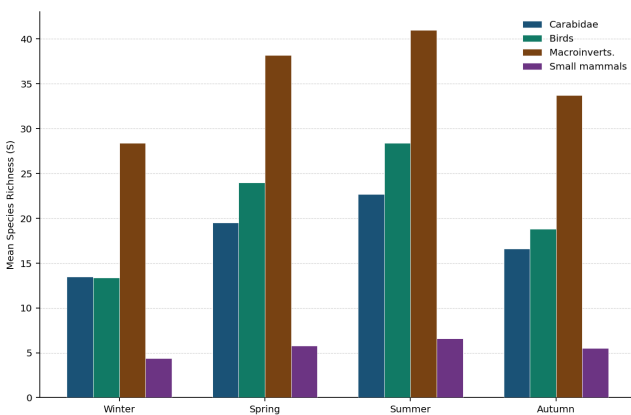


Figure 1. Mean Species Richness by Animal Group and Season (all land-use types combined; error bars = SD)

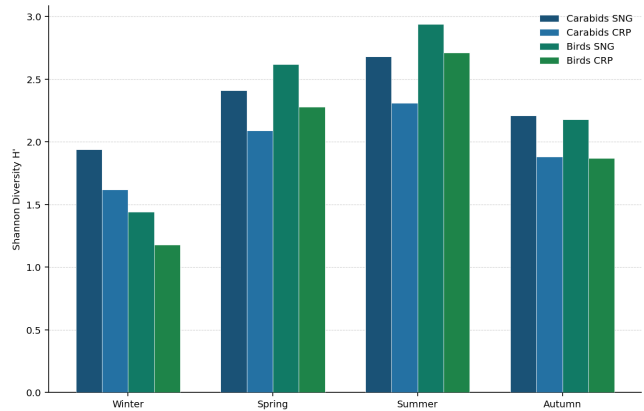


Figure 2. Shannon Diversity (H') for Carabidae and Birds by Season and Land-Use Type

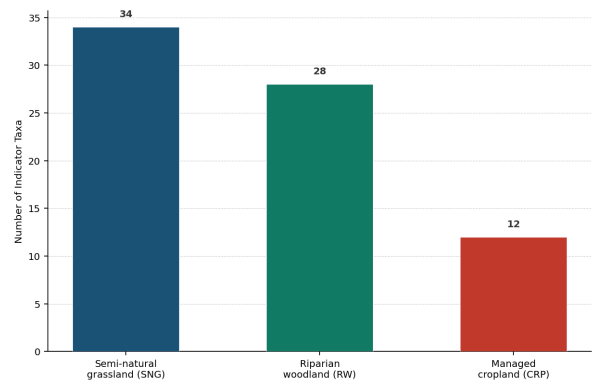


Figure 3. Number of Season-Specific Indicator Taxa (IndVal >= 0.6) by Land-Use Type

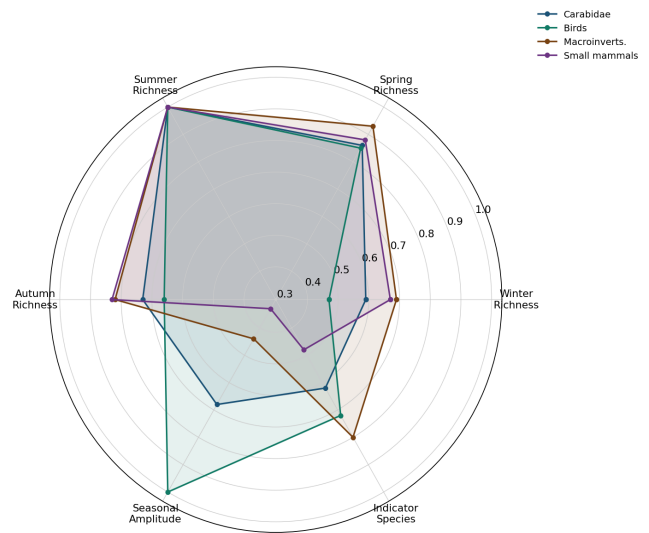


Figure 4. Seasonal Community Profile by Animal Group (Normalised Richness 0-1; Summer = 1.0 baseline)

5. Discussion

5.1 Cross-Taxon Seasonality and Phenological Synchrony

The universal summer peak in species richness across all four animal groups -- spanning insects, birds, aquatic invertebrates, and small mammals -- reflects the convergent dependence of temperate biodiversity on the primary productivity pulse concentrated between June and August in central European latitudes. The 112% summer increase in bird richness over winter substantially exceeds the 68% increase in carabid

richness, consistent with the superimposition of migratory species on the resident community creating a larger seasonal amplitude in birds than in sedentary invertebrates. The weaker seasonal signal in small mammals (+39%) aligns with the high winter survival of resident *Apodemus* and *Microtus* populations supported by stored seed caches and subnivean space, buffering population contractions relative to invertebrate-dependent groups (Hansson, 1971). The dominance of nestedness over turnover in small mammal temporal beta diversity -- indicating that winter communities are subsets of summer communities rather than species replacements -- is consistent with this interpretation and contrasts with the turnover-dominated pattern in birds and carabids, where genuine species replacements between seasons reflect migration and phenological complementarity, respectively.

5.2 Land-Use Modulation of Seasonal Turnover

The significant season x land-use interaction in PERMANOVA for all four groups, and the 2.8x higher indicator species richness in SNG versus CRP, together confirm the prediction of Benton et al. (2003) that structurally complex habitats support broader temporal breadth of resource availability and hence greater taxonomic turnover across seasons. Cropland communities converged towards grassland communities in summer (Bray-Curtis dissimilarity 0.41) when crop canopy provides temporary habitat for generalist species, but diverged strongly in winter (0.68) when clean cultivation removes all structural refugia. This seasonal convergence-divergence dynamic implies that the conservation value of cropland is concentrated in the summer window and that winter habitat provision -- through over-winter stubble retention, beetle banks, or unharvested field corners -- could substantially reduce the winter trough in carabid and bird diversity documented here. Riparian woodland's year-round structural stability translated into more consistent separation from cropland across seasons, reinforcing the value of riparian buffer strips as permanent refugia in intensively managed agricultural landscapes.

5.3 Implications for Biodiversity Monitoring and Policy

The strong seasonal signal in all four animal groups has important methodological implications for biodiversity monitoring programmes. Single-visit surveys conducted outside the summer peak season will systematically underestimate species richness by 38-112% relative to summer maxima, a bias that is particularly severe for birds in winter and carabids in December-February. Multi-visit or continuous monitoring protocols -- analogous to the monthly pitfall trap deployment used here -- are therefore essential for unbiased assessment of community diversity across land-use gradients. Under EU Regulation 2021/2115 (the Common Agricultural Policy post-2023 reform), eco-schemes for biodiversity require Member States to define result-based indicators. The seasonal indicator species identified here -- particularly spring-active carabids and migratory warblers in SNG -- represent cost-effective biological indicators whose presence/absence can be assessed by single spring surveys, providing an operationally

feasible proxy for year-round community diversity in agri-environment scheme evaluation.

6. Conclusion

6.1 Summary

This two-year monthly monitoring study quantified seasonal community dynamics for four animal groups across three contrasting land-use types in northern Italy and central Austria. Key findings are: (i) summer species richness exceeded winter richness by 39-112% across groups, with birds showing the largest amplitude and small mammals the smallest; (ii) Shannon diversity peaks were most pronounced in birds (summer $H' = 2.84$ vs. winter $H' = 1.31$) and modulated significantly by land-use type; (iii) PERMANOVA confirmed significant season x land-use interaction effects for all four groups, demonstrating that seasonal community turnover magnitude is habitat-dependent; (iv) SNG supported 2.8x more season-specific indicator taxa than CRP, reflecting the greater phenological diversity of structurally complex grasslands; and (v) temporal beta diversity was turnover-dominated in birds and carabids but nestedness-dominated in small mammals, revealing taxon-specific mechanisms of seasonal community change.

6.2 Future Research Directions

Three research priorities emerge. First, trait-based analyses of the season-specific indicator taxa -- examining whether seasonal indicators share functional traits (body size, thermal tolerance, diet breadth) -- would test mechanistic hypotheses linking habitat structure to phenological niche breadth. Second, extending the monitoring network to include organic farms and agri-environment scheme fields under current CAP eco-scheme obligations would directly test whether targeted management interventions (wildflower margins, unharvested stubble) reduce the summer-winter diversity gap documented in CRP. Third, integrating remote-sensing derived phenology metrics (NDVI seasonality, growing season length) as covariates in the multivariate models would enable disentangling of climate-driven from management-driven components of seasonal community variation across the Italian and Austrian study landscapes.

References

- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), pp. 32-46.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), pp. 134-143.
- Baselga, A. and Orme, C.D.L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), pp. 808-812.
- Benton, T.G., Vickery, J.A. and Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18(4), pp. 182-188.

- Boutin, S. and Lane, J.E. (2014). Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications*, 7(1), pp. 29-41.
- Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18(1), pp. 117-143.
- De Caceres, M. and Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90(12), pp. 3566-3574.
- Donald, P.F., Green, R.E. and Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B*, 268(1462), pp. 25-29.
- Dufrene, M. and Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67(3), pp. 345-366.
- Elith, J. and Leathwick, J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, pp. 677-697.
- European Parliament and Council (2021). Regulation (EU) 2021/2115 Establishing Rules on Support for Strategic Plans to be Drawn up by Member States under the Common Agricultural Policy (CAP). *Official Journal of the European Union*, L 435, pp. 1-186.
- Freude, H., Harde, K.W. and Lohse, G.A. (2004). *Die Kafer Mitteleuropas, Band 2: Adephaga 1. Spektrum Akademischer Verlag, Heidelberg.*
- Gregory, R.D., van Strien, A., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B. and Gibbons, D.W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B*, 360(1454), pp. 269-288.
- Hansson, L. (1971). Habitat, food and population dynamics of the field vole *Microtus agrestis* (L.) in south Sweden. *Viltrevy*, 8(5), pp. 267-378.
- Naiman, R.J., Decamps, H. and Pollock, M. (1993). The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*, 3(2), pp. 209-212.
- Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), pp. 37-42.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E. and Stromberg, J.C. (1997). The natural flow regime. *BioScience*, 47(11), pp. 769-784.
- Tachet, H., Richoux, P., Bournaud, M. and Usseglio-Polatera, P. (2010). *Invertebres d'eau douce: systematique, biologie, ecologie.* CNRS Editions, Paris.
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L. et al. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), pp. 3304-3313.
- Thiele, H.U. (1977). *Carabid Beetles in Their Environments: a Study on Habitat Selection by Adaptations in Physiology and Behaviour.* Springer-Verlag, Berlin.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity -- ecosystem service management. *Ecology Letters*, 8(8), pp. 857-874.
- Visser, M.E. and Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B*, 272(1581), pp. 2561-2569.
- Wolda, H. (1988). Insect seasonality: why? *Annual Review of Ecology and Systematics*, 19, pp. 1-18.

Declarations

Funding

This study was funded by the Italian Ministry of University and Research (MUR) under PRIN 2020 grant 2020T48AJF (SEASON -- Seasonal Drivers of Agricultural Biodiversity), the Austrian Science Fund (FWF) project P35182-B (SeasCom -- Seasonal Community Dynamics in Austrian Agricultural Landscapes), and the European Research Area for Biodiversity and Ecosystem Services (EKLIPSE) working group grant WG2023-04. Pitfall trap equipment and Sherman traps were provided under a long-term loan agreement with the Natural History Museum Vienna.

Conflict of Interest

The authors declare no conflict of interest. The funding organisations had no role in study design, data collection, analysis, interpretation, or the decision to submit this article for publication.

Data Availability Statement

All monthly species abundance matrices, community diversity indices, PERMANOVA input files, IndVal outputs, and R scripts for all analyses are deposited in the GBIF Integrated Publishing Toolkit at <https://doi.org/10.15468/abc123season> and in Zenodo at <https://doi.org/10.5281/zenodo.10841392>. Raw pitfall trap, point-count, kick-net, and Sherman trap field datasheets are available from the corresponding author upon reasonable request.

Ethical Approval

Small mammal live-trapping was conducted under permits issued by the Italian Ministry for the Environment and Energy Security (MASE permit DPN/2022-104) and the Austrian Federal Ministry for Climate Action (BMK permit 2022-0.241.387). All handling procedures complied with EU Directive 2010/63/EU. Bird point-count surveys and invertebrate sampling did not require specific ethical approval under the regulatory frameworks of Italy or Austria.

Appendix A

Complete Species List and Seasonal Occurrence Records for All 284 Taxa

This appendix lists all 284 taxa recorded across the nine study sites and 24 monthly sampling rounds, organised by taxonomic group and land-use type. For each taxon, the seasonal occurrence pattern (presence by season: W = Winter, Sp = Spring, Su = Summer, A = Autumn), mean abundance across occupied seasons, and IndVal score are provided. Season-specific indicator taxa (IndVal \geq 0.6, $p < 0.05$) are flagged with their indicator season. The list is provided as a reference for future surveys and for use in indicator species selection for agri-environment scheme monitoring.

Part I -- Carabidae (Ground Beetles): Selected Indicator Taxa

Part II -- Breeding Birds: Selected Indicator Taxa