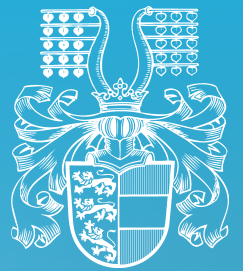


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# From wildlife management to biodiversity assessment: Using camera trap by-catch data to infer species richness

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## ABSTRACT

Camera traps are widely used in wildlife management to monitor focal species such as ungulates. However, the large amount of data on non-target species is rarely analyzed systematically. In this study, we examine whether management-oriented camera trap surveys can be used to infer broader biodiversity patterns. Using camera trap data from four study sites, we recorded 57 species, including 25 mammals and 32 birds. Species richness varied between sites but this was not primarily driven by total sampling effort. Despite substantially greater effort invested, a long-term opportunistic survey detected only slightly more species than a short-term survey using systematic random placement, consistent with spatial coverage, camera density and area size jointly influencing species detection rather than sampling duration alone. We analyzed species accumulation using Michaelis–Menten models fitted to taxa that could be reliably detected by camera traps. Systematic random surveys reached species saturation more rapidly and exhibited faster accumulation than opportunistic designs. The proportion of mammal species listed under the EU Habitats Directive remained consistent across sites, suggesting that camera traps can effectively detect species of conservation significance, even when deployed for management purposes. Late detections of rare or hard-to-detect species disrupted saturation at one site, illustrating the sensitivity of accumulation models to detectability. Overall, our results suggest that camera trap surveys targeting specific species can provide valuable additional information on biodiversity, and that by-catch data should be systematically integrated into wildlife monitoring programs. Systematic random designs may offer efficiency advantages for species inventories, although this comparison is observational and confounded by differences in area size and camera density.

*Vom Wildtiermanagement zur Biodiversitätserfassung:  
Wie sich aus dem Beifang von Kamerafallen auf den Artenreichtum schließen lässt*

## ZUSAMMENFASSUNG

Im Wildtiermanagement werden Kamerafallen häufig zum Monitoring von Zielarten wie Schalenwild eingesetzt. Die dabei anfallenden umfangreichen Daten zu Nicht-Zielarten werden jedoch nur selten systematisch ausgewertet. In dieser Studie untersuchen wir, ob sich solche managementorientierten Erhebungen mit Kamerafallen nutzen lassen, um Rückschlüsse auf die Biodiversität zu ziehen. Mithilfe von Kamerafalldaten aus vier Untersuchungsgebieten konnten insgesamt 57 Tierarten nachgewiesen werden, darunter 25 Säugetier- und 32 Vogelarten. Der Artenreichtum unterschied sich zwischen den Gebieten, war jedoch nicht primär durch den gesamten Stichprobenumfang bestimmt. Trotz des deutlich höheren Erhebungsaufwands wurden in einer langfristigen, opportunistischen Untersuchung nur geringfügig mehr Arten erfasst als in einer kurzzeitigen Erhebung mit systematisch-zufälligem Studiendesign. Dies deutet auf einen Einfluss der räumlichen Verteilung der Kamerafallen hin; der Vergleich ist jedoch dadurch eingeschränkt, dass sich die Gebiete zugleich in Flächengröße und Kameradichte unterschieden. Die Artenakkumulation wurde mithilfe von Michaelis-Menten-Modellen für jene Taxa analysiert, die sich mit Kamerafallen zuverlässig nachweisen lassen. Systematisch-zufällige Erhebungen erreichten die Sättigung der Artenzahl schneller und zeigten eine raschere Artenakkumulation als das opportunistische Design. Der Anteil der nach der FFH-Richtlinie geschützten Säugetierarten war in allen Untersuchungsgebieten ähnlich hoch. Das zeigt, dass sich Kamerafallen auch im Rahmen managementorientierter Studien eignen, um naturschutzrelevante Arten zuverlässig zu erfassen. Späte Nachweise seltener oder schwer detektierbarer Arten führten in einem Gebiet zu Abweichungen vom erwarteten Sättigungsverlauf und verdeutlichen die Abhängigkeit von Akkumulationsmodellen von der artspezifischen Nachweisbarkeit. Unsere Ergebnisse zeigen insgesamt, dass Erhebungen mit Kamerafallen, die auf Zielarten konzentriert sind, wertvolle zusätzliche Informationen zur Biodiversität liefern können. Wir empfehlen daher, Beifang-Daten systematisch auszuwerten und in bestehende Monitoringprogramme zu integrieren. Um die Artenvielfalt zu erfassen, sind systematisch-zufällige Studien von Vorteil. Dieser Vergleich beruht jedoch nur auf Beobachtungen und wird durch Unterschiede in Flächengröße und Kameradichte zwischen den Gebieten verfälscht.

## KEYWORDS

- Camera traps
- EU habitats directive
- Michaelis-Menten equation
- species accumulation rate

## INTRODUCTION

Biodiversity monitoring forms the empirical foundation of nature conservation, spatial planning, and ecological research. Reliable information on species occurrence, community composition, and temporal trends is essential for identifying conservation priorities, evaluating wildlife management measures, and detecting ecological change at an early stage [1], [2]. Without systematic monitoring, fundamental questions remain unresolved: Which species are present in a given area? How complete is the observed species inventory? How does biodiversity respond to land use change, habitat fragmentation, or climate-driven shifts? Increasingly, biodiversity-relevant data are also collected incidentally during wildlife management monitoring programs, raising the question of how such data can be used to support broader biodiversity assessments.

Global studies consistently demonstrate that biodiversity is declining at unprecedented rates, affecting not only rare or specialized species but also widespread and formerly common taxa [3]. Against this background, monitoring approaches must be both methodologically robust and scalable, allowing comparisons across sites and time while remaining feasible under practical constraints such as limited personnel, accessibility, and funding.

A wide range of methods has been developed to assess biodiversity of terrestrial vertebrates, particularly mammals and birds. Traditional approaches include direct observations, point counts, transect surveys, capture-mark-recapture techniques, and various forms of live trapping [4]. While these methods have yielded invaluable long-term datasets, they are often labor-intensive and sensitive to observer bias, weather conditions, and species-specific detectability [5]. More recently, technological advances have expanded the methodological toolbox. Environmental DNA (eDNA) sampling enables the detection of multiple taxa from soil, water, or air samples and provides broad taxonomic coverage, although information on abundance, behavior, and temporal dynamics remains limited [6]. For avifauna, passive acoustic monitoring has become a powerful complement to classical surveys, allowing continuous, standardized recording of vocal activity and increasingly automated species identification through machine-learning approaches [7].

For terrestrial mammals, particularly medium- to large-bodied species, camera trapping has emerged as one of the most widely applied non-invasive monitoring techniques [8]. Camera traps (CT) record animals autonomously, day and night, and generate permanent visual records that can be reanalyzed as taxonomic knowledge or analytical tools improve. Also, CTs allow reliable species identification for most medium- and large-bodied mammals and ground-dwelling birds, which is particularly valuable for species that are difficult to identify acoustically or visually during brief field encounters [8], [9], [10]. Camera-based records further enable the analysis of activity patterns, diel and seasonal behavior, and, under certain conditions, relative abundance indices. Because a single deployment records all passing species, camera traps are well suited to multi-species monitoring; detection probability nevertheless varies markedly among species and with survey design, and reliable multi-species comparisons require this variation to be taken into account [11], [12].

Biodiversity can be quantified using various indices and metrics, each capturing different aspects of community structure. Commonly used measures include species richness, Shannon and Simpson indices [13], and functional or phylogenetic diversity metrics. While diversity indices provide valuable summaries, they are inherently dependent on sampling effort (i.e., the sum of active camera-days across all camera locations) and detection

probability. Species accumulation curves offer a complementary perspective by explicitly linking observed species richness to sampling effort. They allow an assessment of how rapidly new species are detected and whether sampling approaches a saturation point. Asymptotic models, such as the Michaelis–Menten equation [14], are frequently used to estimate the expected maximum species richness and the effort required to approach it [15], [16]. These models are particularly useful for comparing sampling designs, sites, or monitoring methods under standardized frameworks.

A central question in CT-based monitoring concerns the time required to obtain a sufficiently complete species inventory. While common and highly mobile species are often detected rapidly, rare, cryptic, or wide-ranging species may require substantially longer sampling periods [17]. Very small mammals and species with low ground-level activity are often underrepresented, whereas extremely rare or low-density species, such as large carnivores, may remain undetected despite long deployment times [18]. Understanding species accumulation dynamics is important for interpreting CT results and evaluating sampling completeness. Apparent plateaus may reflect either a genuine reduction in the rate of new species detections or methodological limitations related to detectability and sampling design.

Many CT surveys are conducted within wildlife management programs and are primarily designed to address questions related to specific target species, such as ungulates, due to their influence on forest regeneration and forest stability. In the course of such studies, substantial additional data on non-target species (“by-catch” data) are collected, which can be used to address broader biodiversity-related questions. Such by-catch is increasingly recognized as a valuable resource in its own right and has been used, for example, to characterize community composition, species interactions, and activity patterns [19], [20], to model the occupancy of non-target carnivores across biological and anthropogenic gradients [21], and to infer population trends of threatened species [22]. We aim to evaluate whether such data can be systematically used to infer meaningful patterns of biodiversity and species accumulation of the surveyed areas and provide indications of how camera trap records of non-target species may be used to assess and infer patterns of monitored biodiversity.

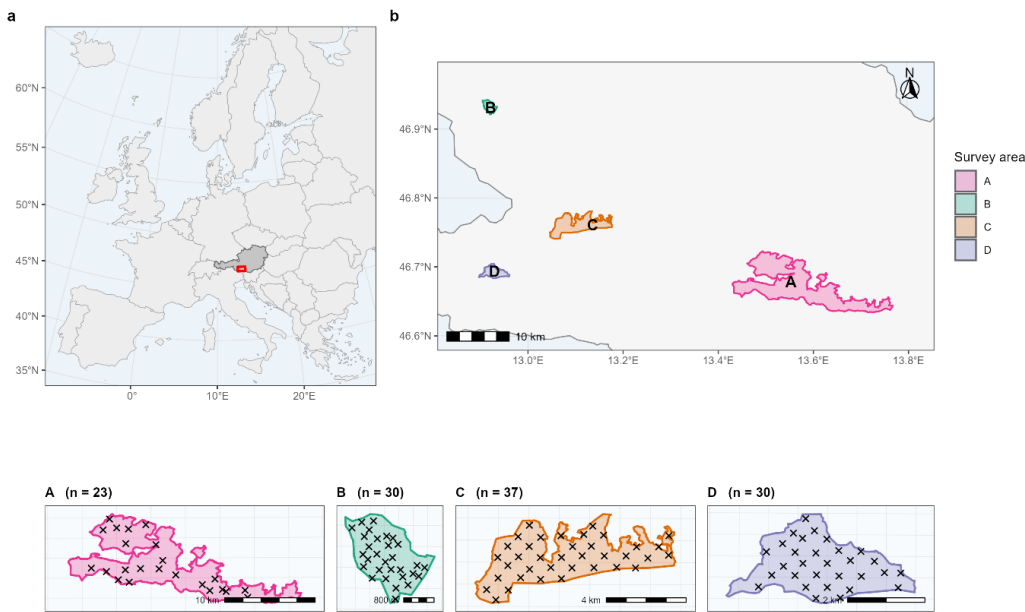
Against this background, the present study investigates species accumulation dynamics derived from CT data across multiple study areas with specific wildlife ecological sampling designs and temporal coverage. Specifically, we address the following questions:

1. When does cumulative species richness derived from camera traps approach a plateau, and how does this vary among sites and sampling designs?
2. To what extent can camera traps detect mammal species of conservation concern?
3. Which conservation-relevant bird species are incidentally recorded by camera traps?

By comparing species accumulation curves and selected model outputs across sites, we aim to explore how observed species detection patterns differ between short-term, systematically designed surveys and a long-term, opportunistic deployment, thereby highlighting potential implications for the interpretation of biodiversity data derived from CTs.

### Survey area

The study was conducted in four survey areas located in the federal state of Carinthia, southern Austria. The location and spatial arrangement of the four sites, including all



**Fig. 1**

CT placement locations, are shown in the study area map (Figure 1). Together, the sites span three floristic regions, reflecting pronounced gradients in climate, topography, and vegetation (Table 1). The combined elevational range of the study areas extends from approximately 600 to 2,200 m a.s.l., with this full gradient being covered primarily by site A, which represents by far the largest spatial extent among the four areas.

**Tab. 1**

Survey	Elevation Range (m a.s.l.)	Area (km <sup>2</sup> )	Floristic Regions [23]	CT Locations	CT/km <sup>2</sup>	Years of Deployment	Active Camera-Days	Deployment Type
A	600-2,200	95.0	3.3 6.1	23	0.2	2015-2020	21,520	Wildlife trails, Baited clearings (salt)
B	1,000-1,700	2.9	1.2	25	8.6	2023-2024	2,462	Systematic-random
C	600-1,850	20.5	3.3	37	1.8	2023-2024	4,046	Systematic-random
D	900-1,600	5.7	6.1	30	5.3	2023-2024	3,282	Systematic-random

According to the forest ecological regionalization of Austria by Kilian et al. [23], the study areas are situated within floristic regions 1.2 (Subcontinental Inner Alps – western part), 3.3 (Southern Intermediate Alps), and 6.1 (Southern Alpine fringe ranges). The first region is characterized by a subcontinental inner-alpine climate with relatively low annual precipitation compared to the northern Alpine margin, pronounced seasonal temperature amplitudes, and a summer precipitation maximum [23]. Vegetation is dominated by montane to subalpine coniferous forests, primarily Norway spruce (*Picea abies*), often accompanied by larch (*Larix decidua*) and, at lower elevations, mixed spruce-fir-beech forests on more mesic sites. Floristic region 3.3 (Southern Intermediate Alps) exhibits a transitional climate influenced by both Alpine and sub-Mediterranean conditions, with generally higher precipitation and milder winters than the inner-alpine regions. Vegetation

**Figure 1:** The four camera trap survey areas in Upper Carinthia, Austria. (a) Location within Europe (red rectangle). (b) Overview of the sites (A–D) in Carinthia. Insets A–D show close-ups of each site with camera trap locations (black crosses). n denotes the number of camera trap locations per site (120 in total). Coordinates are projected in MGI / Austria GK M31 (EPSG:31258).

**Abbildung 1:** Die vier Kamerafallen-Untersuchungsgebiete in Oberkärnten, Österreich. (a) Lage innerhalb Europas (rotes Rechteck). (b) Übersicht der Gebiete (A–D) in Kärnten. Die Ausschnitte A–D zeigen Detailsansichten der einzelnen Gebiete mit den Standorten der Kamerafallen (schwarze Kreuze). n bezeichnet die Anzahl der Kamerafallenstandorte pro Gebiet (insgesamt 120). Die Koordinaten sind in MGI / Austria GK M31 (EPSG:31258) projiziert.

**Table 1:** Overview of the four camera trap survey areas, including elevation range, spatial extent, assigned floristic regions after Kilian et al. [23], deployment period, number of camera trap locations, total active camera-days, and deployment strategy.

**Tabelle 1:** Übersicht der vier Kamerafallen-Untersuchungsgebiete mit Höhenlage, räumlicher Ausdehnung, zugeordneten Wuchsgebieten nach Kilian et al. [23], Erfassungszeitraum, Anzahl der Kamerafallenstandorte, Gesamtzahl der aktiven Kamerafallentage und Ausbringungsstrategie.

includes montane mixed forests dominated by European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and Norway spruce, with a diverse understory and locally extensive broadleaf components, particularly on nutrient-rich substrates. Floristic region 6.1, representing the Southern Alpine fringe ranges, is characterized by comparatively warm and humid climatic conditions with a strong influence from southern air masses. Annual precipitation is high, and snow cover duration is shorter than in inner-alpine regions. Vegetation is dominated by species-rich montane beech forests, often transitioning into mixed beech-fir-spruce forests at higher elevations, while thermophilous broadleaf forests occur locally at lower elevations.

The ungulate community across all study areas is dominated by red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and chamois (*Rupicapra rupicapra*), while wild boar (*Sus scrofa*) occurs only sporadically and at low densities. Large carnivores expected to occur within the study region include the grey wolf (*Canis lupus*), brown bear (*Ursus arctos*), and Eurasian lynx (*Lynx lynx*), all of which are subject to ongoing recolonization dynamics in the Eastern Alps.

## METHODS

### Study design and data origin

The four study sites were surveyed within the framework of commissioned projects aimed at estimating ungulate density, as well as their social structure and activity patterns, using CTs. Consequently, the CT deployment was primarily optimized for the detection of large terrestrial mammals. All additional species recorded by the cameras represent incidental detections—or by-catch—that were subsequently used to address complementary research questions.

### Camera trap equipment and settings

We used multiple camera models, including Bushnell Core DS (Bushnell Outdoor Products, Hyde Park, UT, USA) and Browning Patriot (Browning International S.A., Morgan, UT, USA). CTs were mounted at a height of 50–80 cm above ground level on suitable trees and were preferentially oriented northward to minimize direct sunlight exposure and false triggers. All cameras were programmed to capture eight images per trigger event at a resolution of 4 megapixels, with no delay between consecutive trigger events. This configuration allowed for continuous observation of animals within the detection zone and provided a high temporal resolution of animal movements. Each image was automatically annotated with date, time, temperature, and air pressure at the moment of triggering. All cameras were set to the highest sensitivity level to maximize detection probability. The flash mode was set to “Power Save”. Image data were stored on 32-GB SD cards. Battery levels were checked during each SD card exchange and batteries were replaced when necessary. To reduce false triggers, care was taken to avoid placing cameras where the motion sensor could be activated by dense or tall vegetation moving within the field of view.

### Camera trap placement

#### Study site A

In study site A, CTs were deployed using a non-random, management-oriented approach aimed at increasing the likelihood of detecting ungulates (see Table 1). Camera locations included game trails, salt licks, meadows, and areas adjacent to browsing test sites. Over the course of the long-term monitoring period, camera placement was not static: a subset of locations remained active for extended periods, while others were relocated

periodically or deployed only once for a limited duration of several weeks to months. Deployment duration varied markedly among camera locations, ranging from 113 to 1,828 active camera-days (median 960): seven locations were active for less than one year, whereas nine accumulated images during three to five years of operation. This highly uneven per-location effort strongly influenced the shape of the species accumulation curve for site A. As a result, sampling effort was distributed unevenly across space and time, reflecting an opportunistic deployment strategy rather than a systematically random design. Consequently, data from site A are not directly comparable to those from the short-term surveys in terms of standardized sampling effort but provide complementary, long-term insights derived from repeated and flexible camera deployments.

### Study sites B-D

In study sites B-D, cameras were deployed using a grid-based systematic-random design commonly applied in Random Encounter Model (REM) studies [24]. A regular grid was overlaid on each study area, and CT locations were defined at the grid intersection points. Minor spatial adjustments were permitted where grid points fell on roads, paths, or agricultural land. In contrast to site A, game trails or movement corridors were not explicitly visited, but they weren't specifically avoided either.

### Image processing and data management

After retrieval of the SD cards, image files were processed manually or by using MegaDetector [25] and Timelapse [26] software to remove empty images. Empty images were defined as photographs without animal presence, most commonly triggered by vegetation moving or warmed by sunlight within the camera's detection range.

The filtered image sets were subsequently uploaded to Camelot [27] (site A) or to the Agouti [28] online platform (sites B-D), where images were automatically grouped into independent detection events to facilitate further classification and analysis.

### Taxonomic scope and modelling approach

The Michaelis–Menten model was fitted to taxa for which CTs provide reliable detections and are suitable for asymptotic species accumulation modelling. These included:

- › insectivores
- › rodents
- › carnivores
- › ungulates
- › lagomorphs
- › ground-dwelling birds, specifically all grouse species and woodcock (*Scolopax rusticola*), as well as common songbird species, which were detected in all four areas.

All bat species and other non-terrestrial bird species were excluded from the analysis. Although CTs recorded a substantial number of additional bird species—such as finches, tits and other woodpeckers, which may occasionally forage on the ground—their detection by CTs is considered opportunistic and methodologically unsuitable for saturation-based modelling. Consequently, these species were excluded to ensure biological interpretability and methodological consistency of the fitted models.

## RESULTS

Across all four study sites, camera trapping recorded a total of 57 species, of which 32 were birds and 25 were mammals (Table 2). Species richness differed among sites. The

long-term study site A yielded the highest number of detected species ( $n = 42$ ). The short-term study site B showed comparable richness ( $n = 40$ ), whereas the remaining two sites supported fewer species (site C:  $n = 27$ ; site D:  $n = 28$ ).

Tab. 2

Nr	Taxon	Species	Scientific Name	Survey Area				Annex
				A	B	C	D	
1	insectivores	brown-breasted hedgehog	<i>Erinaceus europaeus</i>				x	
2	bats	bats	Chiroptera	x		x		II;IV
3	rodents	edible dormouse	<i>Glis glis</i>	x		x	x	
4		<b>marmot</b>	<i>Marmota marmota</i>		1			
5		squirrel	<i>Sciurus vulgaris</i>	x	x	x	x	
6		<b>forest dormouse</b>	<i>Dryomys nitedula</i>		3			IV
7		wood mouse	<i>Apodemus</i> sp.	x	x	x		
8	carnivores	badger	<i>Meles meles</i>	128	6	2	5	
9		<b>brown bear</b>	<i>Ursus arctos</i>	1				II;IV
10		<b>golden jackal</b>	<i>Canis aureus</i>		1			V
		marten	<i>Martes martes/foina</i>	127	131	95	84	
11		<b>pine marten</b>	<i>Martes martes</i>	24			2	V
12		<b>polecat</b>	<i>Mustela putorius</i>			1		V
13		red fox	<i>Vulpes vulpes</i>	1,288	457	227	88	
14		stone marten	<i>Martes foina</i>	2	6			
15		weasel	<i>Mustela nivalis/erminea</i>			1	2	
16		<b>wolf</b>	<i>Canis lupus</i>		2		2	V
17	ungulates	<b>chamois</b>	<i>Rupicapra rupicapra</i>	6,600	527	56	11	V
18		mouflon	<i>Ovis gmelini</i>	1				
19		red deer	<i>Cervus elaphus</i>	59,903	624	1,370	313	
20		roe deer	<i>Capreolus capreolus</i>	9,922	406	1,376	1,636	
21	wild boar	<i>Sus scrofa</i>	2					
22	lagomorphs	European hare	<i>Lepus europaeus</i>	2,410	10	8	9	
23		<b>mountain hare</b>	<i>Lepus timidus</i>	28	11	12	4	V

Table 2:

Species detected with camera traps in four survey areas, listed alphabetically by taxonomic group. Bold font indicates species listed under Annex II, IV or V of the EU Habitats Directive and Annex II of the Birds Directive respectively. Numbers indicate the total number of detections, whereas “x” indicates only presence, without exact counts.

Tabelle 2:

Mit Kamerafallen nachgewiesene Arten in vier Untersuchungsgebieten, alphabetisch nach taxonomischer Gruppe geordnet. Fett gedruckte Arten, sind in Anhang II, IV oder V der FFH-Richtlinie bzw. in Anhang II der Vogelschutzrichtlinie gelistet. Die Zahlen geben die Gesamtzahl der Nachweise an, während „x“ lediglich das Vorkommen ohne genaue Zählung angibt.

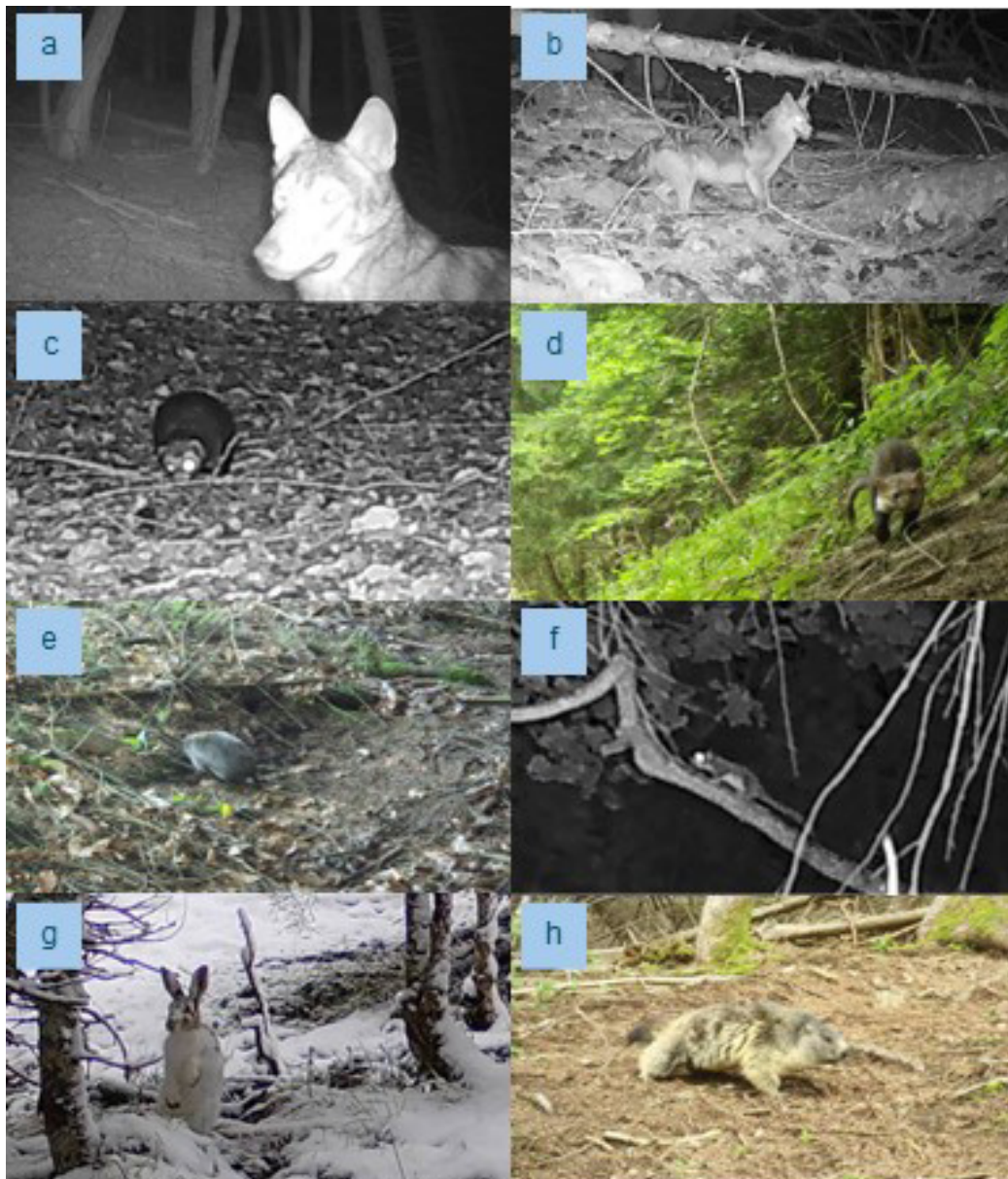
24		blackbird	<i>Turdus merula</i>	x	x	x	x	
25		black woodpecker	<i>Dryocopus martius</i>	37	3		2	I
26		blue tit	<i>Cyanistes caeruleus</i>	x				
27		bullfinch	<i>Pyrrhula pyrrhula</i>		x			
28		buzzard	<i>Buteo buteo</i>	165	3			
29		<b>capercaillie</b>	<i>Tetrao urogallus</i>	108		2	18	I;II
30		chaffinch	<i>Fringilla coelebs</i>	x	x	x		
31		chiffchaff	<i>Phylloscopus collybita</i>		x			
32		crested tit	<i>Lophophanes cristatus</i>	x	x	x		
33		dunnock	<i>Prunella modularis</i>		x			
34		<b>Eurasian jay</b>	<i>Garrulus glandarius</i>	189	18	23	14	II
35		Eurasian sparrowhawk	<i>Accipiter nisus</i>		1			
36		goshawk	<i>Accipiter gentilis</i>	25		1		
37		boreal owl	<i>Aegolius funereus</i>		1			I
38		great tit	<i>Parus major</i>	x	x		x	
39		great-spotted woodpecker	<i>Dendrocopos major</i>	7	4	3	2	
40	birds	green woodpecker	<i>Picus viridis</i>		2			
41		grey-headed woodpecker	<i>Picus canus</i>		1			I
42		<b>hazel grouse</b>	<i>Tetrastes bonasia</i>	1		1	3	I;II
43		long-tailed tit	<i>Aegithalos caudatus</i>	x				
44		<b>mistle thrush</b>	<i>Turdus viscivorus</i>	x	x	x	x	II
45		nutcracker	<i>Nucifraga caryocatactes</i>	x	x	x	x	
46		nuthatch	<i>Sitta europaea</i>	x	x			
47		raven	<i>Corvus corax</i>	1	2			
48		<b>redwing</b>	<i>Turdus iliacus</i>		x			II
49		robin	<i>Erithacus rubecula</i>	x	x	x	x	
50		<b>rock partridge</b>	<i>Alectoris graeca</i>		1		3	I;II
51		<b>song thrush</b>	<i>Turdus philomelos</i>	x	x	x	x	II
52		tawny owl	<i>Strix aluco</i>	32	2		1	
53		whinchat	<i>Saxicola rubetra</i>	x				
54		<b>wood pigeon</b>	<i>Columba palumbus</i>	4,898	x	x	x	II
55		<b>fieldfare</b>	<i>Turdus pilaris</i>	x				II
56		<b>woodcock</b>	<i>Scolopax rusticola</i>	5				II
57	wren	<i>Troglodytes troglodytes</i>	x					
	N species	57		42	40	27	28	
	N species FFH Annex II			2	1	1	1	
	N species FFH Annex IV			2	2	1	1	
	N species FFH Annex V			3	3	3	3	
	N species FFH Annex II, IV or V			5	5	4	4	
	Proportion of FFH-listed species by total number of species			12%	13%	15%	14%	

## Mammals

The 25 mammalian species detected—a selection of which is shown in Figure 2—comprised one insectivore, the brown-breasted hedgehog (*Erinaceus europaeus*), at least one bat species (Order: Chiroptera), five rodent species, ten carnivores, five ungulates, and two lagomorphs. Bat detections occurred at two study sites and were sporadic, but without species-level identification.

Nine mammal species were detected at all four study sites, indicating widespread occurrence across the region. These included squirrel (*Sciurus vulgaris*), badger (*Meles meles*), martens (*Martes martes* and *Martes foina*), red fox (*Vulpes vulpes*), as well as European hare (*Lepus europaeus*) and mountain hare (*Lepus timidus*), in addition to red deer, roe deer, and chamois.

Nine of the recorded mammal species are listed under the EU Habitats Directive (FFH Directive) in one or more annexes. Three species are included in Annex II, four in Annex IV, and four in Annex V. Among these, the forest dormouse (*Dryomys nitedula*) represents one of the seven FFH-listed rodent species known from Austria. The mountain hare was the only lagomorph species found that is listed under the Directive.



**Figure 2:** Selection of mammal species captured with camera traps showing a) wolf (*Canis lupus*), b) golden jackal (*Canis aureus*), c) polecat (*Mustela putorius*), d) pine marten (*Martes martes*), e) brown-breasted hedgehog (*Erinaceus europaeus*), f) forest dormouse (*Dryomys nitedula*), g) mountain hare (*Lepus timidus*) and h) marmot (*Marmota marmota*).

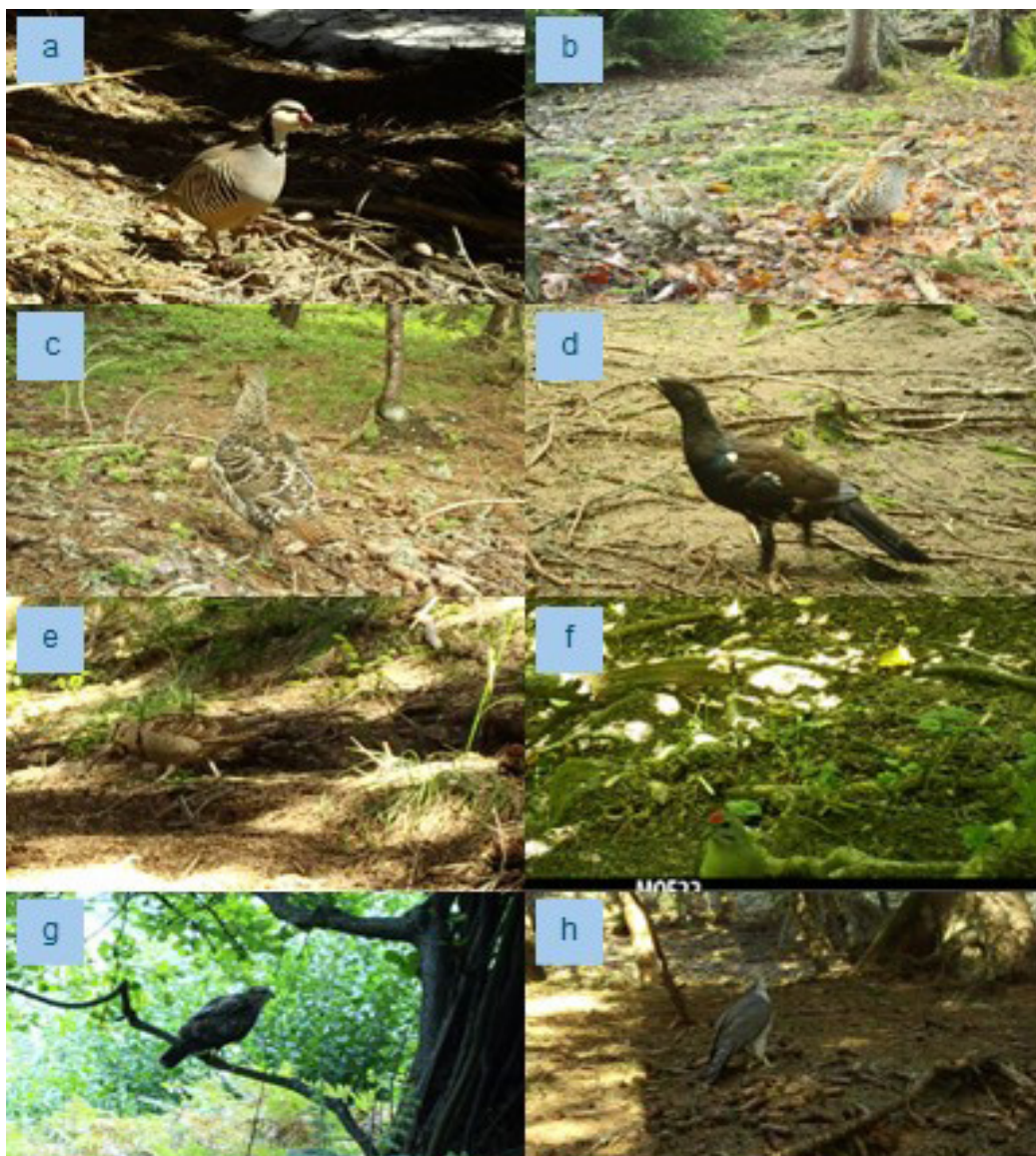
**Abbildung 2:** Auswahl der mit Kamerafallen erfassten Säugetierarten: a) Wolf (*Canis lupus*), b) Goldschakal (*Canis aureus*), c) Iltis (*Mustela putorius*), d) Baummarder (*Martes martes*), e) Braunbrustigel (*Erinaceus europaeus*), f) Baumschläfer (*Dryomys nitedula*), g) Schneehase (*Lepus timidus*) und h) Murmeltier (*Marmota marmota*).

Fig. 2

Five of the recorded carnivores are listed under the EU Habitats Directive: brown bear, wolf, golden jackal (*Canis aureus*), pine marten (*Martes martes*), and polecat (*Mustela putorius*), representing five of the eight FFH-listed carnivores occurring in Austria. Several of these were recorded only as isolated events: brown bear (Annex II/IV) was detected a single time at site A, golden jackal (Annex V) once at site B, and polecat (Annex V) once at site C, while wolf (Annex V) was recorded at two sites (twice each at site B and site D). Notably, when expressed relative to total species richness per site, the proportion of mammal species listed in FFH Annexes II, IV, or V remained within a narrow band of 12–15% across all four study areas (A: 12%, B: 13%, C: 15%, D: 14%). This consistency is a key result of our study: despite the areas differing more than thirty-fold in size (2.9–95 km<sup>2</sup>) and in sampling design, effort, and camera density, the relative representation of conservation-relevant mammals was remarkably stable. This indicates that the conservation-relevant signal carried by CT by-catch is robust to substantial differences in survey design and supports its value as an additional output of focal species monitoring.

### Birds

In total, 32 bird species were detected by CTs (a selection is shown in Figure 3). Of these, 16 species are listed under the EU Birds Directive. Six of the recorded bird species



**Figure 3:** Selection of bird species captured with camera traps, showing a) rock partridge (*Alectoris graeca*), b) hazel grouse male and female (*Tetrastes bonasia*), c) female capercaillie (*Tetrao urogallus*), d) male capercaillie (*Tetrao urogallus*), e) woodcock (*Scolopax rusticicola*), f) grey-headed woodpecker (*Picus canus*), g) buzzard (*Buteo buteo*) and h) goshawk (*Accipiter gentilis*).

**Abbildung 3:** Auswahl der mit Kamerafallen erfassten Vogelarten: a) Steinhuhn (*Alectoris graeca*), b) Haselhuhn, Hahn und Henne (*Tetrastes bonasia*), c) Auerhenne (*Tetrao urogallus*), d) Auerhahn (*Tetrao urogallus*), e) Waldschnepfe (*Scolopax rusticicola*), f) Grauspecht (*Picus canus*), g) Mäusebusard (*Buteo buteo*) und h) Habicht (*Accipiter gentilis*).

Fig. 3

(capercaillie, *Tetrao urogallus*; hazel grouse, *Tetrastes bonasia*; rock partridge, *Alectoris graeca*; boreal owl, *Aegolius funereus*; grey-headed woodpecker, *Picus canus*; black woodpecker, *Dryocopus martius*) are listed in Annex I of the EU Birds Directive and therefore require special conservation measures in Austria. Ten of the recorded bird species are listed in Annex II of the EU Birds Directive.

As with the conservation-relevant mammals, several of these Annex I species were recorded only incidentally and in very low numbers: rock partridge was detected once at site B and three times at site D, grey-headed woodpecker and boreal owl once each at site B, and hazel grouse at three sites in single-digit counts. In contrast, capercaillie and black woodpecker were recorded repeatedly and across multiple sites. That scarce, ground-associated Annex I species appeared at all surveys designed for ungulates further underlines the conservation value of systematically evaluating CT by-catch.

Nocturnal raptors were represented by the boreal owl and the tawny owl (*Strix aluco*), while diurnal raptors included the common buzzard (*Buteo buteo*), Eurasian sparrowhawk (*Accipiter nisus*), and northern goshawk (*Accipiter gentilis*).

### Species Accumulation

Species accumulation was modelled using a Michaelis–Menten equation [14], where  $V_{max}$  represents the expected asymptotic species richness and  $K$  indicates the sampling effort (in camera-days) required to reach half of  $V_{max}$ . Lower  $K$  values therefore reflect a faster accumulation of species. In addition, the sampling effort  $T$  when  $V_{max}$  reached 95 % ( $T V_{max} 95\%$ ) was used as a standardized measure of the sampling effort required to approach species saturation.

Clear differences were observed between the long-term, opportunistic study site (A) and the short-term, systematically random surveys of sites B–D (Table 3). The long-term site A showed a high  $K$  value (2,514.8) and required substantially more sampling effort to approach saturation, as reflected by the markedly delayed  $T V_{max} 95\%$  (47,781.8). In contrast, all three systematically random sites exhibited much lower  $K$  values between 221 and 255 and reached 95% of the estimated  $V_{max}$  considerably earlier with  $T V_{max} 95\%$  between 4,202 and 4,843 camera-days.

**Table 3:** Parameters of Michaelis–Menten species accumulation models for the four study sites, including the estimated asymptotic species richness ( $V_{max}$ ), the sampling effort required to reach half of  $V_{max}$  ( $K$ ), the empirically observed maximum number of species, and the sampling effort at which 95% of  $V_{max}$  was reached ( $T V_{max} 95\%$ ). Results are shown for the long-term, opportunistic deployment (site A) and the short-term, systematically random surveys (sites B–D).

**Tabelle 3:** Parameter der Michaelis-Menten-Artenakkumulationsmodelle für die vier Untersuchungsgebiete, einschließlich des geschätzten asymptotischen Artenreichtums ( $V_{max}$ ), des zum Erreichen der Hälfte von  $V_{max}$  erforderlichen Erfassungsaufwands ( $K$ ), der empirisch beobachteten maximalen Artenzahl sowie des Erfassungsaufwands, bei dem 95 % von  $V_{max}$  erreicht wurden ( $T V_{max} 95\%$ ). Die Ergebnisse sind für die langfristige, opportunistische Ausbringung (Gebiet A) und die kurzfristigen, systematisch-randomisierten Erhebungen (Gebiete B–D) dargestellt.

**Tab. 2**

Site	Sampling design	$V_{max}$ ( $\pm$ SE)	$K$ ( $\pm$ SE)	$V_{max}$ empirical	T first $V_{max}$ empirical	T $V_{max} 95\%$
A	Long-term (multi-year)	25.2 $\pm$ 0.3	2,514.8 $\pm$ 114.8	24	19,544.0	47,781.8
B	4 $\times$ 1 month	23.4 $\pm$ 0.8	222.2 $\pm$ 41.7	23	2,287.2	4,221.1
C	4 $\times$ 1 month	19.3 $\pm$ 0.6	254.9 $\pm$ 48.7	21	4,045.8	4,843.3
D	4 $\times$ 1 month	25.1 $\pm$ 0.3	221.2 $\pm$ 16.9	24	2,757.0	4,202.7

Estimated  $V_{max}$  values were generally close to the empirically observed species richness at sites A, B, and D (Figure 4). Site C deviated from this pattern: late detections of song thrush (*Turdus philomelos*), edible dormouse (*Glis glis*), and capercaillie produced a step-like increase in cumulative richness towards the end of the sampling period, which weakened the Michaelis–Menten fit and even yielded an estimated asymptote below the empirically observed maximum. This case highlights a key limitation of asymptotic accumulation models: when rare or seasonally detectable species are recorded late, the curve fails to saturate and the model becomes unsuitable, irrespective of survey design.

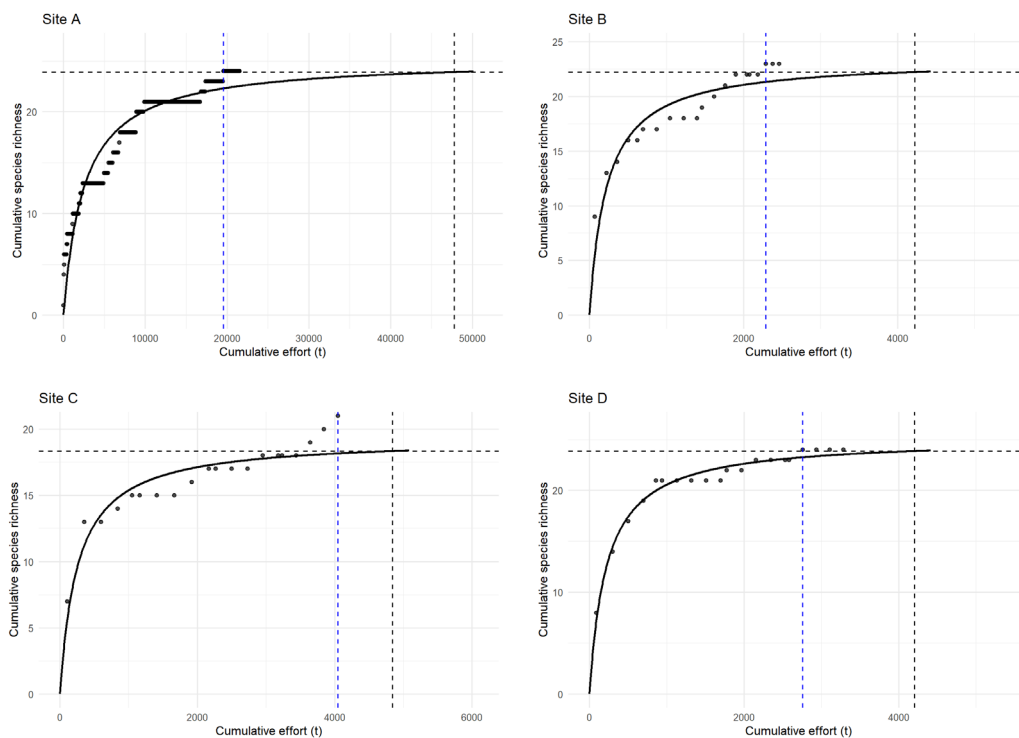


Fig. 4

## DISCUSSION

This study shows that CT data originally collected within wildlife management programs can be effectively used to extract meaningful information on broader biodiversity patterns. Across the four survey sites, camera trapping enabled the detection of a diverse range of terrestrial vertebrates, including mammals from six orders as well as birds, with a total of 57 species recorded. This supports the general suitability of CTs for multi-taxon biodiversity assessments in heterogeneous landscapes. However, species detection was not primarily driven by total sampling effort. Instead, differences in study design appeared to be a key factor shaping species accumulation patterns.

Despite a substantially longer deployment period in site A, which followed an opportunistic and non-random placement strategy, only marginally more species were detected compared to site B, where cameras were placed following a systematic random design. This shows that longer sampling does not necessarily lead to many additional species when camera placement is uneven, and that spatial coverage plays a key role in species detection [9], [17].

However, site A differed from sites B–D not only in placement strategy but simultaneously in spatial extent (95 km<sup>2</sup> versus 2.9–20.5 km<sup>2</sup>), camera trap density (approximately 0.24 versus 1.8–8.6 cameras km<sup>-2</sup>) and habitat heterogeneity. These factors are known to influence species detection independent of placement strategy [12], [29], and our four datasets—originating from independently commissioned projects—do not allow them to be disentangled. The comparison should therefore be regarded as observational rather than as a controlled test of sampling design. Notably, cameras in site A were placed at game trails and baited salt licks, which generally increase per-camera detection rates; the slower species accumulation at this larger site despite such placement is consistent with area size and spatial coverage, rather than placement strategy alone, limiting inventory completeness.

**Figure 4:** Michaelis–Menten species accumulation curves for the four study sites. Points represent empirical cumulative species richness as a function of cumulative sampling effort ( $t$ ), and the solid line shows the fitted Michaelis–Menten model. The horizontal dashed line indicates the modelled asymptotic species richness ( $V_{\max}$ ) derived from the Michaelis–Menten function, not the empirically observed maximum. The blue vertical dashed line marks the sampling effort at which the empirical maximum species richness was first reached. The black vertical dashed line denotes the sampling effort required to reach 95% of the modelled  $V_{\max}$  ( $T V_{\max, 95\%}$ ), providing a standardized measure of the speed at which species saturation is approached.

**Abbildung 4:** Michaelis-Menten-Artensakkumulationskurven für die vier Untersuchungsgebiete. Die Punkte stellen den empirischen kumulativen Artenreichtum als Funktion des kumulativen Erfassungsaufwands ( $t$ ) dar; die durchgezogene Linie zeigt das angepasste Michaelis-Menten-Modell. Die horizontale gestrichelte Linie kennzeichnet den modellierten asymptotischen Artenreichtum ( $V_{\max}$ ) aus der Michaelis-Menten-Funktion, nicht das empirisch beobachtete Maximum. Die blaue vertikale gestrichelte Linie markiert den Erfassungsaufwand, bei dem die empirische maximale Artenzahl erstmals erreicht wurde. Die schwarze vertikale gestrichelte Linie kennzeichnet den zum Erreichen von 95% des modellierten  $V_{\max}$  erforderlichen Erfassungsaufwand ( $T V_{\max, 95\%}$ ) und liefert damit ein standardisiertes Maß für die Geschwindigkeit, mit der sich die Artensättigung annähert.

The proportion of mammal species listed under the EU Habitats Directive (FFH), excluding bats, remained within a narrow band of 12–15% across all four study sites. This stability is striking given that the areas differed more than thirty-fold in size (2.9–95 km<sup>2</sup>) and in sampling design, effort, and camera trap density. It suggests that the conservation-relevant signal carried by camera trap by-catch is largely robust to these design differences, and that even surveys optimized for ungulates capture a representative cross-section of FFH-listed mammals [30, 31]. This robustness is, in our view, the most transferable result of the study: it is precisely what makes by-catch a worthwhile additional output of focal species monitoring, rather than a byproduct to be discarded [30].

For certain species, camera trapping appears particularly well suited. Medium- to large-bodied terrestrial mammals such as mountain hare and chamois were detected consistently, supporting the use of CTs for their monitoring. Of the two FFH-listed ungulate species considered in this study, only chamois was detected. The absence of Alpine ibex (*Capra ibex*) can be explained by the fact that all study sites lie outside the species' natural distribution range. In contrast, species that are primarily nocturnal and morphologically similar, such as polecat and martens, pose identification challenges when infrared cameras are used. For these taxa, white-flash cameras can substantially improve species-level identification and should be preferred when these species are focal targets.

Although bats were detected at two study sites, CT images do not allow reliable species-level identification. Most bat species can only be identified based on species-specific echolocation calls obtained through acoustic monitoring or, in some cases, through morphological examination of captured individuals, including body measurements and diagnostic physical characteristics. Given that more than 20 bat species occur in Carinthia, the records obtained in this study likely represent multiple species rather than a single taxon.

Large carnivores such as brown bear and wolf were detected only sporadically, reflecting both their low densities and wide-ranging behavior. These records illustrate that even rare, wide-ranging, or low-density species of high conservation interest may be detected incidentally in management-oriented CT surveys. However, such sporadic detections should not be interpreted as evidence of established occurrence or population status. During the study period, the protection status of the wolf under the EU Habitats Directive was downgraded from Annex IV to Annex V, highlighting the importance of reliable monitoring data for informing conservation and management decisions. Incidental detections, as observed here, should therefore be interpreted cautiously and cannot replace dedicated monitoring schemes. Targeted, non-random camera placement, often combined with baits, remains necessary for reliable monitoring of these species [32], [33], [34]. For wolf and golden jackal, complementary approaches such as acoustic monitoring and genetic analyses of scat may provide more robust information, as the latter is already common practice for Eurasian otter [32], [35].

Species that are strongly bound to aquatic habitats, such as beaver, are unlikely to be detected consistently in terrestrial CT settings, such as ours. Nevertheless, CTs placed strategically at riverbanks or crossing points can still contribute valuable presence data [36]. Finally, small rodents were largely underrepresented, which is expected given their body size and movement patterns. Their detection would require specialized setups, such as ground-level cameras integrated into non-lethal box traps [37], underscoring that CTs alone cannot comprehensively sample all components of terrestrial vertebrate communities.

Species richness represents the total number of species present, whereas species accumulation describes how this richness is revealed progressively as sampling effort increases. Species accumulation patterns were analyzed using Michaelis–Menten models fitted to a filtered set of species, as described in the Methods section. Accordingly, all accumulation parameters reflect patterns within this detectable subset of the vertebrate community. Across study sites, systematically random camera placements consistently reached 95% of the estimated asymptotic species richness more rapidly than the long-term opportunistic deployment. This indicates that spatially structured camera placement promotes faster accumulation of species, even when overall sampling duration is limited.

The markedly higher K value estimated for site A further underlines this pattern. In the context of the Michaelis–Menten model, a higher K value reflects a slower initial accumulation of species, suggesting that many species required extended sampling time before detection. In contrast, consistently lower K values at the systematically random sites point to more efficient sampling of the community, with a larger fraction of species detected early in the survey period. Together, these results provide strong empirical support for systematic random camera placement as an effective strategy for biodiversity inventories. These findings closely align with findings of Si et al. [17] who showed that species detection in camera trap studies depends more strongly on spatial coverage and camera rotation than on prolonged deployment at a limited number of sites.

Site C deviated from the expected saturating accumulation pattern despite systematic random placement and high spatial replication. Late detections of several species (namely song thrush, edible dormouse and capercaillie) produced a step-like increase late in the sampling period, which substantially reduced the fit of the Michaelis–Menten model and even resulted in an estimated asymptote below the empirical maximum. Such patterns can arise when detectability is strongly time-varying (e.g., seasonal shifts, snow cover), when effort is temporally uneven among camera locations, or when species are rare.

A further important consideration is that species detection depends not only on deployment duration and placement strategy, but also on technical and methodological factors. Camera characteristics such as sensor sensitivity, trigger speed, field of view, camera angle, and mounting height can substantially influence detection probability and therefore affect observed species richness and accumulation dynamics [38]. Small differences in camera positioning may particularly affect the detectability of small-bodied species or species with specific movement behavior. Consequently, variation in technical setup among surveys may partly contribute to differences in species accumulation patterns observed between sites.

In addition, estimates of species saturation are influenced by the analytical approach used to model accumulation curves. In the present study, species accumulation was analyzed using Michaelis–Menten models, which assume an asymptotic saturation process. However, alternative modelling approaches may produce different estimates of saturation thresholds and sampling efficiency. For example, Beukes et al. [39] applied a logistic growth model to estimate species accumulation dynamics in CT surveys. Such methodological differences should be considered when comparing results among studies, as estimates of saturation are partly model-dependent.

### **Methodological limitations and future research directions**

Several methodological limitations of this study should be acknowledged. As in most long-term CT studies, a proportion of cameras failed prematurely due to technical issues such as

battery depletion, limited storage capacity, malfunction, or theft, resulting in unavoidable data loss. To compensate for such losses, we recommend planning for an additional 10–20% of camera units beyond the intended deployment. Differences in camera models, placement heights, and detection settings may also have influenced detection probabilities among sites. Moreover, our datasets originate from wildlife management surveys explicitly designed to monitor ungulates, which constrains the degree to which camera placement and settings could be optimized for broader biodiversity assessment. This represents an inherent limitation of the study and limits the extent to which alternative survey designs can be recommended. Finally, the opportunistic nature of some deployments introduces spatial bias that complicates direct comparisons of species accumulation parameters. Future studies should therefore aim for greater standardization of camera settings and consider stratified placement approaches to ensure a more balanced coverage of different habitat types, where management objectives allow.

### **Practical implications for wildlife management and conservation**

From an applied perspective, our results provide clear guidance for wildlife managers and conservation practitioners. CT surveys designed to monitor one or more focal species, such as ungulates, can simultaneously yield valuable information on broader biodiversity. Failing to systematically analyze and integrate this ancillary information would represent a substantial loss of ecological data. We therefore recommend that the evaluation of non-target species detections be standardized and routinely incorporated into wildlife monitoring programs.

The incidental detection of several bird species listed under Annex II of the EU Birds Directive further illustrates that camera trap surveys conducted for wildlife management purposes can also provide relevant information on game bird species of conservation and management interest.

For broad-scale biodiversity inventories and early detection of community composition, systematic random CT designs are recommended, as they maximize spatial coverage and accelerate species detection. Opportunistic long-term deployments may still be valuable for documenting rare events or behavioral observations, but they are less efficient for estimating species richness.

Camera trapping can be confidently recommended for monitoring medium- and large-bodied terrestrial mammals, including several conservation-relevant species in habitats of very different sizes. However, species-specific adaptations in study design and complementary methods remain essential when monitoring elusive carnivores, aquatic mammals, or small rodents. Overall, camera trapping represents a powerful and flexible tool, but its effectiveness depends critically on thoughtful study design and clearly defined monitoring objectives.

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