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DATA PAPER

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FRUGIVORY CAMTRAP: A dataset of plant–animal interactions recorded with camera traps

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Abstract

Ecological interactions are a key component of biodiversity, essential for understanding ecosystem services and functioning. Recording and quantifying ecological interactions is challenging, frequently requiring complex logistics and substantial effort in the field. Camera traps are routinely used in ecology for various applications, and have proven to be an excellent method for passive and non-invasive sampling of plant–animal interactions. We implemented a standardized camera trap protocol to document vertebrate frugivores-fleshy fruited plants interactions in Doñana National Park, SW Spain, with the central objective of inventorying the diversity of plant–animal ecological interactions providing seed dispersal services. From 2018 to 2023 we recorded pairwise interactions from which we obtained qualitative (presence-absence) and quantitative (frequency of visits) information. Each record in the dataset contains information of a visit by an individual animal to an individual plant, resulting in any form of fleshy-fruit use and provides information on visitation phenology, visit length, and feeding behavior. The dataset presented here includes 10,659 frugivory interaction events for 59 vertebrate species (46 birds, 13 mammals) recorded on 339 plant individuals from 13 different plant species which dominate the fleshy-fruited plant assemblage in the Doñana National Park. The most recorded animal species consuming fruits and playing a legitimate seed dispersal role was *Curruca melanocephala* (1678 records) among birds and *Vulpes vulpes* among mammals (751 records). *Cervus elaphus*, a fruit consumer with a marginal role as legitimate seed disperser, was the most recorded mammal species (1508 records). Avian frugivores, particularly those from the Sylviidae and Turdidae families, are widespread in the region and play a crucial role in maintaining the dispersal service for the fleshy-fruited plant populations in the area. The dataset offers highly versatile quantitative information that can be used to investigate frugivory from the highest resolution scale, the interaction event between pairs of individuals. In addition, other information that can be extracted includes the timing of interactions of animals and plants (their phenological couplings), activity periods of the animals, behavior during the events and preferences for individual plants within populations. There are no copyright restrictions on the data. When using the data from this data paper in publications, we kindly request that you cite the paper accordingly. Additionally, we encourage researchers and educators to inform us about how they are using this data, as we value feedback and would like to be aware of its various applications.

KEYWORDS
artificial intelligence, camera traps, complex networks, Doñana National Park, frugivory, Mediterranean scrubland, mutualism, plant–animal interactions, seed dispersal

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available as Supporting Information. The raw data for camera trap records are also available in the CSIC Open Access repository at https://doi.org/10.20350/digitalCSIC/15623.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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METADATA S1

FRUGIVORY CAMTRAP*:* A dataset of plant-animal interactions recorded with camera traps

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Open Research: Data are available as Supporting Information. The raw data for camera trap records are also available in the CSIC Open Access repository at https://doi.org/10.20350/digitalCSIC/15623.

INTRODUCTION

Ecological interactions among species are at the core of the Web of Life that supports Earth systems (Begon et al. 2006, Thompson 2009) and are therefore essential to understand ecosystem services and functioning (Loreau et al. 2001). There is an urgent need to record, quantify and assess ecological interactions to determine their importance in ecosystem functioning and their robustness to environmental perturbations.

Consumption of fleshy fruits by frugivorous animals is a type of ecological interaction potentially resulting in mutualistic services that are crucial for plant population dynamics and ecosystem functioning, such as natural forest regeneration. But monitoring plant-frugivore interactions is challenging because it is a labor-intensive activity leading to incomplete data samples (Jordano 2016, Chiu et al. 2023) and presents data merging limitations (Quintero et al. 2022). Notwithstanding, recent technological advances have made possible to obtain large amounts of high-quality field data and enough computational power to process them, thus providing the opportunity to study plant-frugivore interactions at the finest scale (i.e., individuals, or even individual parts), beyond the community level.

Over the last two decades, the use of camera traps for wildlife monitoring has significantly enhanced our understanding of vertebrate distributions and ecological relationships (O'Connell et al. 2011, Ahumada et al. 2013). Remote cameras have been used in behavioral studies focused on various aspects, such as activity periods (Suselbeek et al. 2014), daily activity patterns (Leuchtenberger et al. 2014), road crossing behavior (Villalva et al. 2013), human-wildlife conflict (Johnson et al. 2006), and scent marking behavior (Delgado et al. 2011), among others. However, the application of camera traps in behavioral studies (Caravaggi et al. 2017) and plant-animal interactions monitoring (e.g., Da Silva and Dos Reis 2019) is still in its infancy. As an extension of their application, passive sampling with camera traps has proven useful to monitor ecological interactions, providing an enormous added value for field studies requiring extensive sampling schemes, by expanding the spatial (number of sampled individuals) and temporal (day-night) scale of analysis, or by avoiding logistic limitations of direct sampling, among others. However, its application in this context has so far been limited. Data obtained from camera monitoring can be used to estimate interaction occurrence, frequency and, in many cases, detailed data on feeding rates, foraging sequence, fruit handling behavior, etc. In our protocol, plant individuals are passively sampled with camera traps recording the pool of animal species visiting them. These data can be analyzed as individual-based interaction networks (e.g., Isla et al. 2023; Miguel et al. 2018) or pooled by plant species to build species-species interaction networks (Quintero et al. 2022). The continuous-time monitoring provided by the cameras allows the analysis of circadian patterns in visitation and activity of animals at fruiting plants (Ferreiro-Arias et al. 2021), as well as the combined role of diurnal and nocturnal frugivores (Jayasekara et al. 2013, Li et al. 2023).

Efficient pipelines for handling large volumes of videos are currently lacking standardization and are underdeveloped for ecological interaction data. Fortunately, recent advancements in artificial intelligence (AI) applied to image recognition (Leorna and Brinkman 2022, Rigoudy et al. 2022, Velez et al. 2023), coupled with the decreasing cost of camera trap devices, have made it possible to collect and manage high-quality data within a reasonable timeframe and with an affordable budget.

We have created FRUGIVORY CAMTRAP, a dataset that provides detailed data of plant-animal interactions between fleshy-fruited plant species and vertebrate frugivores at the finest resolution, i.e., the interaction event between two individuals. We collected camera trap records of frugivory interactions between fleshy-fruited plant individuals (N= 339) of 13 species and 59 animal species (46 birds and 13 mammals) spanning the fruiting seasons from 2018 to 2023. Overall, this dataset reports 10,659 records (interaction events) between plant individuals and frugivorous animal species. We leverage on flourishing AI-based techniques, to manage large amounts of video records (25,606 sampling days, totaling 614,544 recording hours) to get the most comprehensive camera trap dataset of frugivory interactions ever assembled, to the best of our knowledge, in any geographical area. This data paper provides essential information that can be used to investigate ecological interactions both at the species and individual-level and across multiple temporal and spatial scales.

Class I. Data Set Descriptors

A. Data set identity:

FRUGIVORY CAMTRAP: *A dataset of frugivory interactions recorded with camera traps*

B. Data set identification code:

Data S1.csv

Metadata S1.pdf

C. Data set description

Originators:

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Abstract:
Ecological interactions are a key component of biodiversity, essential for understanding ecosystem services and functioning. Recording and quantifying ecological interactions is challenging, frequently requiring complex logistics and substantial effort in the field. Camera traps are routinely used in ecology for various applications and have proven to be an excellent method for passive and non-invasive sampling of plant-animal interactions. We implemented a standardized camera trap protocol to document vertebrate frugivore-fleshy fruit plant interactions in Doñana National Park, SW Spain with the central objective of inventorying the diversity of plant-animal ecological interactions providing seed dispersal services. From 2018-2023 we recorded pairwise interactions from which we obtained qualitative (presence-absence) and quantitative (frequency of visits) information. Each record in the dataset contains information of a visit by an individual animal to an individual plant, resulting in any form of fleshy-fruit use and provides information on visitation phenology, visit length and feeding behavior. The dataset presented here includes 10,659 frugivory interaction events for 59 vertebrate species (46 birds, 13 mammals) recorded on 339 plant individuals from 13 different plant species which dominate the fleshy-fruited plant assemblage in the Doñana National Park. The most recorded animal species consuming fruits and playing a legitimate seed dispersal role was *Curruca melanocephala* (1678 records) among birds and *Vulpes vulpes* among mammals (751 records). *Cervus elaphus*, a fruit consumer with a marginal role as legitimate seed disperser, was the most recorded mammal species (1508 records). Avian frugivores, particularly those from the Sylviidae and Turdidae families, are widespread in the region and play a crucial role in maintaining the dispersal service for the fleshy-fruited plant populations in the area. The dataset offers highly versatile quantitative information that can be used to investigate frugivory from the highest resolution scale, the interaction event between pairs of individuals. In addition, other information that can be extracted includes the timing of interactions of animals and plants (their phenological couplings), activity periods of the animals, behavior during the events and preferences for individual plants within

populations. There are no copyright restrictions on the data. When using the data from this data paper in publications, we kindly request that you cite the paper accordingly. Additionally, we encourage researchers and educators to inform us about how they are using this data, as we value feedback and would like to be aware of its various applications.

D. Key words/phrases: *Artificial intelligence; camera traps; complex networks; Doñana National Park; frugivory; Mediterranean scrubland; mutualism; plant-animal interactions; seed dispersal.*

Class II. Research origin descriptors

A. **Overall project description:**

See Class II.B.

1. **Identity**:

A dataset of frugivory-interaction events between fleshy-fruited plant individuals and their animal consumers (mammals and birds) collected with cameras in Doñana National Park, SW Spain.

2. **Originators:**

The Doñana frugivory camtrap dataset was created by the Integrative Ecology Group of the Doñana Biological Station as part of the BioInteract work package under the SUMHAL project (LIFEWATCH- 2019-09-CSIC-4). The fieldwork design and coordination were carried out by Pablo Villalva, Blanca Arroyo-Correa, Gemma Calvo, Pablo Homet, Jorge Isla, Irene Mendoza, Eva Moracho, Elena Quintero, Francisco Rodríguez-Sánchez, and Pedro Jordano.

Species identification and validation: Pablo Villalva, Jorge Isla, Pedro Jordano, Elena Quintero, Margaret Hempp, Carlos Gutiérrez Expósito, Irene Mendoza.

3. **Period of study:**

2018-11-21 to 2023-04-17

4. **Objectives:**

The primary objective of this data paper was to compile field data on frugivory interactions using cameras to provide detailed information at different levels: the individual plant and the plant species. From the plant perspective, the monitoring scheme (individual-based frugivory events involving several plant individuals of various species) enables interaction analysis at both the individual and the species level. Interaction presence, visitation frequency and duration can be obtained for each sampled plant individual. An additional set of measures can also be obtained at the individual plant level including animal activity patterns, simultaneous monitoring of ripe fruit availability, and other phenological information. For a community-level approach, data can be pooled by species, allowing for a species-species interaction network analysis for the entire community.

From the animal perspective, only a species-level analysis is possible by now, as differentiating among unmarked animal individuals in the video footage remains challenging. However, species-level data are still invaluable to explore foraging preferences, fruit-handling behavior, circadian activity patterns of visitation, phenological patterns, fine-scale species coexistence, diurnal/nocturnal roles, etc.

The information provided in this study facilitates further research on the dynamics of plant-animal interactions and their implications for both plant and animal communities within Doñana National Park and beyond.

5. Sources of funding:

This study was funded by MICINN through the European Regional Development Fund [SUMHAL, LIFEWATCH-2019-09-CSIC-4, POPE 2014-2020], with additional funding (PJ) from grant PID2022-136812NB-I00 by MCIN/AEI/10.13039/501100011033. IM was supported by the grant PID2020-115129RJ-I00 by MCIN/AEI/10.13039/501100011033.

B. Specific subproject description:

1. *Site description*

The Doñana National Park (SW Spain) is a unique protected area characterized by a rich diversity of natural habitats typical of Mediterranean ecosystems. The provision of fleshy fruits for seed dispersal (the so-called endozoochorous dispersal syndrome) is well represented among Mediterranean woody species in Doñana, where a significant number of these species rely on vertebrates for endozoochorous seed dispersal (Jordano, 2014). As a result, this natural area emerges as a key site for monitoring and studying animal-plant frugivore interactions in the Mediterranean. In addition, aquatic birds have also been reported as important endozoochorous dispersers of plant propagules for many species not producing fleshy fruits (e.g., grasses, aquatic plants, sedges; Soons et al. 2013), yet these non-fleshy fruited species are not considered in this dataset.

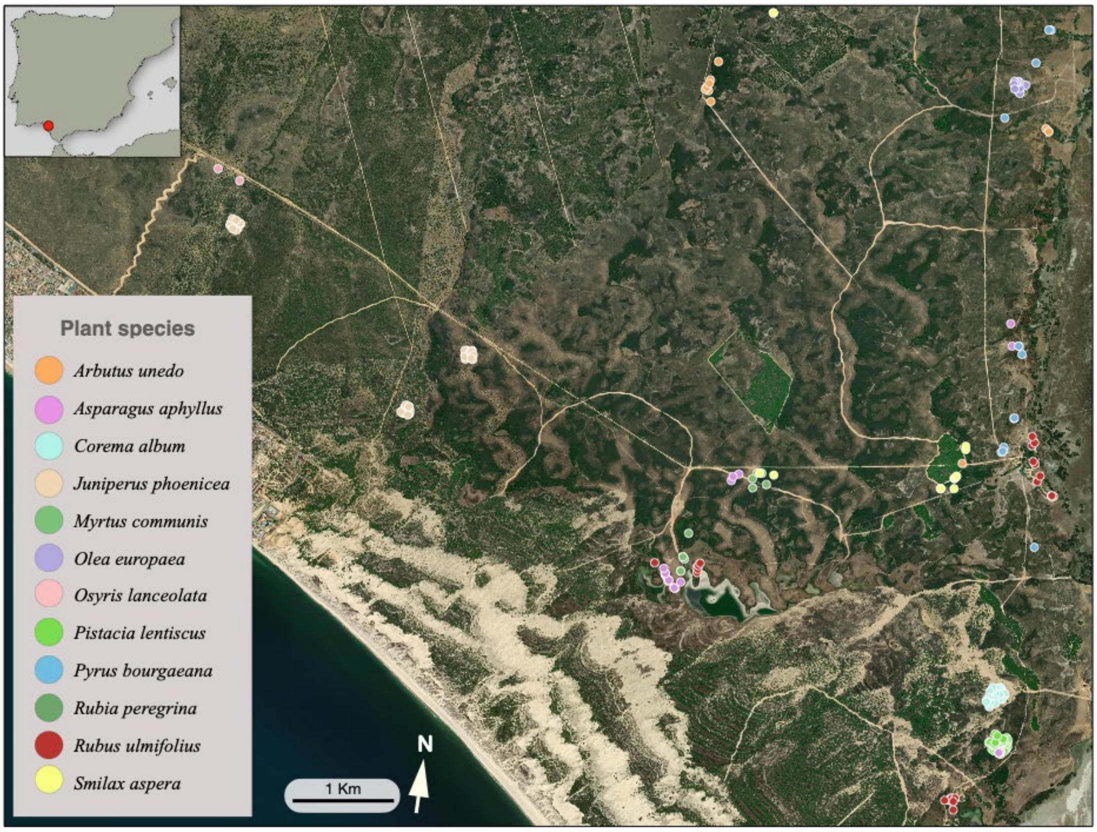


Figure 1. Study area and focal plants monitored within Doñana National Park. The inset shows the location of the study area in the Iberian Peninsula. Dots on the map represent individual plants from 13 different species. Note that the study site for *Juniperus oxycedrus* ssp. *macrocarpa* does not appear on this map as it is located 15 km southeast from the lower limit of the map.

Doñana National Park is located in the Atlantic coast of SW Spain (37° 0' 29" N -6° 30' 24" W, 25 m a.s.l.) within the Mediterranean basin, and represents a remarkable protected area in Europe. It boasts a diverse array of terrestrial and aquatic ecosystems, encompassing pine and cork oak woodlands, scrublands, grasslands, sand dunes, and marshlands. This extensive range of ecosystems provides habitat for a rich biodiversity. Notably, there are over 1,300 plant species in the area, 170 of which are Iberian endemisms, and more than 300 species of birds and 50 species of mammals (Green et al. 2016). Producing fleshy fruits for seed dispersal is a frequent characteristic among Doñana woody plant species. In fact, up to 64% of woody species found in Spanish Mediterranean scrublands, many of which are present in Doñana, have adapted to endozoochorous seed dispersal by vertebrates (Herrera 1984, Jordano 1984), and up to 28 species are found in our study area with additional 2-3 exotic species (not included in our sampling).

The study area is situated within the Doñana Biological Reserve and its immediate surroundings, a core area spanning 6,794 ha within Doñana National Park (Fig. 1). This Reserve boasts a high level of protection and minimal management, representing an exceptional site for investigating ecological and evolutionary processes. Our study encompassed the principal Mediterranean plant communities that harbor a diverse range of fleshy-fruited species in the area (Fig. 2). We monitored with camera traps a total of 13 species out of the 28 fleshy-fruited species recorded in the area, excluding 2-3 exotic species. The plant communities studied include (see e.g., Rivas-Martínez et al. 1980): (i) *Juniperus*-dominated woodlands, (ii) Sclerophyllous scrublands primarily dominated by *Pistacia lentiscus*, alongside other fleshy-fruited species, (iii) Scrublands comprising a variety of fleshy-fruited plant species, occasionally dominated by *Arbutus unedo*, *Olea europaea* var. *sylvestris*, or *Myrtus communis*, (iv) Humid scrublands located in depressions ("monte negro"), predominantly dominated by *Rubus ulmifolius*, and (v) Coastal dunes characterized by dominant species such as *Corema album* or *Juniperus oxycedrus* subsp. *macrocarpa*.

Figure 2. Plant species with fleshy fruits in Doñana Natl. Park (SW Spain). Asterisks indicate the species surveyed with remote cameras, included in this study. a, *Arbutus unedo* (Ericaceae); b, *Arum italicum (*Araceae*);* c, *Asparagus acutifolius* (Asparagaceae); d, *Asparagus aphyllus* (Asparagaceae); e, *Bryonia dioica* (Cucurbitaceae); f, *Chamaerops humilis* (Arecacae); g, *Corema album* (Ericaceae); h, *Crataegus monogyna* (Rosaceae); i, *Daphne gnidium* (Thymaeleaceae); j, Frangula alnus (Rhamnaceae); k, *Ficus carica* (Moraceae); l, *Juniperus oxycedrus* subsp. *macrocarpa* (Cupressaceae); m, *Juniperus phoenicea* (Cupressaceae); n, *Lonicera periclymenum* (Caprifoliaceae); o, *Myrtus communis* (Myrtaceae); p, *Olea europaea*, var. *sylvestris* (Oleaceae); q, *Rubia peregrina* (Rubiaceae); r, *Osyris alba* (Santalaceae); s, *Osyris lanceolata* (Santalaceae); t, *Phillyrea angustifolia* (Oleaceae); u, *Pistacia lentiscus* (Anacardiaceae); v, *Pyrus bourgaeana* (Rosaceae); w, *Rhamnus lycioides* (Rhamnaceae); x, *Ruscus aculeatus* (Asparagaceae); y, *Rubus ulmifolius* (Rosaceae); z, *Smilax aspera* (Smilacaceae); aa, *Tamus communis* (Disocoreaceae); ab, *Vitis vinifera* var. *sylvestris* (Vitaceae). Photograph in panel f by Miguel Jácome-Flores, all other panels by Pedro Jordano.

2. *Experimental and sampling design*

Over a span of 5 years (four complete fruiting seasons; 2018-11-21 to 2023-04-17), we monitored 339 plant individuals belonging to 13 distinct fleshy-fruited plant species, out of a total of 28 species present in the area (Fig. 2). Species not included in the camera-trap set up were scarce, or not found locally, or just not adequate for monitoring by this method when compared with other types of sampling methods. The number of individuals per plant species ranged from 3 to 105 (Table 1). In most cases individual plants for setting up the cameras were selected haphazardly (not randomly) in order to favor plant locations adequate for the visual field of the camera, distance separation between camera and plant, and adequate fruit crop size that could result in visit records. Yet the selection also aimed to include individual plants representative of the growing conditions in the area, i.e., variable canopy openness, local density of conspecifics, variable plant size and crop size. Our monitoring efforts spanned the whole fruiting season of these plant species, resulting in an unequal sampling effort (Fig. 3). Sampling time was variable between plant species, ranging from 20 to 365 days according to variation in fruiting phenology. Fig. 3 shows, at the plant species level, the balance between sampling effort in days and number of interactions detected.

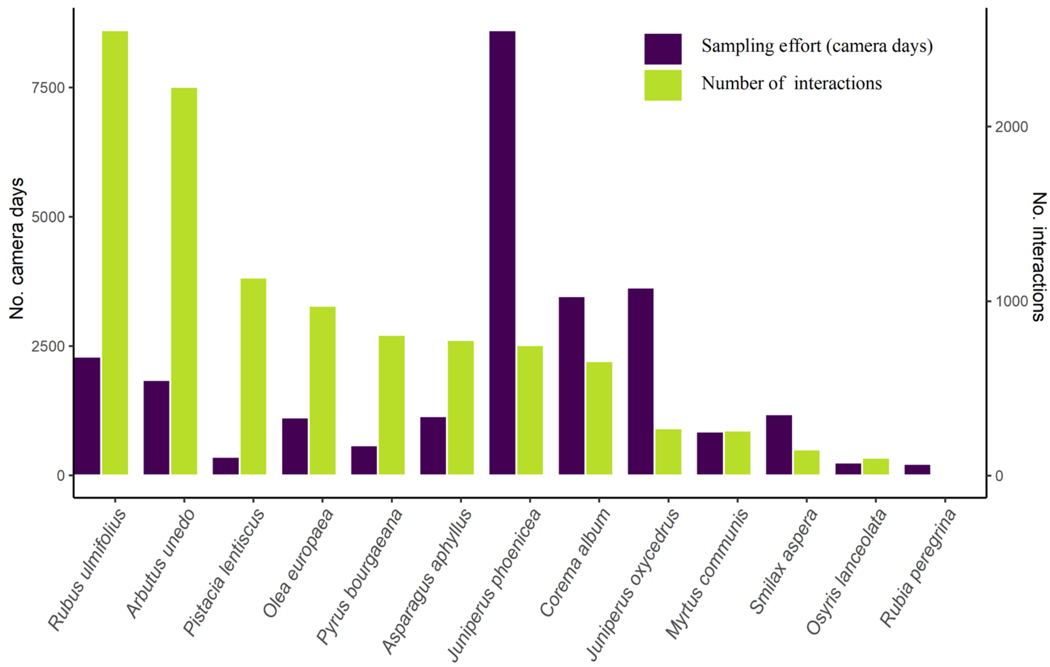


Figure 3. Number of frugivory interactions recorded and the corresponding sampling effort (in days) for each plant species. The left y-axis represents sampling effort, while the right y-axis represents the number of interactions recorded. Note how plant species with high sampling effort do not necessarily record a high number of interactions. e.g., *Juniperus phoenicea* vs. *Rubus ulmifolius*.

The cameras were set in video mode, providing valuable insights for identifying animal species, but also annotating specific foraging behaviors and estimating fruit consumption rates for certain species, as well as fruit-picking and fruit handling behaviors (e.g., Moermond and Denslow 1985, Levey 1987) (see Da Silva and Dos Reis 2019). In our field sampling, we deployed a total of 70 cameras, including 50 Browning Dark Ops®, 10 Bushnell Trophy® cam Aggressor, and 10 GoPro®

cameras. These cameras were strategically positioned towards different plant individuals bearing fleshy fruits. Sensor-triggered camera traps were used for 12 plant species, while continuous recording with GoPro® cameras was used for sampling *Pistacia lentiscus*. Regular checks of the camera traps (batteries and SD-cards restarting) were conducted at regular intervals, either weekly or biweekly, depending on the plant species and the specific period of the year.

Table 1. Summary of sampling method and experimental results. The table includes information on the number of individuals sampled, the seasons during which sampling occurred, the duration of the sampling period in months, the plant's phenology, the overall sampling effort for each species, and the survey method employed (ST-CT, which stands for Sensor-Triggered Camera-Trap, and Go-Pro, which involves continuous recording with surveillance-type cameras). It also presents the number of interactions and the count of animal species recorded for each plant species.

Plant species	No. indiv.	Sampling seasons	Sampling duration (months)	Plant phenology	Sampling effort (days)	Method	No. interactions	No. species	Fruit type
Asparagus aphyllus	24	2021-22	6	Oct - Dec	1144	ST-CT	777	13	Berry
Arbutus unedo	19	2021-23	8	Dec - Jan	1846	ST-CT	2229	24	Berry
Corema album	25	2020-21	12	Jul - Oct	3465	ST-CT	656	18	Drupe
Juniperus oxycedrus	29	2020-23	9	Dec - Mar*	3632	ST-CT	270	9	Cone
Juniperus phoenicea	105	2018-20	17	Sep - Feb*	8610	ST-CT	806	17	Cone
Myrtus communis	12	2021-23	9	Dec - Feb	849	ST-CT	257	12	Berry
Olea europaea var. sylvestris	16	2021-23	8	Nov - Dec	1119	ST-CT	967	20	Drupe
Osyris lanceolata	3	2022-23	6	Sep - Feb*	247	ST-CT	102	9	Drupe
Pyrus bourgaeana	12	2021	4	Sep - Nov	584	ST-CT	806	16	Pome
Pistacia lentiscus	42	2018-20	8	Sep - Mar	358**	Go-Pro	1134	22	Drupe
Rubia peregrina	3	2021	2	Sep - Nov	224	ST-CT	5	3	Berry
Rubus ulmifolius	35	2021-22	7	Jul - Aug	2299	ST-CT	2555	37	Poli drupe
Smilax aspera	14	2021-23	10	Oct - Mar	1187	ST-CT	150	11	Berry

*Species produce ripe fruits almost continuously (*O. lanceolata*) or may keep ripe fruits from one year to the next in mast years (*Juniperus*). In the case of junipers, surveys were restricted to the fruit production peak periods.
** The sampling effort is referenced in terms of sampling days, with the important caveat that each day corresponds to 2.2 hours of recording per individual.

3. *Research methods*

3.1 Field sampling design

We selected potential target species to be monitored through cameras aiming to include all the fleshy-fruit producing species (Valdés et al. 2007; Fig. 2); yet not all species are amenable to monitor with camera traps due to differences in growth-habit, fruiting display, growing site, etc. that in certain cases prevent an adequate set up of the cameras. After selecting the target species, we created a phenology timeline to help organize camera deployment in the field. Later we exhaustively searched and selected plant individuals bearing ripe fruit on the field. As mentioned above, plants were not randomly selected because this would have caused the inclusion of individuals not adequate for monitoring with cameras either because of small fruit crops, visibility/cover conditions, orientation, etc. Yet the selection of individual plants included a broad range of growing conditions and adequately captured the environmental variance of the plants growing sites. This selection was a continuous process maintained throughout the entire survey. Cameras were placed in front of selected individuals without manipulating the plant or its surroundings to maintain unaltered the natural conditions of the potential interactions. Each camera was placed on a pole framing the entire individual or just a portion of it where the fruits were located (e.g., for *Juniperus* sp. the whole individual was in the field of view, while for *Rubus ulmifolius* only a portion of it). When the camera could not capture complete images of an individual (canopy + ground), we placed at least two cameras to obtain information on animal species feeding on the canopy as well as fallen fruits on the ground.

3.2 Data extraction protocol

We developed an image processing workflow specifically designed for integrating video recordings and creating extensive and accurate databases of frugivore interactions using camera traps. To effectively manage the large and complex dataset, we adapted the structure of the Camera Trap Data package (Bubnicki et al. 2023), a standardized structure for managing camera trap data, to our sampling design. This *ad hoc* structure provides a well-organized framework for controlling camera-trap ecological-interaction data across three levels, which are represented in three plain text files: *Deployments*, *Revisions*, and *Observations*.

The *Deployment* table contains all metadata regarding deployment, location and setup of each camera. The Revision table documents the video file batches obtained during each revision, which corresponds to field visits for tasks such as changing batteries and/or memory cards. The *Observation* table provides the deeper level of detail at the video level following the review of each video file. This structured methodology enables us to efficiently handle and analyze the data extracted from the video recordings.

Collecting data through camera trap video sampling presents challenges, particularly regarding data storage and management due to the large volume of information generated. One common issue encountered in camera trap monitoring is the generation of numerous empty video batches, especially in environments with high wind levels where camera activation can be erroneously triggered by the movement of vegetation, such as grasses and tree branches. To address this challenge, we developed a streamlined protocol that facilitates the creation of extensive databases from video recordings while reducing the time and effort required.

In order to remove empty videos lacking animal presence, we employed the computer vision model *Megadetector* (Beery et al. 2019). We used MD.v.4 during the first fruiting season (year 2020-21) and upgraded to MD.v.5 for the second fruiting season (2022-23) following the release of the enhanced version. For analyzing the video recordings of *Pistacia lentiscus*, we utilized the *DeepMeerkat* software developed by Weinstein (2018) to detect animal visits and then analyzed all videos manually to identify bird species and consumption behavior.

Our protocol encompasses three key stages. In the first stage, *pre-processing*, we established a standardized protocol for camera trap settings, video dumping, and control of sampling effort. This ensures consistency and accuracy in data collection. During the second stage, *processing*, we implemented automatic image recognition to classify empty videos and enhance video visualization to identify species and their behaviors through the *Timelapse* program (Greenberg, 2020). This stage allows us to optimize time and extract meaningful information efficiently. In the third stage, *post-processing*, we integrate diverse datasets from different video batches (different seasons, focal species and cameras) and consolidate them for comprehensive analysis obtaining a cohesive dataset for further exploration and interpretation. A detailed description of our ecological interaction sampling protocol using camera traps is available in Villalva & Jordano (2023).

Camera traps were set up to record ten-second videos to capture plant-animal interaction events and the resulting fruit use, if any. In case of multiple animals showing up in a single 10s video (e.g., bird flocks), we counted each animal and annotated the number of individuals in a unique record. However, the 10s duration for the videos resulted in instances where multiple sequential videos captured the same interaction event (i.e., a single visit by an individual animal), leading to high temporal autocorrelation in the data and potential overestimation of visit rates if each 10s video is counted as an interaction. In order to address this issue and ensure independent sampling of interaction events, we collapsed all sequential videos where the same species appeared and recorded within up to a 5-min interval (and thus, likely attributable to the same individual animal) as a single visit event by the same frugivorous animal. We must point out that choosing different aggregation intervals could result in different visit rate estimators, i.e., visit rates might be overestimated (by using short time intervals) or underestimated (by using long time intervals). Thanks to our experience with observations at focal plants and visit duration, 5 min appears adequate as a compromise to avoid pseudoreplication and overestimation of interaction frequencies (Hjel et al. 1990). As a result, we merged a total of 7,734 videos, yielding 3,541 five-min events (single visitation events to individual plants); this implies that the aggregation affected 41% of all the 18,840 videos sampled. Most of these cases (74% of the collapsed records) were for mammal species (e.g., *Vulpes vulpes*, *Cervus elaphus*) typically with long visits when the camera is sequentially triggered multiple times. For the birds, most cases involved warbler species (*Curruca communis*, *C. melanocepahala*) and the *Turdus merula* (30%, 21%, and 17%, respectively), all of them with short visits to the plants and involving the collapse of few sequences (2-5 successive videos for a single visit record). Thus, in most cases, aggregating at 5 min intervals would not result in serious bias in the estimation of the actual interaction frequency, as most visits by frugivores tend to be very short (<< 5 min in duration) and the aggregation mostly affected recordings of longer visits by mammals; in turn, this would avoid the obvious overestimation bias of recording a single record in a 10 s clip as a single interaction (see e.g., Hjel et al. 1990). Careful consideration should be given to those aspects of pseudoreplication and redundant recordings when comparing across datasets with the objective of estimating visit rates. In this way, we reduced the number of records to approximate the number of actual visits (interaction events) by frugivores to plants (Fig. 4). While this protocol was used for camera trap monitoring with 10 s-triggered recordings, the continuous surveillance mentioned for *P. lentiscus* enabled the recording of complete visitation sequences, without requiring collapsing independent video clips.

Whenever available, the duration of the consumption event can be used as an indicator of the interaction strength, providing valuable information on the intensity of the interaction, especially when combined with the fruit consumption rate for the species (Vázquez et al. 2005). Overall, the dataset comprises 10,659 records for 46 bird species and 13 mammal species (Fig. 4, Table 2).

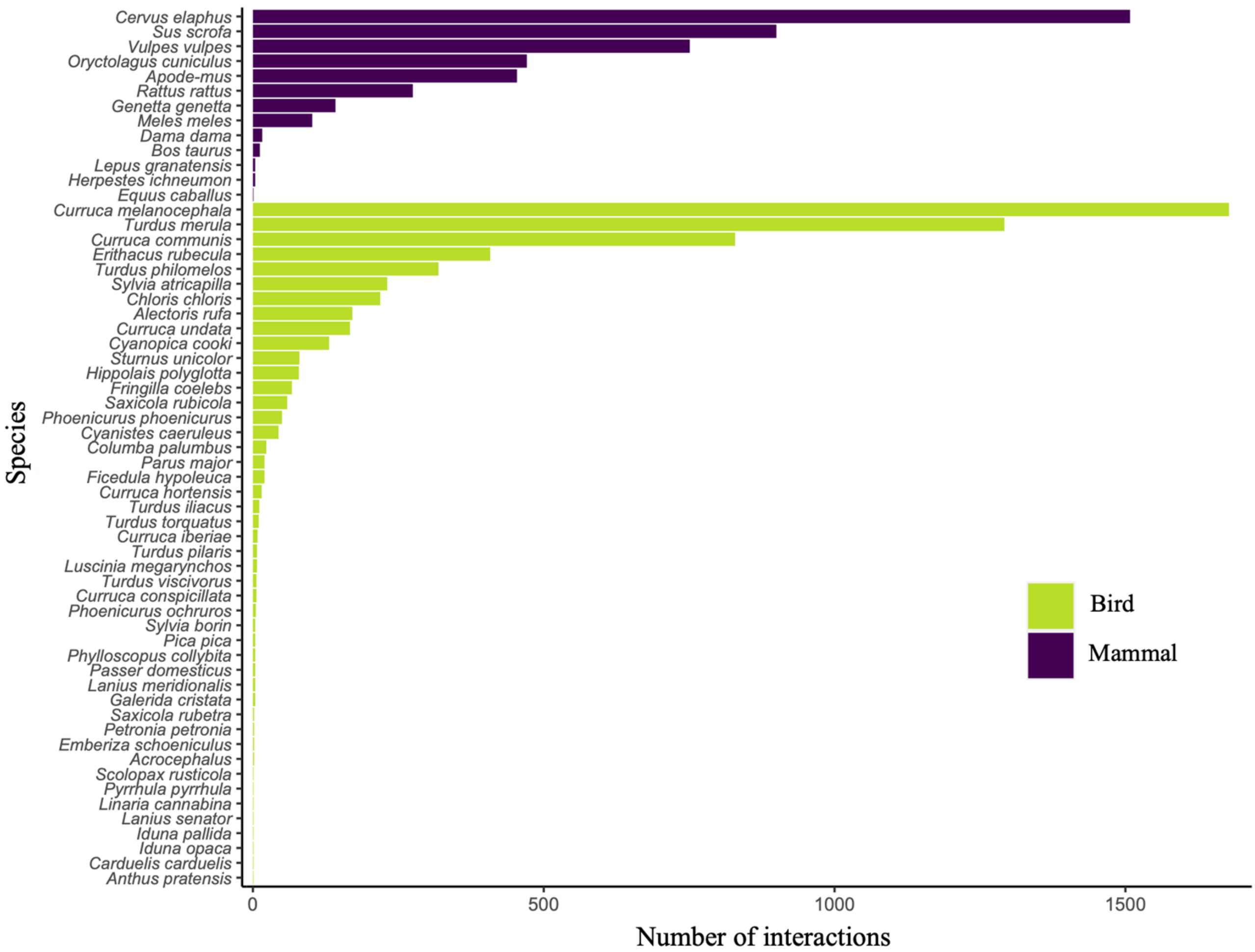


Figure 4. Total number of interactions recorded for different frugivore species in the study area. The frugivore species assemblage in the study area exhibited a total of 10,659 recorded interactions, including 13 mammal species and 46 bird species.

4. *Taxonomic Data*

Identification of species was assessed by experienced researchers. Species names for animals and plants are included in Table 2 (also see Fig. 5), according to standard lists of plants (WCVP 2022), and animals (birds, Gill et al. 2023; mammals, Wilson et al. 2019).

Table 2. Scientific names and taxonomic arrangement of species included in this study.

BIRD SPECIES

Family	Scientific name	Family	Scientific name
Acrocephalidae	*Acrocephalus scirpaceus*	Muscicapidae	*Saxicola rubicola*
Acrocephalidae	*Hippolais polyglotta*	Paridae	*Cyanistes caeruleus*
Acrocephalidae	*Iduna opaca*	Paridae	*Parus major*
Acrocephalidae	*Iduna pallida*	Passeridae	*Passer domesticus*
Alaudidae	*Galerida cristata*	Passeridae	*Petronia petronia*
Columbidae	*Columba palumbus*	Phasianidae	*Alectoris rufa*
Corvidae	*Cyanopica cooki*	Phylloscopidae	*Phylloscopus collybita*
Corvidae	*Pica pica*	Scolopacidae	*Scolopax rusticola*
Emberizidae	*Emberiza schoeniclus*	Sturnidae	*Sturnus unicolor*
Fringillidae	*Carduelis carduelis*	Sylviidae	*Sylvia atricapilla*
Fringillidae	*Chloris chloris*	Sylviidae	*Sylvia borin*
Fringillidae	*Fringilla coelebs*	Sylviidae	*Curruca iberiae*
Fringillidae	*Linaria cannabina*	Sylviidae	*Curruca communis*
Fringillidae	*Pyrrhula pyrrhula*	Sylviidae	*Curruca conspicillata*
Laniidae	*Lanius meridionalis*	Sylviidae	*Curruca hortensis*
Laniidae	*Lanius senator*	Sylviidae	*Curruca melanocephala*
Motacillidae	*Anthus pratensis*	Sylviidae	*Curruca undata*
Muscicapidae	*Erithacus rubecula*	Turdidae	*Turdus iliacus*
Muscicapidae	*Ficedula hypoleuca*	Turdidae	*Turdus merula*
Muscicapidae	*Luscinia megarhynchos*	Turdidae	*Turdus philomelos*
Muscicapidae	*Phoenicurus ochruros*	Turdidae	*Turdus pilaris*
Muscicapidae	*Phoenicurus phoenicurus*	Turdidae	*Turdus torquatus*
Muscicapidae	*Saxicola rubetra*	Turdidae	*Turdus viscivorus*

MAMMAL SPECIES		PLANT SPECIES	
Family	**Scientific name**	**Family**	**Scientific name**
Bovidae	*Bos taurus*	Asparagaceae	*Asparagus aphyllus*
Canidae	*Vulpes vulpes*	Ericaceae	*Arbutus unedo*
Cervidae	*Cervus elaphus*	Ericaceae	*Corema album*
Cervidae	*Dama dama*	Cupressaceae	*Juniperus oxycedrus* subsp. *macrocarpa*
Equidae	*Equus caballus*	Cupressaceae	*Juniperus phoenicea*
Herpestidae	*Herpestes ichneumon*	Myrtaceae	*Myrtus communis*
Leporidae	*Oryctolagus cuniculus*	Oleaceae	*Olea europaea* var. *sylvestris*
Leporidae	*Lepus granatensis*	Santalaceae	*Osyris lanceolata*
Muridae	*Rattus rattus*	Rosaceae	*Pyrus bourgaeana*
Muridae	*Apodemus sylvaticus/Mus spretus*	Anacardiaceae	*Pistacia lentiscus*
Mustelidae	*Meles meles*	Rubiaceae	*Rubia peregrina*
Suidae	*Sus scrofa*	Rosaceae	*Rubus ulmifolius*
Viverridae	*Genetta genetta*	Smilacaceae	*Smilax aspera*

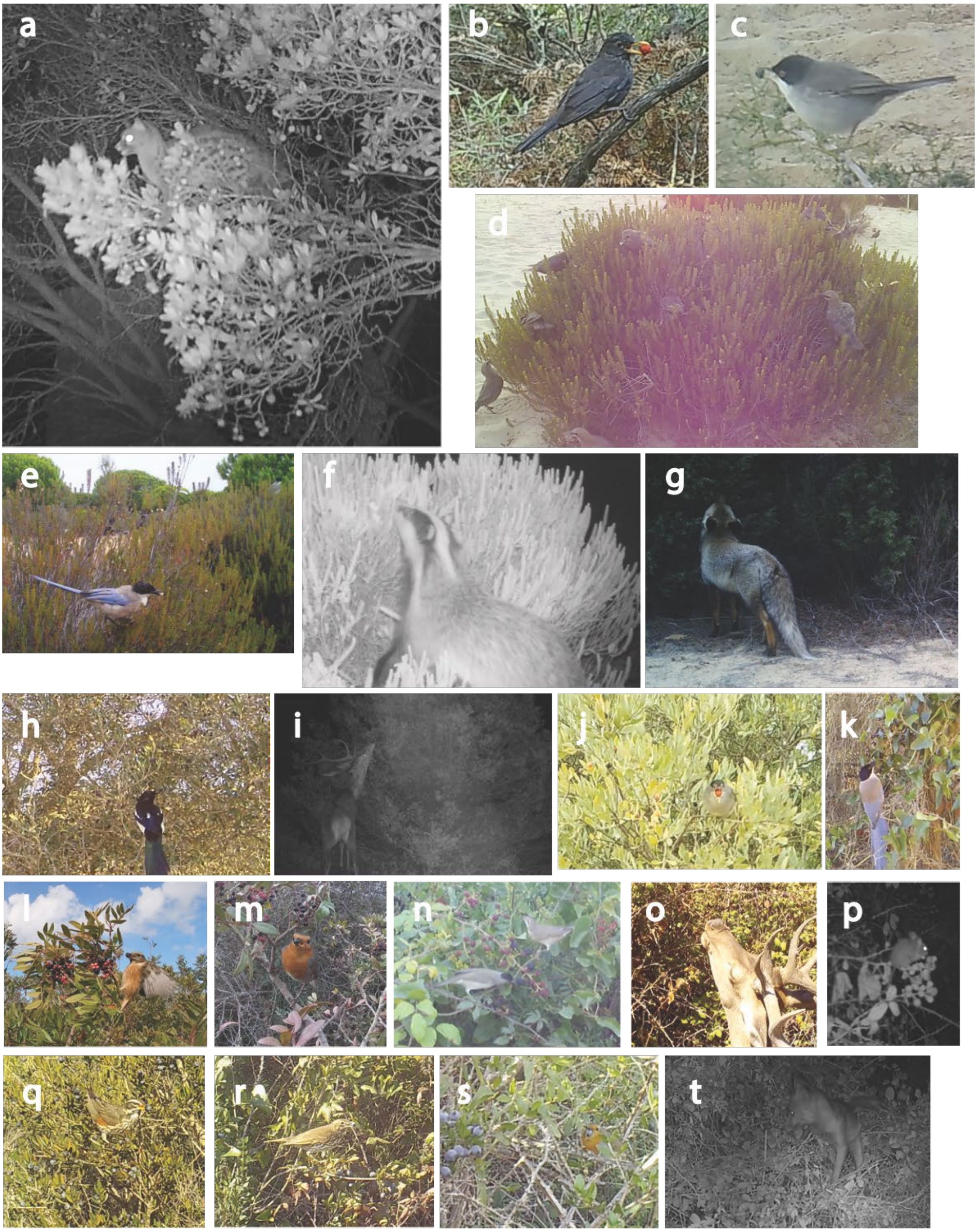


Figure 5. Examples of frugivore visits recorded with camera traps at the studied plant species in Doñana Natl. Park (SW Spain). a, *Arbutus unedo* - *Genetta genetta*; b, *A. unedo* - *Turdus merula*; c, *Asparagus aphyllus* - *Curruca melanocephala*; d, *Corema album* - *Sturnus unicolor*; e, *C. album* - *Cyanopica cooki*; f, *Juniperus phoenicea* - *Meles meles*; g, *J. phoenicea* - *Vulpes vulpes*; h, *Olea europaea* var. *sylvestris* - *Pica pica*; i, *O. europaea* - *Cervus elaphus*; j, *Osyris lanceolata* - *Sylvia atricapilla*; k, *Smilax aspera* - *Cyanopica cooki*; l, *Pistacia lentiscus* - *Saxicola rubicola*; m, *P. lentiscus* - *Erithacus rubecula*; n, *Rubus ulmifolius* - *Sylvia atricapilla* and *S. borin*; o, *R. ulmifolius* - *Cervus elaphus*; p, *R. ulmifolius* - *Apodemus sylvaticus*; t, *R. ulmifolius* - *Vulpes vulpes*; q, *Myrtus communis* - *Turdus iliacus*; r, *M. communis* - *Turdus philomelos*; s, *M. communis* - *Erithacus rubecula*. Photograph in panel g by Jorge Isla, panels l and m by Elena Quintero, all other panels by Pablo Villalva.

C. **Data Limitations and Potential Enhancements:**

This dataset offers valuable insights for individual-level and community-level (e.g., Fig. 6 and 7) as well as zoocentric approaches (e.g., activity daily patterns), allowing for a broader understanding of plant-animal interactions in the ecosystem. Beyond the limitations described below, the utility of this dataset lies in the high-resolution interaction recording at the level of the interaction event, which allows us to more deeply understand frugivory patterns at different temporal (inter-annual, intra-annual and circadian variation) as well as spatial scales. For comparative analyses among plant species, we advise users to take into account imbalances in sampling effort and the number of focal

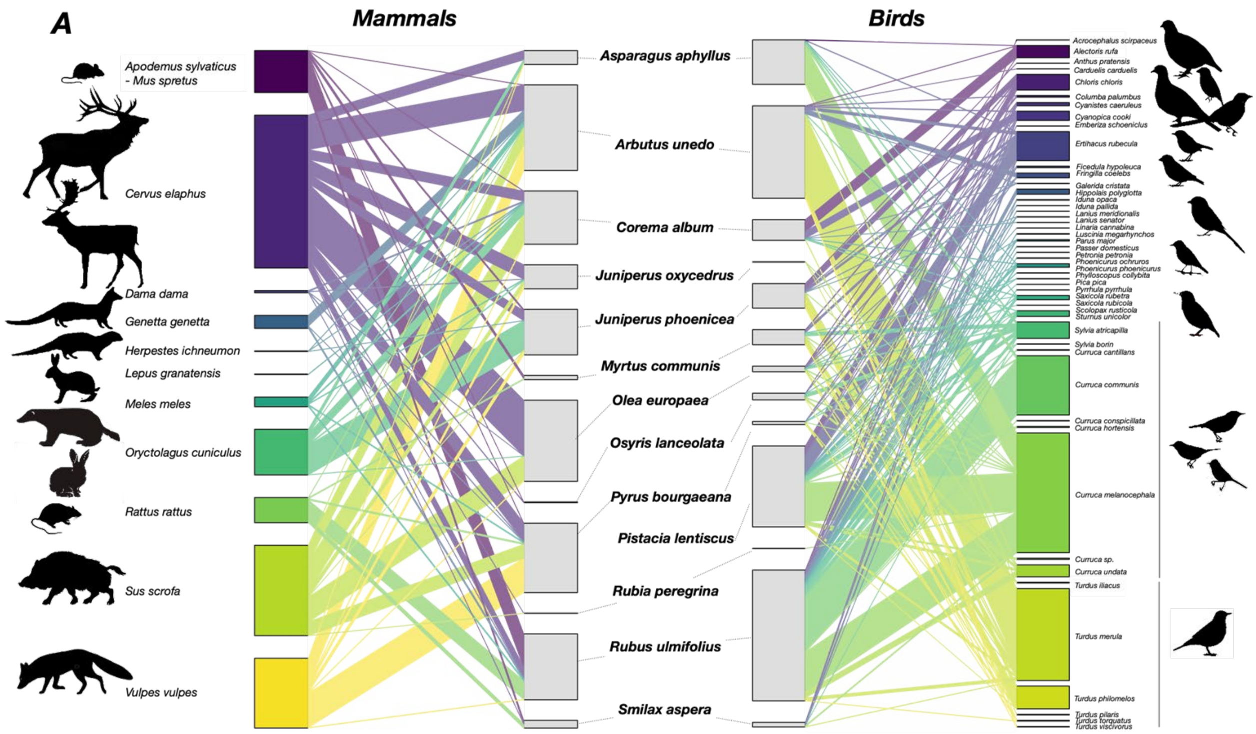


Figure 6. Interaction networks between animal consumers and plant species included in this dataset. The size of the nodes (rectangles) and links in the network (lines) are proportional to the number of frugivore events (mammal species, left; avian species, right) recorded for each plant species, providing a visual representation of the dataset's composition. Additionally, this diagram demonstrates the potential for analyzing the dataset using a community-level approach by assessing species-level interaction patterns. The species-level frugivore assemblages were estimated by summing up all interactions recorded on the monitored plant individuals of each plant species.

plants sampled per plant species (particularly, *Pistacia lentiscus* and *Juniperus phoenicea* were both more exhaustively sampled in terms of number of plant individuals than other species) as we will state below.

It is worth emphasizing that camera-trap sampling can be biased for certain species for which other sampling methods could be more adequate. In any case, it is the combination of sampling methods that provides the most complete record of ecological interactions in this species assemblage (Quintero et al. 2022). For example, compared to fecal-based sampling (using either direct analysis of fruit/seed contents or DNA-barcoding techniques), records from camera traps may fail to detect very rare interactions, especially those involving rare plant species in the area which may be more difficult to cover with cameras. This dataset has the potential to be enriched from a community-scale perspective by integrating various methods used in plant-animal interaction surveys conducted in the same area and time span. The combination of direct observations at focal plant individuals, and identification of frugivore species by DNA-barcoding of regurgitated/defecated seeds in scats, with camera trap

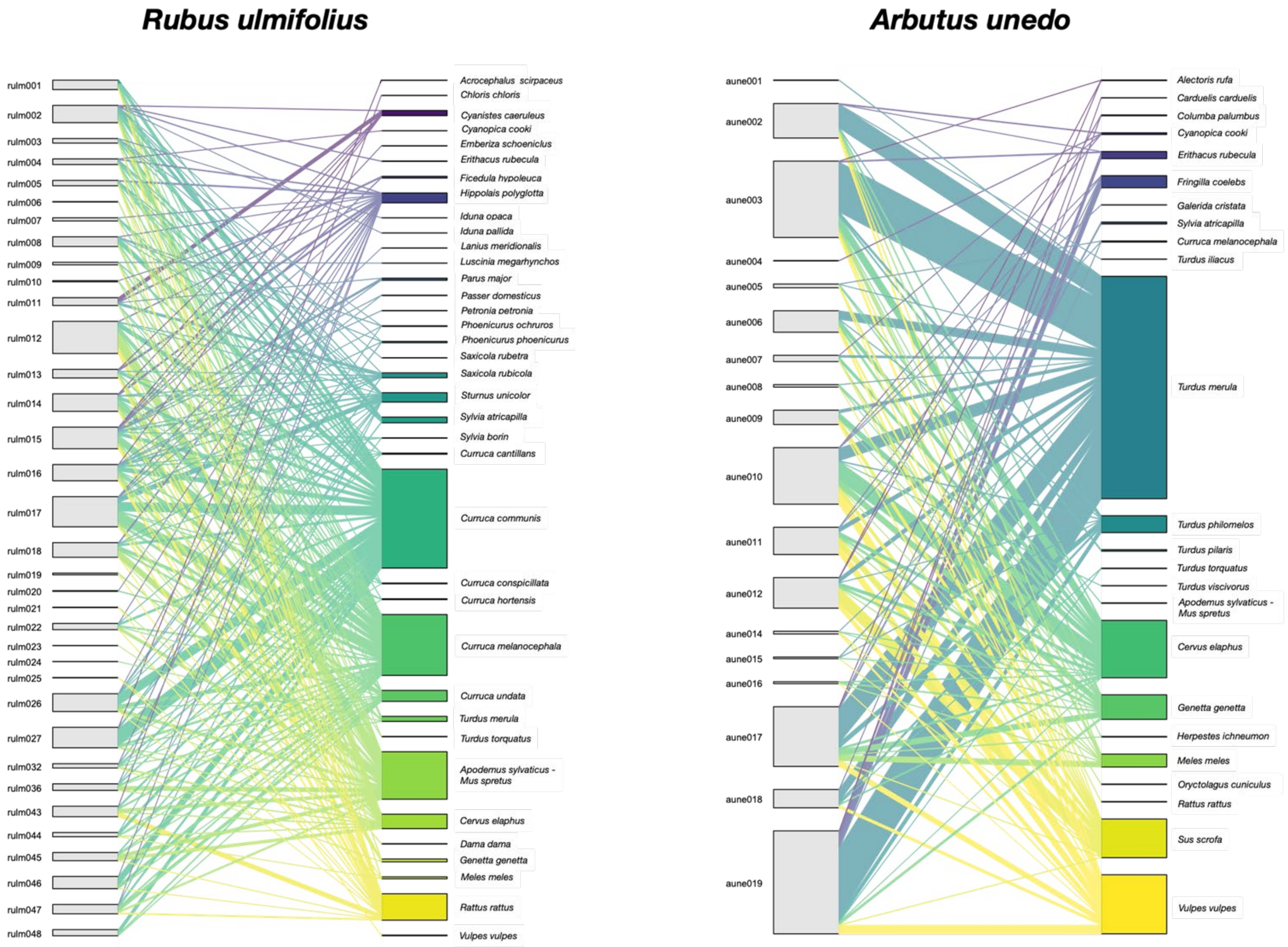


Figure 7. Examples of interaction networks between animal consumers and individual plants (spatially-isolated clones, in the case of *Rubus*) for *Rubus ulmifolius* and *Arbutus unedo*. The node and link width is proportional to the total number of frugivore events recorded on each individual plant of the species (rectangles in gray) or for animal species (rectangles in color). This figure shows how the dataset can be analyzed within an individual-level approach. Link widths indicate the relative strength (in terms of proportion of visitation records) of use of different individual plants by different frugivorous animal species.

data will provide a more comprehensive and complementary dataset (Quintero et al. 2022). Beyond limitations of species sensitivity to different sampling methods, the robustness of all these sampling schemes crucially depends on sampling effort (Jordano 2016), as usually occurs in biodiversity monitoring.

Reliance on AI algorithms for identification of empty videos (i.e., the camera triggered by wind or accident) with no animal visits imposes additional issues, especially in relation to the automatic filtering of empty videos or videos with animal presence but unrelated to fruit consumption (i.e., false negatives and false positives, respectively). For instance, false negatives (i.e., failure to record some interactions, either because the deployment is not suitable to capture them, or computer vision failed to detect them); and false positives (i.e., visitation without actual fruit handling or consumption). Beyond unbalanced sampling effort, that information on false negatives and positives is important to detect possible biases in the number of interactions recorded for some animal or plant species.

Regarding sampling completeness, we have estimated the accumulation curve for the interaction richness (number of unique species-species interactions) accumulation curve of the overall sampling across species, suggesting that the overall effort at the community level was adequate to effectively capture the interaction richness in the plant-frugivore assemblage with our camera trap approach (Fig. 8). However, some species appeared to be undersampled by this method, either because of their low abundance during the monitoring period, or because they could be better

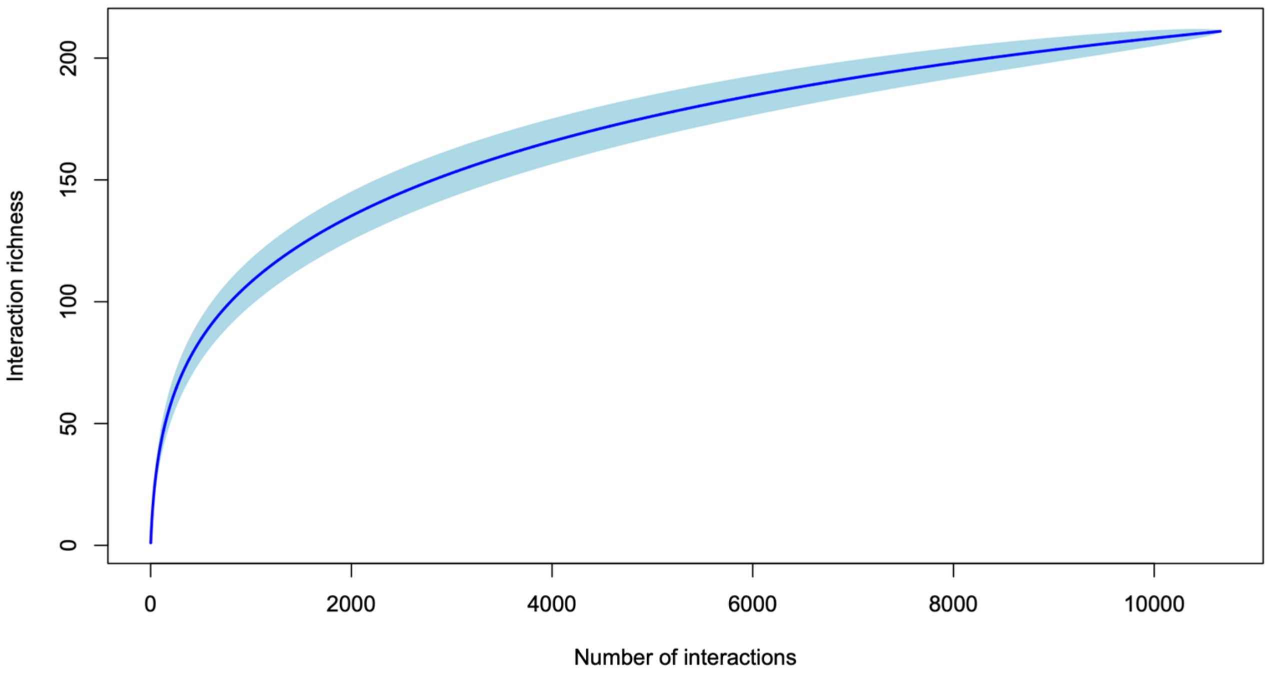
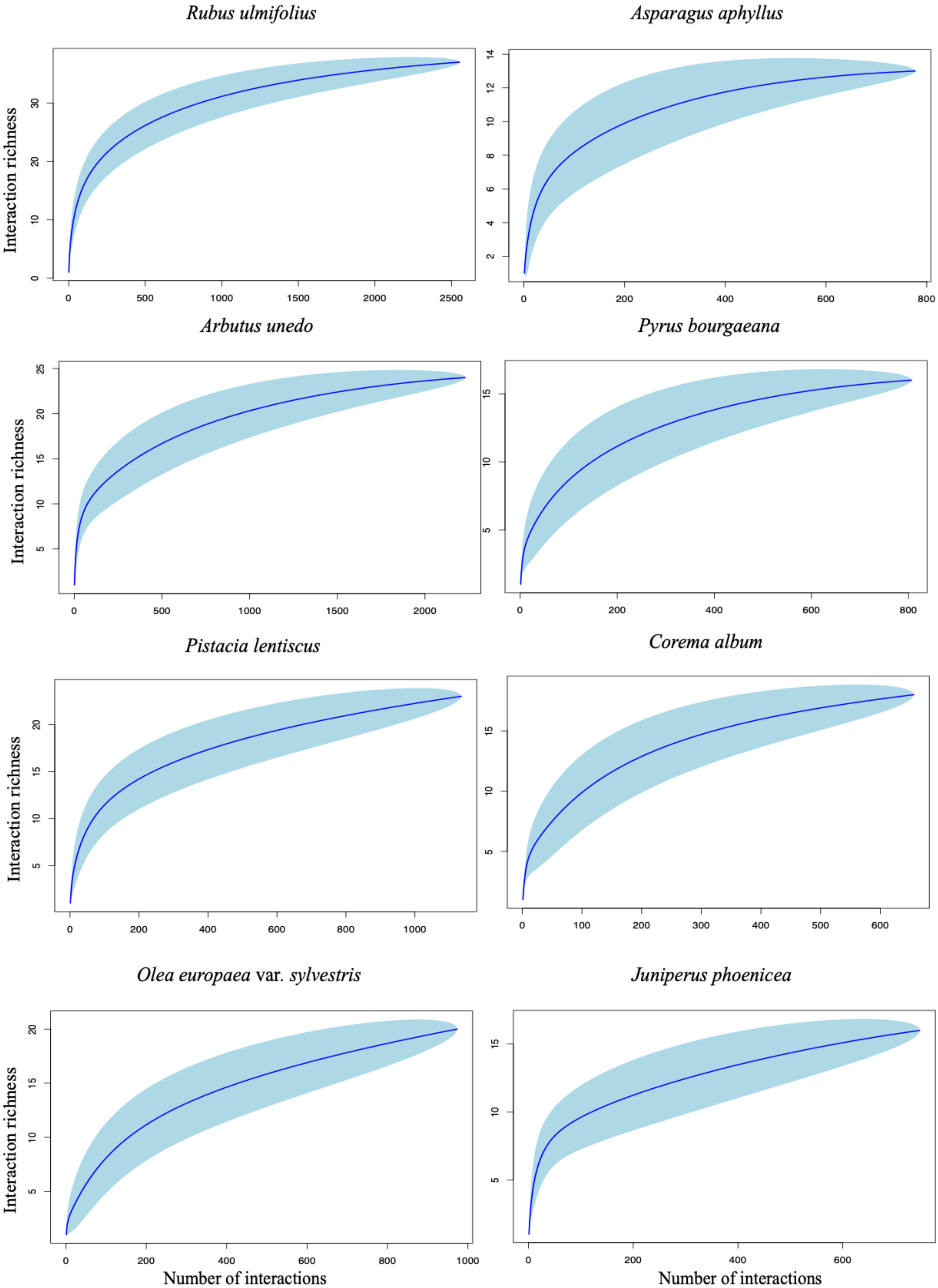


Figure 8. Sampling completeness at community level. Accumulation curve of interaction richness (IAC, number of distinct, species-species, pairwise interactions recorded) in relation to increasing sampling effort in terms of number of interactions recorded. This accumulation curve is analogous to species diversity accumulation curves (SAC, for the cumulative number of species sampled in relation to increasing number of individuals sampled) routinely used in biodiversity sampling (Gotelli and Colwell 2011, Chacoff et al. 2012, Jordano 2016). In our sample, the curve approaches an asymptote, indicating that further sampling efforts are unlikely to reveal a significant number of new interactions between frugivores and plant species. The blue line represents the mean estimate, and the light blue shadow represents the 95% confidence interval surrounding the estimate. The IAC was estimated with package vegan (Oksanen et al. 2022).

monitored using other approaches (Fig. 9). Thus, alternative sampling methods could ideally complement interaction recording for these species.


Rubus ulmifolius
Asparagus aphyllus
Arbutus unedo
Pyrus bourgaeana
Pistacia lentiscus
Corema album
Olea europaea var. sylvestris
Juniperus phoenicea
Interaction richness
Interaction richness
Interaction richness
Interaction richness
Number of interactions
Number of interactions

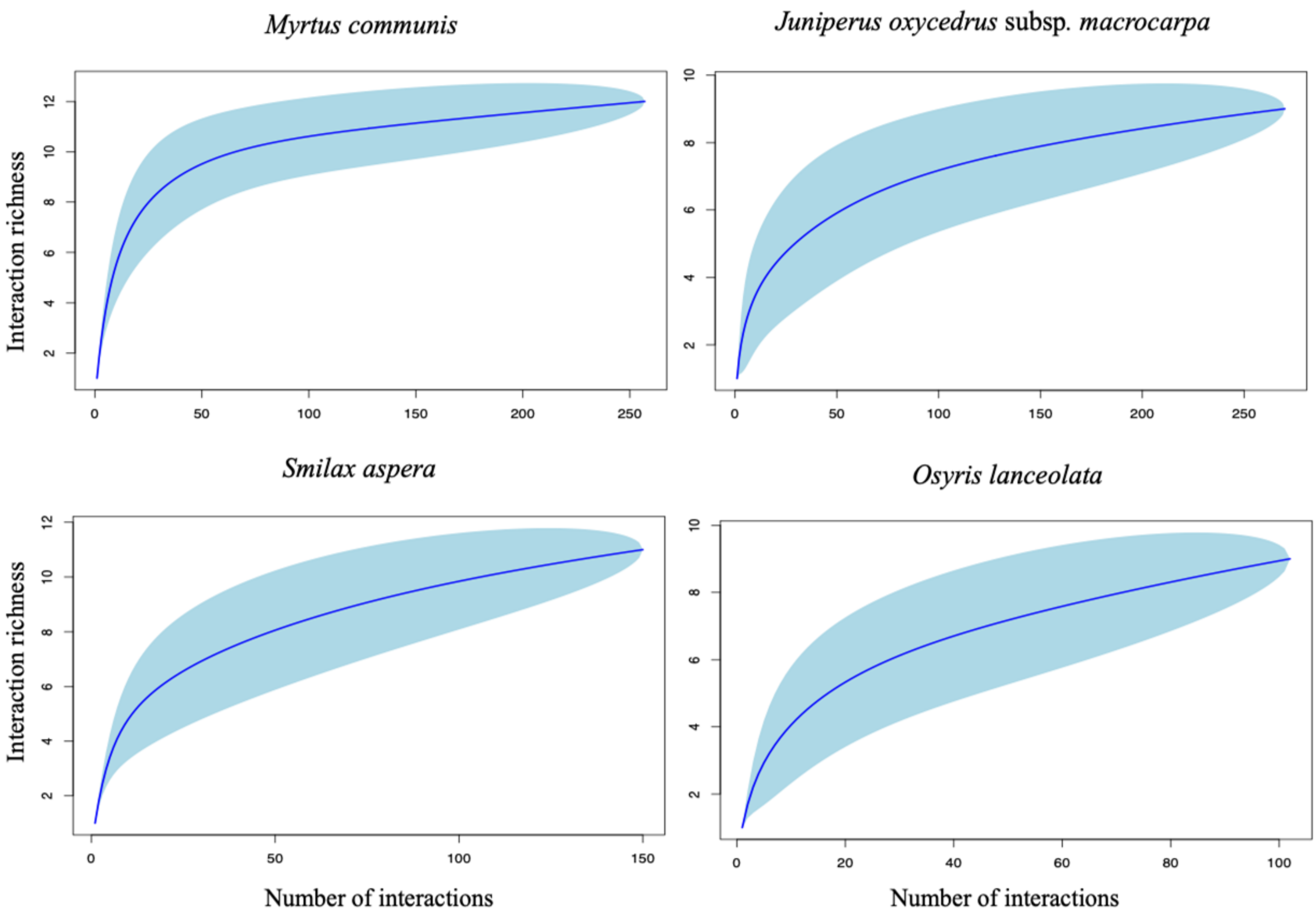


Figure 9. Sampling completeness at the species level: Accumulation curves for interaction richness (IAC) in relation with sampling effort (number of interaction events recorded).

It is worth noting the difference in methodology between *Pistacia lentiscus* and the rest of plant species, for which instead of using camera traps, we employed continuous-monitoring GoPro® cameras to record interactions. This resulted in significant differences in sampling effort and the detection of interaction events. While plants monitored by camera traps were continuously recorded for several weeks, the GoPro® cameras were active for 2.2 h d^{-1} in *Pistacia lentiscus* during the maximum foraging activity in the early morning for around 10 non-consecutive days. This continuous-recording protocol is advisable for plant species where interactions with nocturnal frugivores are rare or absent (e.g., avian-dispersed species), as it has proved to be very efficient, capturing a significant number of interactions with less sampling effort in the field compared to the camera traps. However, it is important to consider this methodology does not operate 24 h a day and may not be useful for some analyses such as those addressing daily activity patterns. In contrast, the method seems to be best suited for research questions on foraging behavior and fruit handling. Therefore, interactions recorded for *Pistacia lentiscus* in our database only involve diurnal species (mainly frugivorous birds), limiting the inclusion of other nocturnal or crepuscular animals, such as foxes or rodents, which are known to be extremely infrequent frugivores for this plant species (Perea et al. 2013).

Class III. Data set status and accessibility

A. **Status:**

1. Latest update: 26/09/2023

2. Latest archive date: 26/09/2023

3. Metadata status: Latest update on 26/09/2023 refers to the submitted version of the revision process.

4. Data verification: 26/09/2023

B. **Accessibility:**

1. Storage location and medium:

The original dataset, along with any updated versions and complementary material, can be freely accessed on the GitHub repository (https://github.com/PJordano-Lab/frugivory-camtrap) hosted by GitHub Inc., and Digital-CSIC archiving system (https://doi.org/10.20350/digitalCSIC/15623). The data are provided for public use and can be used for research purposes. The dataset will be periodically updated in the GitHub repository and archived in Digital-CSIC.

2. Contact person:

Pedro Jordano, Dept. Integrative Ecology, Estación Biológica de Doñana – CSIC – Av. Américo Vespucio 26, Sevilla, Spain. E-mail: jordano@ebd.csic.es

3. Copyright restrictions: None

4. Proprietary restrictions:

When using the data from this data paper in publications, we kindly request that you cite the paper accordingly. Additionally, we encourage researchers and educators to inform us about how they are using this data, as we value feedback and would like to be aware of its various applications.

Class IV. Data structural descriptors

A. **Data set file:**

1. Identity:

   DataS1.csv

2. Size:

   10,659 records, 14 columns, 1.5 MB

3. Format and storage mode:

   Comma-separated values (.csv)

B. **Variable information:**

Identity	**Definition**	**Data type**	**Example**
PlantSp	Plant species scientific name.	string	*Arbutus unedo*
PlantID	Plant individual unique identifier. A unique code identifying the plant individual sampled.	string	AUNE003
AnimalSp	Scientific name of the interacting animal species.	string	*Vulpes vulpes*
DateTime	Date and time when recording started. Formatted as an ISO 8601 string YYYY-MM-DD hh:mm:ss	datetime	2015-01-01 03:38:40
Behavior	Foraging behavior of the interacting animal.	string	eating
Count	Number of animal individuals recorded in the scene.	integer	1
Coexistence	Another animal is recorded foraging in the same scene.	boolean	TRUE
NCam	Number of cameras installed at the same PlantId.	integer	2
EffortSpecies	Sampling effort at species level. Number of days a plant species was recorded.	numeric	584
EffortInd	Sampling effort at individual level. Number of days a focal plant individual was recorded.	numeric	29,8
Duration	Duration of the recording event in seconds. It can be considered as a proxy of interaction intensity.	numeric	20,93
Longitude	Longitude of the deployment location in decimal degrees, using the WGS84 datum.	numeric	-6,44453
Latitude	Latitude of the deployment location in decimal degrees, using the WGS84 datum.	numeric	37,02329
SpeciesType	Type of animal: mammal or bird.	string	bird

D. **Data anomalies:**

If there is no available information for a specific record, it is indicated as 'NA'.

Class V. Supplemental descriptors

A. **Data acquisition:**

1. Data forms or acquisition methods:

The video files (both empty videos and videos with animals) are stored in external hard drives with a backup mirror. The datasets including file and revision information are stored in a hierarchical structure as explained in section 3 (comprehensively explained in Villalva & Jordano, 2023). The data resulting from image recognition using *Megadetector* (Beery et al. 2019) were saved in *.json* format for each model run (corresponding to a video batch organized by season or plant species). Therefore, there is a single *.json* file for each batch, stored in a folder named "Megadetector" in the mentioned GitHub repository. The output files generated by *Timelapse* were saved as *.csv* files for each batch, resulting in multiple *Timelapse* outputs stored in the "Timelapse results" folder. The script associated to this publication uses these results as inputs to perform the following tasks:

ii. Harmonize all datasets by resolving inconsistencies, applying filters, and collapsing data into 5-minute intervals for consistency.

iii. Integrate all datasets into a single one and include information about sampling effort and coordinates.

2. Location of completed data forms:

All data forms can be freely accessed by contacting the authors.

3. Data entry verification procedures:

All changes and verification procedures performed to the original data are traceable through R code (R Development Core Team 2022) accessible in the GitHub repository for Villalva & Jordano (2023). A toy dataset and illustrative code can be found in the data-paper repository to demonstrate the complete procedure. R packages used in the analyses and code development are included in the reference list.

B. **Quality assurance/quality control procedures:**

The dataset underwent thorough scrutiny, with a focus on summarizing and analyzing interactions to ensure ecological consistency of the results. Additional validation measures were implemented for each column of the dataset, placing particular emphasis on the recording dates. Camera traps can occasionally exhibit incorrect date or time due to malfunctions or misconfigurations in the setup. In our pipeline, instances of Timestamp Issues (TI) were mostly identified and flagged in the field, with the correct date and time set based on the nearest camera. In cases where TI went undetected in the field, the dataset was examined for events outside the sampled date range, and these missing dates were rectified following the same procedure as for previous Timestamp Issues. We used the AI-model entitled *Megadetector* (Beery et al. 2019) to remove videos without animals in the scene, obtaining a high accuracy with an assignment confidence of >95% for identifying empty videos coming from accidentally-triggered cameras.

C. **Related materials:**

None.

D. **Computer programs and data-processing algorithms:**

Juniperus phoenicea recordings were manually reviewed by human operators alone. To help the visualization of *Pistacia lentiscus* video recordings, we used *DeepMeerkat* software developed by Weinstein (2018). For the rest of plant species in order to remove empty videos lacking animal presence, we employed *Megadetector* (Beery et al. 2019) MD.v.4 during the first fruiting season (year 2020-21) and upgraded to MD.v.5 for the second fruiting season (2022-23) following the release of the enhanced version.

E. **Archiving:**

This dataset is freely downloadable as supplementary material in this publication and new data will be updated on the GitHub Inc. repository on a regular basis (https://github.com/PJordano-Lab/frugivory-camtrap) and archived in Digital-CSIC (https://doi.org/10.20350/digitalCSIC/15623). It is also possible to obtain the dataset by contacting the authors of this manuscript. The data published in these repositories are free to use and are fully available for public use and research purposes.

F. **Publications and results:**

Quintero, E., F. Rodríguez-Sánchez and P. Jordano. 2023. Reciprocity and interaction effectiveness in generalised mutualisms among free-living species. Ecology Letters 26: 132–146. https://doi.org/10.1111/ele.14141

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G. **History of data set usage:**

The PhD thesis projects of Elena Quintero and Jorge Isla used a portion of the present dataset. Elena Quintero focused on studying *Pistacia lentiscus*, while Jorge Isla worked with data on *Juniperus phoenicea*. Both have published several papers focused on each focal species (see publications and results section). Additionally, a combination of part of the dataset with other interaction datasets was employed to provide a comprehensive methodological overview of merging best practices for ecological interactions data (Quintero et al. 2022). This dataset is also being integrated in a more comprehensive dataset obtained through various interactions sampling methods, resulting in a new, forthcoming data paper focused on the community-level frugivore assemblage of Doñana National Park. Additionally, this dataset is being employed to assess the performance of Artificial Intelligence for image recognition in different plant species.

H. **Data request history:** None.

1. Data set update history: None.
2. Review history: None.
3. Questions and comments from secondary users: None.

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