Received: 12 April 2023 | Revised: 12 October 2023 | Accepted: 10 November 2023

DOI: 10.1002/ecy.4236

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Behavioral interactions are modulated by facilitation along a heterotrophic succession

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Funding information
MCIN/AEI/ 10.13039/501100011033 and ESF Investing in your future, Grant/Award Number: RYC2019-027216-I; Generalitat Valenciana and the European Social Fund, Grant/Award Numbers: ACIF/2019/056, SEJI/2018/024

Handling Editor: Evan L. Preisser

Abstract

Competition and facilitation drive ecological succession but are often hard to quantify. In this sense, behavioral data may be a key tool to analyze interaction networks, providing insights into temporal trends in facilitation and competition processes within animal heterotrophic succession. Here, we perform the first in-depth analysis of the factors driving temporal dynamics of carcass consumption by analyzing behavioral patterns (i.e., interactions) and community dynamics metrics (i.e., species richness, abundance, turnover, and diversity) in a Neotropical scavenger guild. For this purpose, we monitored goat carcasses using automatic cameras. From 573 reviewed videos, we registered 1784 intraspecific and 624 interspecific interactions, using intraspecific and interspecific aggressions ($n = 2048$) as a behavioral proxy of competition intensity. Our results show that resource availability shapes behavioral interactions between vultures, with a specific effect of the different species on behavioral and competition dynamics, showing the existence of a hierarchy between species. Furthermore, behavioral processes linked to carcass opening tended to be facilitative, related to moments of higher tolerance (i.e., lower aggressiveness), thus reducing competition intensity and also affecting community structure and dynamics. This novel framework demonstrates complex ephemeral successional processes characterized by a fluctuation in facilitation and competition intensity during the consumption of an unpredictable resource linked to key ecosystem processes.

KEYWORDS
animal behavior, carrion consumption, community dynamics, community ecology, competition, ephemeral resource, facilitation, heterotrophic succession, scavenger, species interactions

INTRODUCTION

Ecological succession is one of the most studied processes in community ecology, being defined as a sequence of changes in an ecological community that are observable in time and space (Begon & Townsend, 2020; Connell & Slatyer, 1977). Two different types of succession have been described. On the one hand, autotrophic succession starts with an ecosystem with low biomass due to a disturbance that increases over time as species colonization

occurs, also increasing the flow of energy in the ecosystem. On the other hand, heterotrophic succession begins from an ephemeral resource (e.g., dung, carrion, fruit) and thus experiences a peak in resource availability that disintegrates as succession progresses, resulting in the disappearance of the community (Begon & Townsend, 2020).

Succession provides a conceptual framework for comprehending community and ecosystem dynamics (Prach & Walker, 2011). Thus, understanding how succession occurs is still essential in modern ecology because disturbance regimes are being altered, putting biodiversity at risk and thus modifying ecosystem services (Chang & Turner, 2019; Pulsford et al., 2016). Several theoretical frameworks have been proposed to describe the colonization of species along succession (Connell & Slatyer, 1977; Koffel et al., 2018; Pulsford et al., 2016). In particular, the Facilitation and Inhibition Models, developed by Connell and Slatyer (1977), should be highlighted. The Facilitation Model established that the succession process begins with the colonization of the early species (i.e., pioneer species), which modifies the environment, making it less suitable for the establishment of other pioneering species, but enhancing the establishment of late species. In contrast, the Inhibition or Competition Model establishes that the modifications made by pioneer species favor them and prevent the establishment of late species. Nevertheless, most of these classical models of community ecology have been tested using time-static measurements (e.g., comparing communities at different stages of succession at selected time points, with noncontinuous measurements over time). However, with the development of new techniques and analytical tools, the importance of understanding the dynamics of communities over time and succession as a continuous process has become evident (Collins et al., 2008).

In classical ecology, two species sharing the same requirements will develop different strategies to avoid high levels of competition, for example, niche differentiation. Alternatively, it has also been assumed that the intensity of competition has an inverse relationship to phylogenetic relatedness between species that coexist (Rangel et al., 2018). However, one of the limitations in studies on community dynamics (i.e., succession) is the difficulty of measuring variations in the intensity of competition between species that coexist and have the same ecological requirements (Pulsford et al., 2016). This problem could be addressed in animal communities through behavioral studies, because the most immediate response of animals to any change is at the behavioral level (Bro-Jørgensen et al., 2019). In the last decade, behavioral biology has been included in the study of animal networks because the behavior of a single species influences the behavior of other species through interspecies interactions, leading to cascading effects at the community level, and determining ecological processes (Gil et al., 2018; Rahman & Candolin, 2022). Indeed, the need to refine the study of functional relationships between organisms by measuring traits based on behavioral measures has become evident (Schleuning et al., 2023; Spiegel et al., 2017). Specifically, aggressive behaviors have been associated in the literature with competition for a limited resource. Because some aggressive interactions can be harmful or fatal, animals will often reserve them for situations in which the perceived risk is high (Kilgour et al., 2020; Mohamad et al., 2010). Thus, by studying behavioral patterns, and, specifically, trends over time in aggressive interactions among organisms that coexist, share a resource, and are phylogenetically related (e.g., obligate scavengers), we might understand changes in the intensity of competition between species through resource consumption (Kilgour et al., 2020; Wilson et al., 2020). Nevertheless, this requires observational studies in natural situations, because other indirect methods (e.g., radiotracking) cannot provide information at the scale needed to discern patterns of interactions between species.

The decomposition of organic matter is fundamental in all ecosystems, as it is a key element in the cycle of matter and energy (Benbow et al., 2019; Moore et al., 2004). Specifically, carrion is a unique resource due to its high nutritional content and its ephemeral and unpredictable nature, both temporally and spatially (Barton et al., 2013, 2019). Nevertheless, most of the scientific work has focused on autotrophic succession (Chang & Turner, 2019; Rezende et al., 2021). Furthermore, the study of succession that occurs during the consumption and decomposition of the bodies of dead organisms has focused on invertebrate species and microorganisms (Dawson et al., 2022; Moura et al., 2005; Pechal et al., 2013; Sladecek et al., 2021). But, although the role of these organisms is very important in certain systems, vertebrate scavengers consume the greatest amount of vertebrate carrion biomass, playing a key role in carrion recycling (DeVault et al., 2003; Gutiérrez-Cánovas et al., 2020). Carrion of a certain size allows the consumption of multiple individuals of different species at the same time (Moleón et al., 2015), which implies very high levels of competition, occurring among both conspecific and heterospecific individuals (Moreno-Opo et al., 2020; Naves-Alegre, Morales-Reyes, Sánchez-Zapata, & Sebastián-González, 2022; Ruxton & Houston, 2004). Furthermore, different facilitative processes have also been described in scavenger communities, in the provision of carrion by carnivores (Allen et al., 2014), in the location of the carcass

(Kane et al., 2014; Kane & Kendall, 2017; Naves-Alegre, Morales-Reyes, Sanchez-Zapata, et al., 2022) and for carcass opening (Naves-Alegre, Morales-Reyes, Sánchez-Zapata, & Sebastián-González, 2022; Orr et al., 2019; Selva et al., 2003). The process of carcass opening refers to tearing apart the hard ungulate skin, which can only be done by a few scavenger species (e.g., those with the largest body size, or with powerful beaks), and thus giving access to the inside of the carcass for all scavengers. But this event has only been studied with time-static measurements, relating it to the total time of carrion consumption (Orr et al., 2019; Selva et al., 2003), association patterns between species with different skin-opening abilities (Kendall, 2013; Naves-Alegre, Morales-Reyes, Sánchez-Zapata, & Sebastián-González, 2022) or the relationship between the number of skin apertures and the frequency of feeding of a given species (Alvarez et al., 1976). Therefore, carrion is an ideal system to study temporal changes in the competition and facilitative processes that occur within vertebrate organisms during a heterotrophic succession because the community changes rapidly over time and carcasses could be easily monitored.

In this study, we investigate the underlying dynamics of heterotrophic succession in a Neotropical vertebrate scavenger community, comparing it with a classical theoretical background (Connell & Slatyer, 1977; Pulsford et al., 2016). First, we analyze changes over time in the scavenger assemblage to understand the temporal dynamics of this ephemeral succession (Collins et al., 2008; Rezende et al., 2021). Second, we identified temporal variations in the intensity of aggressiveness and tolerance between scavengers to assess the competitive and facilitative interactions that drive the dynamics of carrion consumption. In this way, we assume a direct relationship between levels of aggressiveness and competition, while moments of reduced aggressiveness may reflect higher tolerance and/or facilitative processes (Kilgour et al., 2020; Mohamad et al., 2010). We establish specific hypotheses related to these objectives based on heterotrophic succession theory and the two classical Facilitation and Inhibition Models of species colonization (see Table 1 for hypotheses and further details).

MATERIALS AND METHODS

Study system

The study was carried out in the Neotropical savanna called Cerrado, in the northeastern of Brazil (state of Piauí). The Brazilian Cerrado is one of the largest biodiversity hotspots on the planet, with an extension of over 2 million km^2 (Klink & Machado, 2005). We focused on the species of avian scavenger that had been recorded consuming large carcasses in this community (Naves-Alegre et al., 2021). Thus, we considered four vulture species (i.e., obligate scavengers): turkey (*Cathartes aura*), lesser yellow-headed (*Cathartes burrovianus*), black (*Coragyps atratus*), and king (*Sarcoramphus papa*) vultures; and two species of facultative avian scavengers: Southern caracara (*Caracara plancus*) and Yellow-headed caracara (*Milvago chimachima*).

Study design and general variables

In November 2018, we placed 11 goat carcasses ranging from 20 to 40 kg in weight and at least 1.5 km apart to maximize spatial independence. Each carcass was monitored by two automatic cameras (Browning Strike Force pro HD model), one configured to take photographs and the other to record video (see Naves-Alegre et al., 2021 for more details on the fieldwork design). In this way, we obtained, in total, 2501 videos and 27,448 images (hereafter when we refer to an "archive" we will mean one datum, either an image or a video file).

We assigned an ID to each archive, and we registered the following variables: (1) the carcass to which it belongs, (2) date and time, (3) richness (i.e., number of species present), (4) the abundance of each species present (i.e., maximum number of unequivocally different individuals of a species registered in the archive) and (5) the number of individuals actively feeding of each species, defined as those individuals that were observed feeding for at least one-third of the duration of the video (i.e., over 20 s). Furthermore, to estimate the moment of consumption of the carcass, we calculated the variable (6) percentage of total carcass consumption for each archive. To this end, we considered the time because carcass detection (i.e., the time elapsed between the detection of the carrion and the time the file was taken) and the time of complete carcass consumption (i.e., the time elapsed between the detection of the carrion and the complete consumption of the carcass) (Wenting et al., 2022). Thus, we calculated:

$$PC_{ik} = \frac{T_{ik} - CD_k}{CC_k - CD_k} \times 100,$$

where PC_{ik} is the percentage of total carcass consumption of an archive i from a carcass k. T_{ik} is the data and time of the archive i in carcass k. CD_k is the time of carcass detection and CC_k is the time of complete carcass consumption (see Appendix S1: Table S1 for details on the variables). This variable allowed us to normalize the

TABLE 1 Hypotheses explaining potential competition and facilitative processes through behavioral changes in the intensity of aggressiveness of the interactions between species and variables influencing heterotrophic succession dynamics in a vertebrate scavenger assemblage in the Neotropics.

Theoretical background	Hypothesis	Expected pattern	References
Heterotrophic succession (e.g., animal succession) starts from an ephemeral resource that becomes available to the community. The resource begins to be colonized and consumed by different species. The community itself consumes the entire resource, leading to the collapse of the succession	(1) Community assembly and dynamics will vary as the heterotrophic succession progresses, until the complete disappearance of the resource, which will lead to the disappearance of the community	Scavenger richness, abundance, and diversity will show a bimodal trend along the carcass consumption process. There will be an increase in these variables at the beginning of the succession, as the recruitment of individuals of different species occurs. This trend will reach a maximum when the carcass community reaches its carrying capacity. Then, the biomass of the resource will begin to decrease until the disappearance of the community Species turnover will be large at first as more species are recruited. At the end of the succession, when the carrion is practically consumed, the turnover will increase again because the composition of the community will be less stable, with a higher species loss	Collins et al., 2008; Magurran & Henderson, 2010; Rezende et al., 2021
Facilitation Model: pioneer species alter the conditions and make the environment less favorable for them, but more suitable for later successional species. This succession model occurs most often in autotrophic succession and animal succession	(2) The dynamics of the heterotrophic succession that occurs during the consumption of a medium-/large-sized carcass will be driven by a facilitation process produced by the opening of the carcass skin. This aperture can only be carried out by some of the species of the community, which will make the entire resource biomass available to the rest	Pioneer species will be present during the first part of the succession, and will not inhibit the establishment of later species Scavenger richness, abundance, and diversity will be higher when the carcass is opened because this is the time when all species in the community will be able to consume the resource Turnover will be higher when the carcass is opened and the resource is fully available, allowing more species to come and consume it Aggressiveness levels will be higher before carcass opening, because the availability of the resource will be limited. Once the	Alvarez et al., 1976; Connell & Slatyer, 1997; Kendall, 2013; Naves-Alegre, Morales-Reyes, Sánchez-Zapata, & Sebastián-González, 2022; Selva et al., 2003

TABLE 1 (Continued)

Theoretical background	Hypothesis	Expected pattern	References
		carcass is opened, competition levels will decrease, because more resources will be available	
Inhibition Model: pioneer species modify the environment in such a way that it becomes less suitable for the colonization of other, later species. This model establishes that succession will, therefore, be driven by the dominant species	(3) Competition levels will remain high throughout the carrion consumption process, so that when the species with the highest competitive abilities reaches the carcass, general levels of aggressiveness will increase among the individuals of other species that will not be able to access the resource	Pioneer species will be present during the first part of the succession and will inhibit the establishment of later species As succession progresses and the resource becomes colonized, we expect that competition among individuals for the resource will increase, leading to a corresponding increase in aggression levels. However, once a certain point of the succession is reached, aggression levels will decrease as individuals become satiated or because there is not enough resources available	Allen et al., 2014; Brown, 1964; Connell & Slatyer, 1997; Kilgour et al., 2020; Mohamad et al., 2010; Moreno-Opo et al., 2020
	(4) Aggressiveness will be driven by the dominant species	King vulture will drive aggressive interactions, as it has been described as the dominant species in the Neotropical scavenger hierarchy due to its larger size	

Note: The heterotrophic succession hypothesis does not exclude the Facilitation or Inhibition Models, and they may be complementary.

different consumption times of the carcasses (mean ± SD: 48.41 ± 14.41 h).

We used 20,656 archives for general community analyses, with records of all scavenger species present and their abundance. Maximum time of the consumption process of each carcass was recorded (i.e., from PC = 0 to PC = 100), eliminating files after the complete consumption of the carcass. For behavioral analysis, we used only the videos, which were 1 min long and set to be taken every 3 min. We discarded one carcass because the videos were poorly focused. From the resulting videos, we first selected those videos in which more than one individual appeared, as our main objective was to focus on interactions. Second, we took a sample of videos from each carcass by selecting them in an alternating pattern (e.g., viewing one out of three videos) so that they covered the entire process of carcass consumption ($n = 573$ videos; see Appendix S1: Table S2 for further details).

Moreover, to determine whether there was a change in the pattern of interactions before and after the carcass opening, we established the time of carcass opening for each carcass, at which the ventral part of the carcass had an aperture large enough to consider that all species (regardless of their capacity, i.e., body size, size of the carcass) could dispose of the total biomass of the carcass. This variable was determined through observational evidence when an individual king vulture was first observed slitting the skin (i.e., the only species capable of tearing the goat skin in this community). The opening of carcasses was highly variable; however, it was located on average at 25% of the PC (minimum: 0.54%, maximum: 67.18%; see Appendix S1: Table S3). Consequently, we first considered carcass opening as a static event, so we defined a binomial variable "carcass opening status," whereby videos with date and time before the time of carcass opening were classified into closed ($n = 149$) and videos after the opening date and time were classified as open ($n = 424$).

In order to investigate the potentially dynamic nature of carcass opening, we second calculated a continuous variable termed "time to/from carcass opening" (Appendix S1: Figure S1). Nevertheless, we discarded this approach and, therefore, this variable for two reasons. First, we observed a high correlation between this variable and the PC (Pearson's $|r| = 0.70$). Second, the Bayesian mixed models (see the *Statistical analyses* section) that incorporated this variable, and when PC was excluded in order to avoid correlation, exhibited a higher widely applicable information criterion (WAIC) compared with those that considered PC and carcass opening status as a binomial variable (WAIC of the model for time to/from carcass opening vs. the model for PC and carcass opening status: 977.8 vs. 957.8). For this reason, we decided to treat this variable as a static event over time and only consider the carcass opening status variable.

Community dynamics metrics

To understand how the scavenger community changes throughout the succession process and the effect of the possible facilitation process due to carcass opening (hypotheses 1 and 2), we initially calculated (1) the richness and (2) the total abundance of species present in the different points of percentage of total carcass consumption (i.e., PC). For this section, we used the data from the 20,656 archives. Then, we conducted community dynamics analyses by using the *codyn* R package (Hallett et al., 2016) using the PC as the time variable and the carcass as the replicate variable. In this way, we calculated (3) dynamic changes in species richness throughout the process of carcass consumption considering both species losses and gains, that is, total turnover (turnover function; Appendix S1: Section S1). To estimate total turnover, we used unit-to-unit changes in the percentage of carcass consumption (i.e., PC), for example, from 1% to 2%, from 2% to 3%, and so on. Additionally, we calculated (4) the Shannon–Wiener diversity index along the carcass consumption process using the community_diversity function (see Appendix S1: Section S1). As a result, we obtained 376 data for each of these two variables after using the functions of the *codyn* R package.

Behavioral data collection

For the extraction of behavioral data, we only considered vulture species because they monopolized the consumption of large carcasses (Appendix S1: Table S4). Interactions with the rest of the species were scarce; in addition, vultures play a major role in the processes of facilitation and competition in this community (Naves-Alegre, Morales-Reyes, Sánchez-Zapata, & Sebastián-González, 2022). We defined interaction as any action between two vultures that involved one responding to the presence or activity of the other, whether by intentional (e.g., direct attack) or unintentional (e.g., displacement) behavior of the initiator individual (Table 2) (Moreno-Opo et al., 2020). We did not distinguish between individuals, given the difficulty of tracking them throughout the playback of a video, as individuals move in and out of the camera's field of view, and because most of these species lack patterns that would allow us to identify individuals easily. For this reason, we quantified the total number of interactions between all the individuals observed in a video (regardless of their identity), that is, focal-animal sampling (Altmann, 1974). Furthermore, we sampled several kinds of

TABLE 2 Overview of the different variables and interactions registered between New World vultures during the observation of the videos recorded by the camera traps.

Behavioral term	Definition
1. Agonistic interactions	
Attack	Aggression or attempted aggression by using the beak, claws, or open wings, with the intention of displacing the target individual from its position or to avoid being displaced
Theft	Remove or attempt to remove food from the beak or claws of another individual that is feeding at that moment
Retreat	One of the individuals moves away (victim) in the presence of the other (initiator), without any aggressive gesture or conflict, by giving up his position
2. Nonagonistic interactions	
Affiliative	Nonaggressive intent, may involve feather preening, or food sharing (the latter commonly between individuals of the same species of different ages)
3. Role in the interaction	
Initiator	Individual who intentionally or unintentionally initiates interaction with another individual
Victim	Individual who receives the interaction
4. Classification according to the participants	
Intraspecific interaction	The initiator and the victim of the interaction belong to the same species
Interspecific interaction	The initiator and the victim of the interaction belong to different species

interactions indicating different levels of aggressiveness and hierarchy between individuals, differentiating interactions initiated by the different vulture species (i.e., turkey, lesser yellow-headed, black, and king vultures; Table 2). Given the very small sample of interactions obtained for vultures of the genus Cathartes, that is, turkey and lesser yellow-headed vultures, we considered these two species together (hereafter designated Cathartes vultures) because of the similarity in their behavioral traits and scavenging efficiency (Houston, 1988). Behavioral data extraction from the videos was carried out by a single person, to increase consistency in the interpretation of the behaviors.

Statistical analyses

We used Bayesian mixed models to analyze changes in some of the community dynamics metrics and fluctuations in the competition levels throughout the carcass consumption process. On the one hand, to determine whether changes in community richness and abundance occurred during carcass consumption and the effect of carcass opening (hypotheses 1 and 2), we modeled (1) species richness (Poisson distribution, link = "log"; $n = 20{,}656$), (2) total species abundance (Poisson distribution, link = "log"; $n = 20{,}656$), and (3) total turnover (Gaussian distribution, link = "identity"; $n = 376$). Moreover, to determine changes in community diversity, we also modeled (4) the Shannon index (Gaussian distribution, link = "identity"; $n = 376$). We initially included in all models the explanatory variables: (1) PC (included as a polynomial to account for its nonlinear effect) and (2) carcass opening status. Moreover, to determine the variation in the abundance of each species along the carcass consumption, we used univariate models, using as response variables (1) the abundance of Cathartes vultures, (2) the abundance of black vultures and (3) the abundance of king vultures; and as explanatory variable (1) PC (all fitted with a Poisson distribution, link = "log").

On the other hand, to analyze possible changes in the intensity of competition (hypotheses 2 and 3), we considered attack and theft interactions together (henceforth referred to as "aggressive interactions") as those are the two types of interactions that involved the highest level of aggressiveness and intentionality, and are therefore a good proxy to measure the level of competition. Thus, we assumed that the remaining interactions, that is, affiliative and retreat interactions (henceforth referred to as "nonaggressive interactions"), would represent less competitive situations, indicating facilitative processes and/or moments of higher tolerance between individuals, as these kinds of interactions represent nonaggressive relationships, avoiding direct confrontations, and thus reflecting a certain degree of tolerance and the existence of pre-established hierarchies among individuals (Grossel et al., 2022; Mohamad et al., 2010). We analyzed (4) the total number of interactions, regardless of the kind of interaction, to determine general changes in interaction numbers between individuals through the carcass consumption process. In this case, in addition to the previously mentioned predictors (i.e., PC as a polynomial and carcass opening status), we also added (3) total abundance, or (4) Cathartes vultures' abundance, (5) black vultures' abundance, and (6) king vultures' abundance separately as explanatory variables. We fitted these models to a Poisson distribution (link = "log"). We did not include the number of individuals of each species actively feeding in any of the models because these variables were highly correlated (Pearson's $|r| > 0.70$) with each species' abundance (see Appendix S1: Figures S2 and S3).

Second, we evaluated the changes in aggressiveness intensity (i.e., competition intensity) along the whole process of carcass consumption. We used mixed aggregated binomial regression models (link = "logit"), where the response variable was modeled as: $y_{\text{interaction}\,i} \sim \text{Binomial}(y_{\text{total}\,i}, p_i)$, where $y_{\text{interaction}}$ was the number of an interaction type in a i video recorded, y_{total} was the total number of interactions recorded in this i video, and p_i was the probability that all recorded interactions were of the type of interaction we model, that is, $p_i \sim \text{uniform}(0,1)$. In this way, we analyzed: (1) the proportion of aggressive interactions, (2) the proportion of nonaggressive interactions, (3) the proportion of interspecific aggressive interactions, and (4) the proportion of interspecific nonaggressive interactions. We included as explanatory variables: (1) PC as a polynomial, (2) the carcass opening status, (3) the total abundance of all species considered together, or (4) Cathartes vultures, (5) black vultures, and (6) king vultures' abundances separately. We built a full model for each previous response variable following the form:

$$\begin{aligned}\text{logit}(p_i) = {} & \alpha_{0i} + \beta_1 \text{PC} + \beta_2 \text{PC}^2 + \beta_3 \text{PC}^3 + \beta_4 \text{CarcassStatus}_i \\ & + \beta_5 \text{CathartesVultures}_i + \beta_6 \text{BlackVulture}_i \\ & + \beta_7 \text{KingVulture}_i + \epsilon,\end{aligned}$$

where p_i is the probability that a type of interaction is recorded in video i. α_{0i} refers to the intercept, y β are the parameters of the different covariates considered. The model can also be of the form that includes the total abundance (i.e., of all species together) and not the sum of the abundances of each species separately. These two variables were not incorporated together in the same model.

PC was modeled as a polynomial in all models to determine whether its effect was not linear (hypothesis 3). Also, we included carcass as random intercept in all models to consider the differences in the consumption of each carcass and the differences in their initial size (i.e., initial biomass). We built all possible models for each response variable by testing all combinations of variables, selecting the best model (i.e., top-ranking model) by comparing its fit using the widely applicable information criterion WAIC (Gelman et al., 2014), selecting the model with the lower WAIC value. We fitted all mixed models within a Bayesian approach using the "brm" function from the *brms* package (Bürkner, 2017), using nonexplicative default Student *t* priors (df = 3, mean = 0, scaling factor = 10). All Bayesian models consisted of four chains, each with a minimum of 2000 iterations and 1000 burn-in samples. We confirmed the convergence of the models by inspecting the mixed of the Markov chains and making sure that in all cases the maximum Gelman–Rubin statistic (i.e., Rhat value) was 1.0 (Hilbe et al., 2009). We determined a strong statistical effect of model parameter when the 95% Bayesian credible interval (CI) did not overlap zero. All models were fitted in R (R Core Team, 2022).

RESULTS

Community dynamics and species abundances

On average, we registered 2.02 ± 0.84 species per archive (i.e., video or image), with a total abundance of 6.82 ± 6.57 individuals per archive. The results of the models did not show statistical support for the influence of PC on richness, although this variable was included in the best model (i.e., lower WAIC; Appendix S1: Table S5). However, when the carcass was closed, the richness was statistically lower than when the carcass was open (Figure 1). Furthermore, the overall abundance of species was statistically affected by PC, so that as carcasses were consumed, abundance decreased (see Appendix S1: Figure S4 for details). Similarly, the opening status also had a strong statistical effect on the abundance, which was higher once the carcass was opened (Figure 1). These apparently conflicting results are due to the high variability of the opening times of the 11 carcasses (see Appendix S1: Table S3). Specifically, the models analyzing separately the abundances of the species showed a strong influence of PC on all of them (Appendix S1: Figure S7 and Table S6). Finally, we found that the Shannon–Wiener diversity index and total turnover varied along the PC, with PC having a strong nonlinear effect on both, while we did not find an effect of the carcass opening status on diversity (Figure 1).

Behavior throughout carcass consumption

In the 573 reviewed videos, we recorded 2048 aggressive interactions (529 interspecific and 1519 intraspecific), 356 retreats (95 interspecific and 261 intraspecific), and four affiliative interactions (all of them intraspecific) (see Appendix S1: Table S7 for further details). Bayesian mixed models performed for the whole carcass consumption process showed that PC had strong statistical support in most of the variables. Thus, we found a cubic effect of this variable in the number of total interactions recorded, the proportion of interspecific displacements, the proportion of aggressive interactions and the proportion of interspecific aggressive interactions. Conversely, our results showed that the proportion of interspecific nonaggressive interactions was not influenced by this variable (Figure 2). Furthermore, we found a notable effect of the carcass opening status, with a higher number of total interactions and a higher proportion of aggressive interactions when the carcass was open. In contrast, we found the opposite effect when we analyzed the proportion of nonaggressive interactions, which was higher when the carcass was closed (see Appendix S1: Table S8).

The American black vulture initiated most of the aggressive interactions (68.4%), followed by the king vulture (28.9%) and finally, the Cathartes vultures, initiating only 2.7% of the aggressive interactions recorded (see Appendix S1: Table S7). In this way, top-ranking models did not include the total abundance of the species, but the models did show an effect of the abundance of each species separately (see Figure 2). In fact, each species had a different influence on the behavioral dynamics throughout carcass consumption. Black vultures had a positive effect on the proportion of aggressive interactions recorded, whereas Cathartes had a strong negative effect. Finally, the presence of the king vulture had a positive influence on the proportion of interspecific interactions, both for nonaggressive and aggressive interactions (Figure 2; Appendix S1: Table S8).

DISCUSSION

The relationship between competitive and facilitative interactions within and between species in succession determines its dynamics, so it is essential to use temporal analytical approximations to study these processes and understand what factors influence them. In this study, we provide the first in-depth analysis of the community

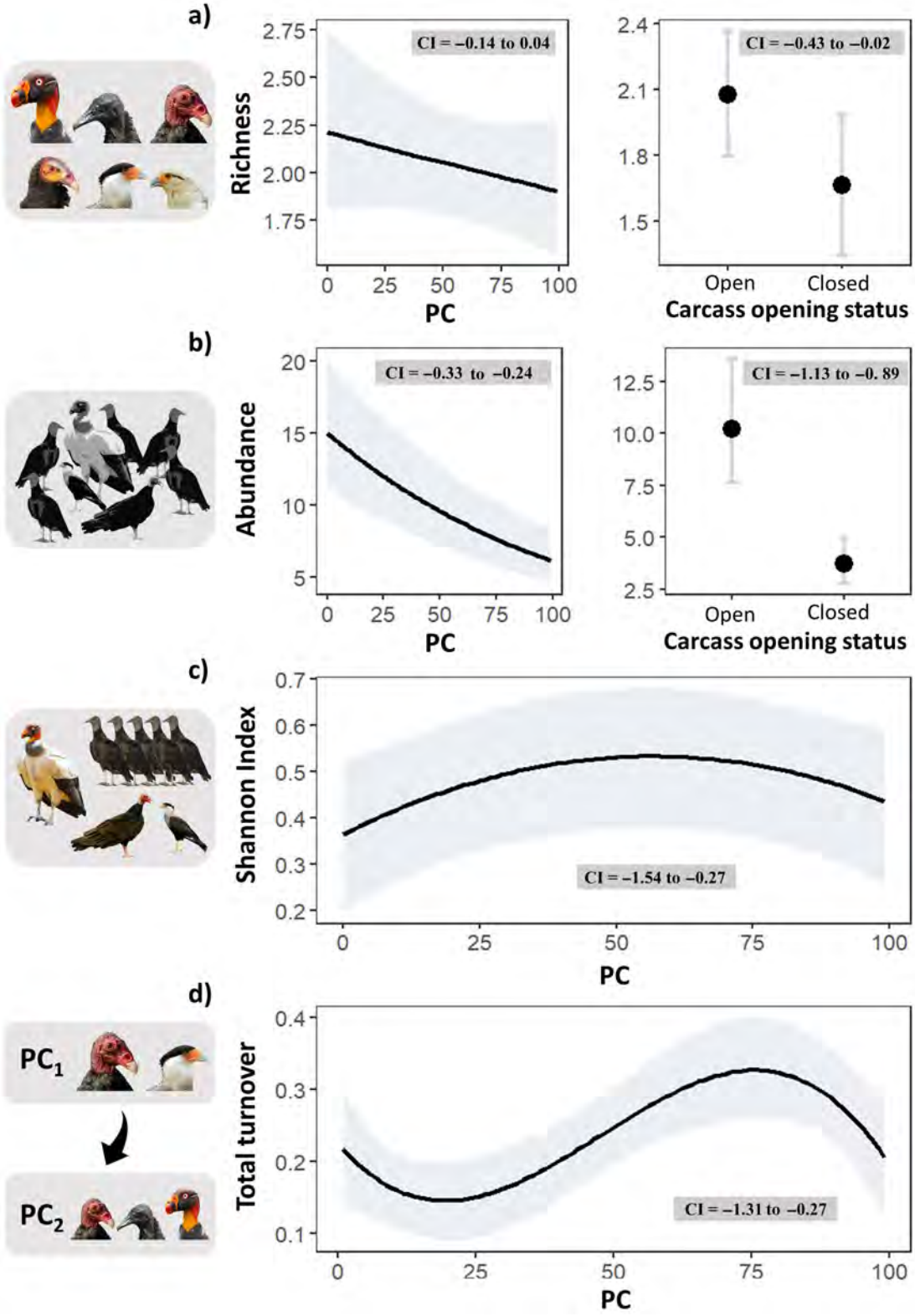

FIGURE 1 Conditional effects of all the explanatory variables included in the best models (i.e., lower WAIC) obtained for community dynamics analyses: (a) richness, (b) abundance (c) Shannon–Wiener diversity index and (d) total turnover. Black lines represent predicted posterior means, and shadow bands and gray boxes show 95% confidence intervals (i.e., CI) obtained in the top-ranking Bayesian mixed models (i.e., lower WAIC). For more details, see Appendix S1: Table S5 and Figure S5. Illustration credits: Lara Naves-Alegre.

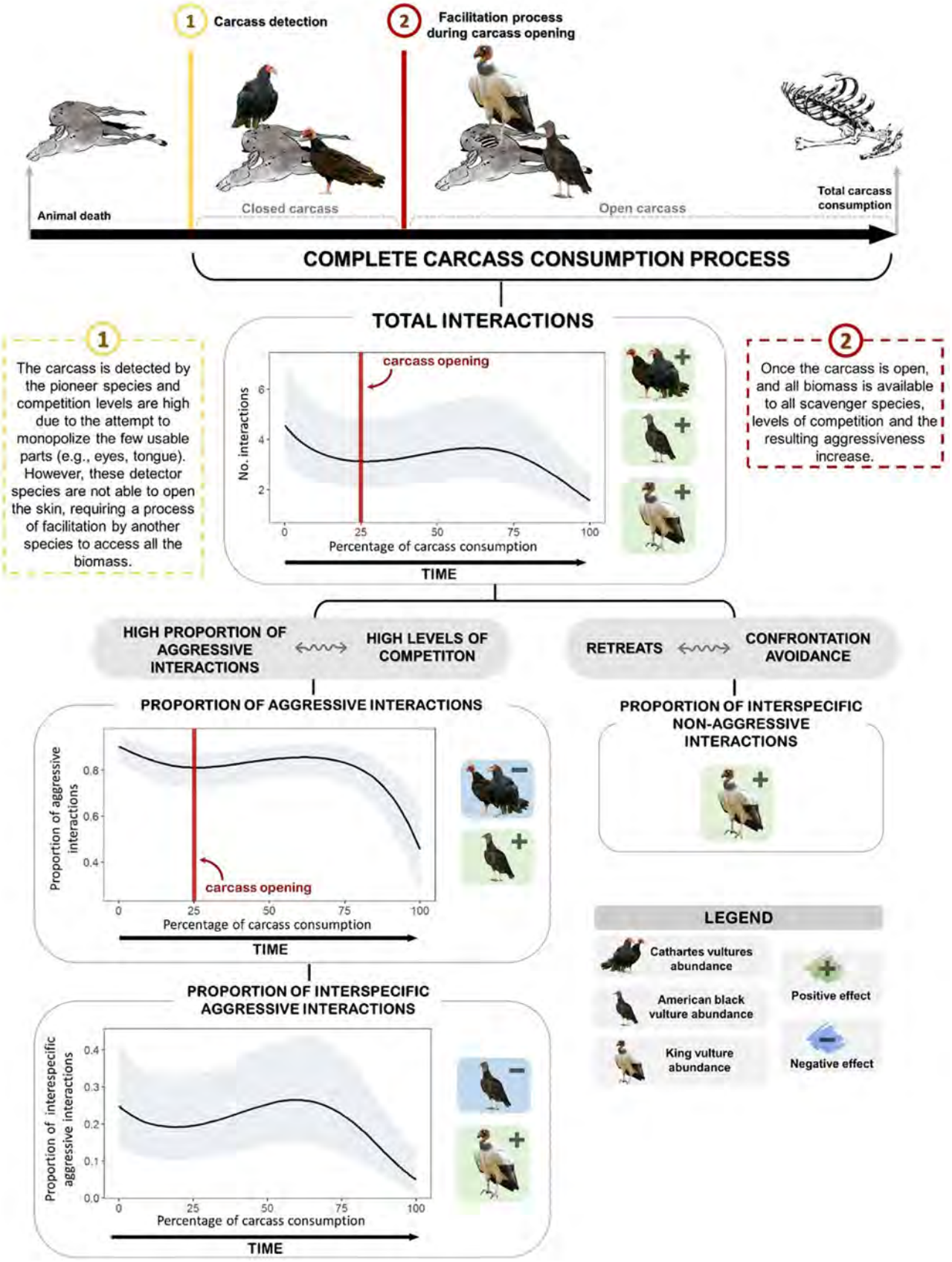

FIGURE 2 Legend on next page.

dynamics of a vertebrate heterotrophic successional sequence. We determine changes in the intensity of competition, which remains a challenge in autotrophic succession (Pulsford et al., 2016), and the existence of a key facilitation event along the process of carrion consumption and resource availability, by combining temporal and behavioral analyses. Our results show high overall competition levels (i.e., high aggressiveness) that varied throughout the succession, being influenced by the facilitation process resulting from carcass opening, as well as by the community composition at the carcass at a given time.

Vertebrate community composition during heterotrophic succession

Supporting our first hypothesis, we found that species abundance, diversity, and turnover changed as the process of carcass consumption progressed, showing very different patterns. First, we detected a linear decrease in the abundance of individuals as the resource was being consumed, contrary to what has been described for autotrophic succession, in which abundance initially tends to increase when colonization begins (Begon & Townsend, 2020). We did not find an initial increase in abundance, perhaps because scavenger recruitment at carcasses in our study system is very fast (i.e., 10–30 min) (Naves-Alegre, Morales-Reyes, Sanchez-Zapata, et al., 2022). Second, species diversity also varied over time, with a concave-down trend, so the scavenger community reached its highest diversity at the midpoint of the successional sequence. Third, we also found that species turnover changed following a complex pattern (i.e., cubic form), contrasting with the patterns found in autotrophic succession, in which the highest turnover rates are recorded at the early stages (Kaarlejärvi et al., 2021). Species turnover has been related to productivity in plant communities, so it would therefore be necessary to analyze whether higher levels of turnover indicate higher rates of carrion consumption (Chalcraft et al., 2004). Moreover, we found no support for our prediction that species richness changes along the carcass consumption process, contrary to what has been found in studies on insect succession (Moura et al., 2005). This may be because we only registered six scavenger species present in the carcass, two of which (i.e., king and black vultures) dominated the carcass during practically the entire succession. Future research in more diverse scavenger assemblages may elucidate whether there are changes in richness trends over resource consumption.

The influence of facilitative processes on succession dynamics

Carcass opening has already been established as a facilitative process in vertebrate scavenger communities in other ecosystems, although it has only been described with time-static measurements (Alvarez et al., 1976; Naves-Alegre, Morales-Reyes, Sánchez-Zapata, & Sebastián-González, 2022; Orr et al., 2019; Selva et al., 2003). The time of carcass opening was highly variable between carcasses, as it relied on the arrival of the only species strong enough to slit the skin, that is, the king vulture. This aspect might differ in other systems, in which multiple species could potentially access the carcass interior independently, speeding up carcass opening times. As expected if the Facilitation Model was the main process that drives this succession (hypothesis 2), pioneer species (i.e., those with a higher foraging ability due to their sense of smell: Cathartes vultures) did not prevent the arrival of the later ones. Thus, species with greater competitive ability (either because of their social characteristic or their larger size, i.e., American black and king vultures, respectively; Wallace & Temple, 1987) dominated the middle and final stages of the succession (Dawson et al., 2022; Menéndez & Gutiérrez, 1999). This

FIGURE 2 Conceptual illustration (above) and main results of the Bayesian mixed models showing fluctuations in behavioral interactions (below) during a heterotrophic succession that drives the consumption of large carcasses in a Neotropical scavenger community. We consider the beginning of the succession when the carcass is found by the first individual (i.e., pioneer species; yellow) until it is completely consumed (i.e., only the bones and skin remain). Our results showed that this community dynamics are mainly driven by a facilitation process due to the opening of the carcass skin (represented as a red line at 25% of carrion consumption, i.e., the average value for all carcasses, in those top-ranking models when this variable was included). Through the study of interactions, we can discern variations in the intensity of competition, so a high proportion of aggressive interactions reflect high levels of competition, while nonaggressive interactions (i.e., those that avoid confrontation) reflect higher levels of tolerance. Thus, the effects of PC (i.e., percentage of carcass consumption) on the total number of interactions, the proportion of aggressive interactions and the proportion of interspecific aggressive and nonaggressive interactions are represented. Black lines symbolize predicted means, while the gray bands indicate the 95% credible intervals. The positive (green) and negative (blue) effects of the abundances of the different scavenger species on the interactions recorded in this succession are displayed. Only those variables that had strong statistical support, that is, whose confidence intervals did not overlap 0, are shown. For more details, see Appendix S1: Table S8 and Figure S6. Illustration credits: Lara Naves-Alegre.

pattern may also be partly related to local enhancement (i.e., a facilitation process in which pioneer species signal the presence of carrion to other species) previously demonstrated in this community, and not, or not only, by the carcass opening process (Naves-Alegre, Morales-Reyes, Sanchez-Zapata, et al., 2022). Moreover, as expected, the carcass opening also had an effect on species richness and abundance. These two variables were statistically larger once the carcass was opened, which may be due to the resource being available for the entire assemblage from that moment on, in agreement with what has been previously established (Selva et al., 2003). In contrast, neither species diversity nor species turnover through succession were influenced by this process.

Furthermore, this facilitation process not only influenced the structure of the community, but also affected behavioral patterns. Consequently, the total number of interactions recorded, and the proportion of aggressive ones were also influenced by carcass opening, being both larger when the body was open than when it was closed. This indicates that when the carcass is closed, tolerance levels between species are higher, perhaps because of their inability to access the resource (Kilgour et al., 2020). Once the carcass is opened by the species with the largest body size (i.e., king vulture), the levels of aggressiveness increase again, because the entire resource becomes available for all species (Kendall, 2013). These findings suggest that this process has generally led to a reduction of competition within this scavenger guild by increasing tolerance among individuals at the earliest stages of scavenger consumption. Nevertheless, once the carcass is opened, the Inhibition Model is a better descriptor of this succession, as the levels of competition increase. However, additional data would be needed to determine whether some species are excluded from the carcass due to these negative interactions. Thus, these results support previous assumptions that ephemeral succession is initially driven by the Facilitation Model (Connell & Slatyer, 1977; Menéndez & Gutiérrez, 1999). However, this also contrasts with previous research on succession of dung and carrion-insect communities, where it is evident that facilitation is not the main successional mechanism in these ephemeral communities (Michaud & Moreau, 2017; Sladecek et al., 2021).

Finally, it is important to note that, in addition to carcass opening, other key facilitation processes might occur during carrion consumption dynamics, such as the previously mentioned process related to carcass location. In this specific system, previous studies have demonstrated information transmission between vultures with olfactory skills (i.e., pioneer species) and other raptor species (Naves-Alegre, Morales-Reyes, Sanchez-Zapata, et al., 2022). Similar processes have been observed in Old World systems, where species gain information from heterospecifics, including both raptors and mammals, in multiple ways (Jackson et al., 2020; Kane et al., 2014; Spiegel et al., 2013).

Competition intensity over the consumption of an ephemeral resource

Complex patterns of competitive mechanisms have been established in plant communities depending on the availability of limiting resources (Koffel et al., 2018). Our results show how the competition between scavengers, both conspecifics and heterospecifics, varies during the consumption process of this ephemeral resource. Aggressiveness starts from very high levels at the beginning of carcass colonization, probably because pioneer individuals defend the resource when they find it. This is consistent with that demonstrated in other studies, which establishes that in nondominated resources, that is, without an "owner," more aggressive individuals have a greater competitive capacity and, therefore, greater probability of dominating and exploiting the resource (Brown, 1964; Kilgour et al., 2020). However, after this initial stage of highly competitive intensity, we observed a decrease in this aggressiveness as the species present were not able to fully exploit the carcass. This is consistent with our results, which showed how the closed state of the carcass supported lower levels of competition in general.

In autotrophic communities it has been established that the identity of the species forming the assemblages does not influence the general dynamics of the succession (Maggi et al., 2011). In contrast, our results show a specific effect of the different species on behavioral and competition dynamics, showing the existence of a hierarchy between species (Houston, 1988; Wallace & Temple, 1987). On the one hand, the abundance of larger and competitively superior species (i.e., king vulture) did not influence the general levels of aggressiveness recorded, although it was the only species that positively affected the proportion of interspecific aggression. On the other hand, the role of the black vulture in the general levels of aggressiveness is highlighted, because this species led practically all intraspecific aggressions, the most frequent interaction type, because of its gregariousness behavior and not because of its physical dominance (Buckley, 1996). Therefore, the presence of these two species increases the levels of competition during carrion consumption, evidencing the importance of certain functional traits (i.e., body size and sociality) in the species hierarchy and, therefore, the competitive dynamics of this succession, supporting the Competition Model (Connell & Slatyer, 1977).

Concluding remarks and future perspectives

Our study highlights the importance of monitoring behaviors that are directly transferable to community functions (e.g., those related to foraging and resource consumption) (Wilson et al., 2020), also considering the dynamics of succession over time, rather than just comparing time-static measurements at different stages of the succession. In particular, we provide valuable insights into the factors that influence the dynamics of carrion consumption, a key process in the structure and functioning of ecosystems (Benbow et al., 2019). First, we demonstrate that competition intensity does not remain constant throughout the succession, being influenced by both resource availability and the facilitation process of carcass opening. Second, facilitative processes influence the community from its structure to the behavioral level, thus showing the possible importance that facilitation may have in other systems (e.g., with the presence of large carnivores or when tougher-skinned ungulate carrion is available) (Allen et al., 2014; Kendall, 2013; Moleón et al., 2015; Selva et al., 2003). Future research could benefit from a more comprehensive and integrated approach that considers the complex and dynamic behavioral interactions between scavenger species, together with factors related to species traits, the resource (e.g., carcass size) and environmental factors (e.g., habitat characteristics). In addition, we considered the carcass opening process as a static event in time because it better explained the behavioral and community dynamics throughout the process of consumption of the experimental carcasses we used. However, it is essential to study the dynamics and influence of this process in carcasses with thicker skin (e.g., megaherbivores carcasses), as there could be a progressive and nonstatic opening process of the carcass (i.e., enlargement of the aperture), or there could also occur different openings in a single carcass at different consumption times. Globally, it would be necessary to integrate behavioral approaches in the study of the functioning and structure of ecological communities. Understanding the mechanisms underlying these successional processes at different scales is fundamental because of their implications for ecosystem health and functioning (Rezende et al., 2021; Wenting et al., 2022), allowing us to assess the deterioration of functioning in highly human-impacted systems (Loreau & de Mazancourt, 2013).

ACKNOWLEDGMENTS

Lara Naves-Alegre, and Esther Sebastián-González were supported by the Generalitat Valenciana and the European Social Fund (ACIF/2019/056, SEJI/2018/024, respectively). Esther Sebastián-González also received the grant RYC2019-027216-I funded by MCIN/AEI/10.13039/501100011033 and by ESF Investing in Your Future.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Naves-Alegre et al., 2023) are available in Figshare at https://doi.org/10.6084/m9.figshare.22581982.

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SUPPORTING INFORMATION

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

How to cite this article: Naves-Alegre, Lara, Esther Sebastián-González, and José Antonio Sánchez-Zapata. 2024. "Behavioral Interactions are Modulated by Facilitation along a Heterotrophic Succession." *Ecology* e4236. https://doi.org/10.1002/ecy.4236