RESEARCH ARTICLE

Drivers of individual-based, antagonistic interaction networks during plant range expansion

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Abstract

1. Range expansion in plant populations, especially at the colonization front, can be either limited by disproportionately large effects of antagonistic interactions or facilitated by their release. How the strength of antagonistic interactions changes along successional gradients during range expansion is still poorly documented, especially when diverse assemblages of plant antagonists (rodents, invertebrates and birds) combine within interaction networks.

2. We study the changes in individual-based, predispersal seed–pulp predator networks along a colonization gradient in a rapidly expanding *Juniperus phoenicea* population in Doñana National Park (SW Spain). Additionally, we analysed the role of individual plant traits and neighbourhood attributes in network configuration by using Exponential Random Graph Models.

3. Seven seed–pulp consumer animal species varied significantly in their frequency of interaction and prevalence. While invertebrate species were well-established in old and intermediately mature stands, greenfinch *Chloris chloris* was dominant at the colonization front. Variable species roles and spread of interactions among individual plants generated changes in the configuration of interactions during plant expansion.

4. Individual plant traits strongly determined the topology of these networks, although with differences between stands. Increasing individual crop size and seeds per cone increased the interaction odds of individual plants, while seed viability showed the opposite effect. The network topology at the colonization front appeared less driven by individual traits, possibly because of the short interaction history of this recently established area. The disproportionately large effect of *C. chloris* in these recently established stands, potentially resulted in large seed losses during range expansion.

5. *Synthesis.* Turnover of antagonistic interactions, characterized the colonization front, resulting in more heterogeneous interaction strengths among individual plants. We found no evidence for a complete or sizeable antagonistic release of *J. phoenicea* at the colonization front promoting this rapid expansion. It becomes necessary to explore interactions with seed dispersers to understand

how antagonistic and mutualistic plant–animal interactions balance during range expansion. Our study highlights the importance of an individual-based approach in understanding how interactions are structured and driven in natural changing landscapes.

1 | INTRODUCTION

Fast-paced global change is currently impacting a number of crucial ecological factors that trigger plant range shifts. Recently, robustly supported evidences including spatial mismatches among interacting species caused by climate change (Schweiger et al., 2008), natural recolonization of abandoned agricultural lands (Escribano-Avila et al., 2014) or natural expansion (García et al., 2014) have shown plant abilities to naturally regenerate, disperse and colonize new habitats over short time spans. In most cases, a clear involvement of a diverse array of plant–animal interactions has been documented shaping the plant movements. For instance, mutualistic interactions such as animal-mediated seed dispersal are necessary to trigger rapid responses for plants to respond efficiently to global change drivers (González-Varo et al., 2021). However, the role that antagonistic interactions may play in limiting or facilitating plant range shifts in response to these factors is largely unknown.

Plant populations in natural range expansion scenarios are characterized by a mature population that acts as a source of propagules heading towards recently established areas, known as the colonization front (Shigesada & Kawasaki, 2002). Plant stand features such as individual density, spatial cover or demographic and genetic structure vary in these range shift processes (Excoffier et al., 2009; Petit, 2011; Shigesada & Kawasaki, 2002). Population expansion often involves a complex network of interactions with animals that either facilitate expansion (e.g. seed dispersers, pollinators) or constrain it (e.g. herbivores, seed predators). The outcome and balance between positive (mutualistic) and negative (antagonistic) interactions with other effects (e.g. interspecific competition) may pervasively determine the dynamics of plant movements (Svenning et al., 2014). It is important to explicitly represent interspecific interactions in forecasts of dynamic range expansion when most interacting species show correlated spatio-temporal trends in their effects and the number of interacting species is low (Svenning et al., 2014). The presence of active expansion fronts necessarily associates with such spatial and geographical variation in interaction conditions (Travis, 1996). One of the possible hypotheses linking natural expansion processes and plant–animal interactions is the enemy release hypothesis (Keane & Crawley, 2002). This release from enemies facilitates the expansion through a reduction or elimination of antagonistic agents, repeatedly documented during expansions of alien species (Meijer et al., 2016). Antagonistic plant–animal interactions

related to reproductive fitness play a key role during processes restructuring plant populations. For example, by increasing interactions intensity or releasing their pressure, these could constrain or allow early regeneration processes (Keane & Crawley, 2002; Svenning et al., 2014) or determine species richness (Janzen, 1970). These are likely processes during colonization from source stands, yet we still have a limited understanding regarding how biotic interactions and ecological factors result in observed range dynamics.

Antagonistic interactions with animals and their effect on plants can deeply affect plant reproductive output (Sallabanks & Courtney, 1992; Strauss & Irwin, 2004). These interactions could determine seed source limitation: plants are simply unable to produce enough propagules to 'fill' available target microsites for recruitment (Münzbergová & Herben, 2005; Schupp, 2002). Antagonistic and mutualistic interactions in nature are embedded, building complex networks with species from very different taxa (Fontaine et al., 2011; Morris et al., 2014) and result in combined effects on plant fitness (Harper, 1977). Predispersal seed predation occurs in advance to other potentially limiting effects that act on seed dispersal, such as recruitment or regeneration limitation (Nathan & Muller-Landau, 2000; Schupp, 2002). In fleshy fruited species, predispersal predation interactions may involve direct seed destruction (Fuentes & Schupp, 1998; González-Varo, 2010), fruit infestation by insect pests and other pathogens (García, 1998) and fruit/seed damage by pulp peckers and seed predators (Simmons et al., 2018; Snow & Snow, 1988). Subsequently, predation on dispersed seeds is performed by major seed predators and non-legitimate seed dispersers including insects, mammals and birds (Hulme & Benckman, 2002; Janzen, 1971). The magnitudes of predispersal seed predation are usually relatively low (Janzen, 1971; Kolb et al., 2007; Xu et al., 2015), although sometimes can compromise a large part of the available propagules (Crawley, 2000; Guido & Roques, 1996). How assemblages of predispersal seed–pulp predators are reshaped along plant regeneration gradients remains underexplored (Sallabanks & Courtney, 1992).

Tools from ecological networks theory have recently proven most effective in assessing the complex patterns of plant–animal interactions (Bascompte & Jordano, 2014). However, network models are typically built on species-averaged estimators, ignoring variability among individuals in their interaction patterns (Dupont et al., 2014; Melián et al., 2014). By averaging, the importance of individual biotic and abiotic context in the establishment of interactions

is neglected (Rodríguez-Rodríguez et al., 2017; Thompson, 1988; Valverde et al., 2016). This approach has pervasive consequences for the inferences and results interpretation. For example, aggregated data from many individuals subject to spatio-temporal variation are used to produce species-level averages, which marginalize away the relevant (process-level) scale (Clark et al., 2011). It is important to note that the partners in interactions in nature are individuals, not the species to which they belong. This fine scale is the most appropriate when assessing factors structuring interaction networks between plants and animals (Dupont et al., 2011). An individual-based approach is a powerful tool to understand the role of predispersal antagonistic interactions during plant range expansion, and factors that structure them. Any interaction shaped by individual phenotypes (with heritable potential) that could modify individual plant fitness can be an important selective force for trait evolution (Strauss et al., 2005; Strauss & Irwin, 2004). At the intra-population level, both intrinsic and extrinsic individual plant attributes play a role in interactions with predispersal antagonists (Schupp et al., 2019). The main intrinsic traits are those related to individual fecundity, plant physical features and seed–fruit traits. Meanwhile, extrinsic plant attributes such as location, isolation and neighbourhood also play a role in the assembly of antagonists (Schupp et al., 2019).

Novel analytical tools like Exponential Random Graph Models (ERGMs) allow us to unravel the determining factors of the complex structure of interaction networks (Morris et al., 2008; Saul & Filkov, 2007) and are extremely effective in addressing individual-scale variation. Analogously to a generalized linear model, ERGMs are based on a response variable which is the structure of the network itself (link distribution among nodes), and predictor variables with information associated with each specific network node (i.e. plant attributes). Thus, it is possible to compare the structure of an observed network with that generated by models that include or exclude specific node information. These models have been recently introduced in ecological research (Arroyo-Correa et al., 2021; Miguel et al., 2018), providing ways to infer causes determining the distribution of the interactions among network nodes (Kolaczyk & Csárdi, 2014). The relative roles of intrinsic and extrinsic traits in interaction network structures have been evaluated for mutualistic networks (Arroyo-Correa et al., 2021; Miguel et al., 2018; also see Gómez et al., 2011; Valverde et al., 2016), although how these factors drive antagonistic network topologies at the individual level remains unexplored.

In this study, we focused on the predispersal antagonistic assemblage of seed–pulp predators of *Juniperus phoenicea* subsp. *turbinata*. *Juniperus phoenicea* is considered as a foundation species (Whitham et al., 2006) and has undergone a rapid expansion since the protection of Doñana National Park five decades ago (García et al., 2014). This plant range expansion setting, involving a diverse assemblage of predispersal antagonists, is ideal for examining how interaction networks are restructured at the individual level across colonization stages, and the factors that determine these shifts in network structure. We expect a reconfiguration of interaction networks along the colonization gradient that would explain the rapid expansion of

this population (e.g. through a release of antagonistic interactions in recently established stands). Furthermore, we hypothesize that the individual-based network topologies are being driven by individual traits and neighbourhood context. Specifically, the main goals in this study were: (i) Describe the individual-based network of *J. phoenicea* and its assemblage of predispersal seed–pulp predators. (ii) Examine how these interactions are reshaped along a natural gradient of colonization through basic network descriptors and the species and the spread of interactions across individual plants. (iii) Assess the role of plant traits and neighbourhood context as drivers of network topology. (iv) Evaluate the consistency of network topology drivers during plant range expansion.

2 | MATERIALS AND METHODS

2.1 | Study site and study species

The study area is located on the southwestern edge of the Reserva Biológica de Doñana (RBD) within the limits of the Doñana National Park (Figure S1). Until its protection in 1969, this area was managed by local inhabitants for wood harvesting, livestock and hunting (Granados et al., 1988). Since then, several plant species, notably *J. phoenicea*, have significantly expanded their distribution in the area by natural regeneration (García et al., 2014). Locally, its expansion process has produced a natural colonization gradient from mature stands to early colonization fronts, where *J. phoenicea* enters areas dominated by low sclerophyllous shrubland.

Juniperus phoenicea subsp. *turbinata* (Guss.) Nyman (Cupressaceae) is a gymnosperm shrub inhabiting coastal dunes and rocky habitats in the western Mediterranean and in the Macronesian archipelagos (Adams, 2011). Species of the genus *Juniperus* are considered as foundation species in semi-arid Mediterranean ecosystems (Whitham et al., 2006) and the juniper-dominated woodlands on stabilized dunes are listed as Habitat of Community Interest (DOCE, 1992). *Juniperus phoenicea* is an anemophilous species characterized by very productive mast seasons occurring among years with very limited cone production (Jordano, 1993; Roques et al., 1984). Its reproductive cycle spans 2 years, and adult trees produce transformed fleshy cones also called galbules or arcestides (hereafter, cones). Cones are brown-red coloured when ripe (Figure S2) with an average of five seeds per cone, consumed and dispersed by several thrush species and medium-sized generalist mammals, such as *Meles meles* and *Vulpes vulpes* (Jordano, 1993; Perea et al., 2012).

Several invertebrate consumers have been recorded feeding on the cones and seeds all along the *J. phoenicea* distribution area (Roques et al., 1984; Turgeon et al., 1994; Ribes & Askew, 2009). The effects of each specific interaction are variable (Figure 1; Table S1). For example, the wasp *Megastigmus amicorum* (Hymenoptera: Torymidae) feeds on the seed embryo, while the larvae of the beetle *Nanodiscus transversus* (Coleoptera: Nanophyidae) feeds on the cone pulp. The antagonistic mammal assemblage is mainly

FIGURE 1 The pre-dispersive consumers of *Juniperus phoenicea* pulp and seeds found in the Doñana Biological Reserve. In addition, the recorded parasitoid species or morphospecies are included. The lines starting from the consumers go to the cone pulp or seed depending on their specific target. Modified from Ribes and Askew (2009).
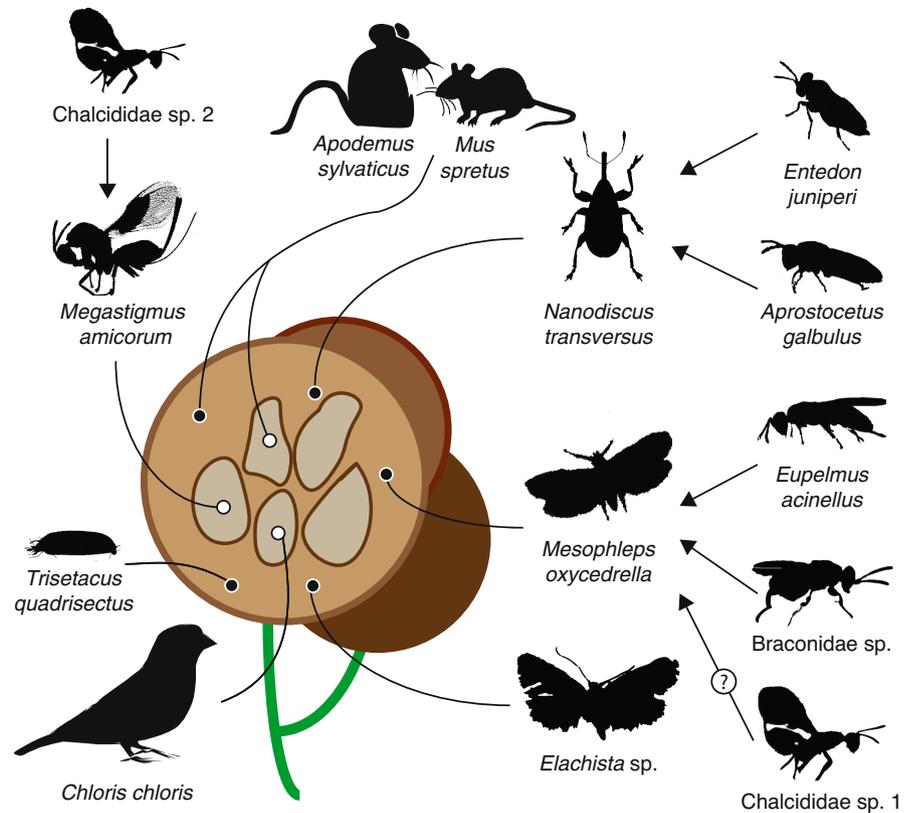
composed by mice *Apodemus sylvaticus* and *Mus spretus* (Rodentia: Muridae) that destroy the seeds to feed on the energy-rich embryo of juniper species, although rodents can consume the outer pulp (García et al., 2000; Santos & Tellería, 1994). In the study area, larger mammal species including lagomorphs, carnivores and ungulates, may also play a role as seed predators (also as seed dispersers) of *J. phoenicea*, damaging a variable percentage of seeds when feeding on cones (Perea et al., 2012). However, we exclude these species since their role as seed predators occurs in late stages of recruitment. Finally, the only reported seed predatory bird species is the greenfinch *Chloris chloris* (Passeriformes: Fringillidae; Santos & Tellería, 1994).

2.2 | Sampling design

Our sampling design consisted of three 1-ha plots along a natural regeneration gradient (Figure S1). These plots have all junipers individually identified and georeferenced. The mature stand is located in a mature juniper forest named '*Sabinar del Marqués*' (MAR), with dominance of junipers and a high density of individuals (10,520 individuals/ha). The intermediate stand, named '*Sabinar del Ojillo*' (OJI), is a dense juniper stand (9010 individuals/ha) also composed of mediterranean scrubland. The colonization front stand, '*Sabinar de Colonización*' (COL) is characterized by scattered juniper individuals of recent formation and with the lowest density (2030 individuals/ha). We established five subplots [mean ($\pm 1 SD$) of $522 \pm 115 \mathrm{m}^2$ subplots area] within each of the three main 1 ha plots, distributed regularly throughout the main plot. We used the individuals located in each subplot to randomly select 35 individual plants per stand ($N = 105$ plants in total). Focal plants were characterized and monitored for individual interactions during two fruiting seasons: October 2018–May 2019 and October 2019–June 2020.

2.3 | Sampling interactions

We monitored each of the 105 focal plants during the two consecutive study seasons, using different methods (see Suppl. Mat. for details). To collect data on rodent interactions, we combined two sampling methods: camera-trap survey and live-trapping. We conducted eight direct night-time trapping campaigns and the photo-trapping sampling effort involved a total of 201,600 h of recording, both methods evenly distributed among focal plants. For both methods we consider the presence of a species under a focal plant as a potential interaction. We quantified invertebrate interactions by dissecting 50 mature cones from each focal plant per season (number of analysed cones = 7906 cones). We identified antagonistic species and their markings based on Roques et al. (1984). When a parasitoid was recorded (Figure 1), we assigned the event as a detection of the host species, and indicative of one interaction of the plant with the corresponding host pulp–seed predator species (Table S1). Finally, *C. chloris* interactions were quantified by seed-traps placed under focal plants to collect the remnants of cones falling during their visits. Based on video records of foraging finches during full visits to the plants [mean ($\pm 1 SD$) of 4.5 ± 2.6 cones consumed per visit], we

estimated that every four damaged cones found in the seed-traps conservatively indicate one visit event by *C. chloris* in an individual plant. We carried out 35 checks of the seed-trap during the entire sampling, in which we counted the number of cones attacked, and emptied the trap. To handle the same interaction units for all data, we calculated the frequency of occurrence of each animal interaction for its survey. For example, how frequently an insect species was present in a cone relative to all the analysed cones, or how frequently we detected at least one *C. chloris* visit during weekly seed-traps checks.

2.4 | Plant characteristics

We thoroughly sampled a set of intrinsic and extrinsic plant traits known to influence animal preferences across the 105 focal plants (Table S2). We considered plant traits that could drive interactions with predispersal seed–pulp predators hierarchically (Sallabanks, 1993): first, the individual neighbourhood context, then general plant traits and finally at a higher scale of detail, cone quality traits. To characterize the juniper neighbourhood density and productivity of each plant we used the georeferenced location of all the individuals in each stand and estimated by direct count the cone production in all the juniper individuals growing in a buffer area of 100 m^2 surrounding each focal individual. For each focal individual, we recorded its height, the two maximum diameters of its canopy projection, canopy area and total cone crop size. Direct counts of cones were carried out by scanning the whole plant canopy area and counting the cones with a hand-counter. We used the harvested cones (50 cones per plant) to measure cone traits. For each plant, we measured the average values of maximum length and diameter of the cones, total fresh mass, pulp mass, seed mass, one-seed mass, number of seeds per cone and seed viability was estimated by flotation procedure (Table S2; Figures S4–S6).

2.5 | Individual-based, antagonistic interaction networks of *J. phoenicea*

We constructed four weighted, individual-based, bipartite networks between *J. phoenicea* focal plants and their predator species, one for each of the studied stands and a general one with all the data combined. Notice that our networks are partially individual networks (i.e. bipartite networks with two modes, plants and animals), with one of their modes (plant nodes) being represented by individual plants, but the other mode (animal nodes) represented by the antagonistic animal species. However, we use a phytocentric approach where the individual-based scale is only applied to plants and their individual assemblages. We used the three per-stand networks to evaluate changes in network configuration and node strength distribution during plant range expansion. We pooled data collected from the three stands (105 focal plants) into an overall network that was useful as a 'big picture' to detect general trends in the effect of cone

and plant-level traits in the network topology. In addition, per-stand networks were also used to assess among-stand variation in the role of individual traits and neighbourhood attributes on the detected network topologies across the colonization gradient.

To detect structural changes in interaction organization between the three study areas a pool of network metrics was computed. To evaluate how the weight of interactions was spread out or concentrated in a few plants we calculated species strength. This metric was also calculated for predator species, to assess their role in each network. This node-level metric measures the importance of each node of one mode in the network from the perspective of the other mode nodes (Bascompte et al., 2006). In addition, as a measure of how extensively the interactions with each animal species are distributed among plant individuals in each stand, we calculated the prevalence of predator species (% plants with specific interaction recorded). At the network level, we calculated metrics that would allow us to detect changes in the overall network topology (weighted connectance, weighted nestedness and modularity). To assess the antagonistic load in each stand we calculated Weighted Connectance (wC), the number of links in the whole network relative to the total possible number of links (Bersier et al., 2002). To determine the amount of hierarchical structure in a network, we computed Weighted Nestedness (wNODF). High wNODF strengthens a core of highly connected nodes which, coupled with increased connectance of peripheral nodes, provides a cohesive structure to the network (Bascompte et al., 2003). To detect densely connected groups of nodes (e.g. animal species that tend to interact with the same subset of individual plants), with sparse connections to nodes in other groups, we calculated Modularity (Olesen et al., 2007). Both network-level and node-level metrics were computed with ʀ package BIPARTITE, and in the case of modularity we use the Beckett algorithm (Dormann et al., 2008; Dormann & Strauss, 2014). To address network similarities, we computed the Hamming distance between network graphs, which relies on the minimum number of link additions/deletions required to mutate one network into the other (Butts & Carley, 2005). In this context, higher Hamming distance between networks A-B than between A-C indicates that the topology of A is more similar to C than it is to B. Statistical significance of network metrics was calculated by comparison with a null model, contrasting the observed networks with 100 randomly generated networks using null models which maintain network connectance ('vaznull' function in the ʀ package BIPARTITE, Dormann et al., 2009). We used bootstrapping with replacement to estimate 95% confidence intervals (CIs) for network metrics and to assess possible overlap in estimated metrics values between the three study networks.

2.6 | Assessing drivers of network topology

To analyse the effect of individual and neighbourhood plant traits on network topology we estimated an Exponential Random Graph Model (ERGM; Kolaczyk & Csárdi, 2014; Lusher et al., 2013). Before fitting ERGM models on network structure and performing

multivariate discriminant analyses on plant traits (see below) we tested for multicollinearity among predictor variables using a variance inflation factor (VIF) procedure. Multicollinearity was computed using the VIF R package (Lin, 2012) and it allowed us to discard five variables of the initial dataset that showed strong multicollinearity. We set a threshold of VIF = 3, and we discarded redundant variables above this value. Two variables were removed at the plant level (plant diameter and plant cover), and three variables at the cone level (cone mass, pulp mass and total seed mass; Table S2). We tested for differences in cone traits among plants of the three stands by means of linear discriminant analysis carried out with the 'lda' function of the MASS package (Venables & Ripley, 2002). We used discriminant analysis to find a linear combination of traits that maximizes variation among plants within the three distinct sampled stands. Traits, when combined with others, provided the best discrimination power were selected through the Wilks' lambda criterion, using the 'greedy. wilks' function in the R package KLAR (Heino et al., 2015).

2.6.1 | ERGM theory

ERGM has been used recently in ecological research for the analysis of individual-based mutualistic interaction networks (Arroyo-Correa et al., 2021; Miguel et al., 2018). The ERGM design is analogous to a GLM and implements a Markov chain Monte Carlo maximum likelihood parameter estimation. These models allow us to test hypotheses about the underlying mechanisms shaping networks by modelling how the number of links is affected by specific predictor variables associated with the network nodes (node covariates). In common with other models, ERGMs require a link function that captures the underlying distribution of the data (here, interaction strength distribution). In addition to node covariates, to take into account aspects of network topology like link weights, the ERGM allows to consider these structural covariates in parameter estimation. The structural term representing the total number of link weights, referred to as 'sum' in ERGMs, models the general propensity of nodes to be connected to other nodes, and it is equivalent to having an intercept within a GLM.

2.6.2 | ERGM interpretation

In a weighted ERGM, the coefficient estimates of node covariates must be interpreted in terms of the effect on the probability of increasing (or decreasing) the strength of pairwise interactions. They indicate the expected change in the logged number of any pairwise interaction increasing (or decreasing) as a function of a given one-unit change in a specific node attribute (Arroyo-Correa et al., 2021; Kolaczyk & Csárdi, 2014). In our case these predictor variables are directly associated with the node (plants) attributes (e.g. cone crop size, seed mass) and model how these traits affect the number of links that each node establishes in the network. By associating network topology to specific plant attributes, we aimed to assess

the contribution of each node (plant) attribute to the overall network configuration. The underlying Poisson distribution of interactions allows the interpretation of the coefficients as the increase or decrease in the frequency that each plant–animal pair interacts (logged). In this way, plant traits, as node attributes, affect animal preferences that ultimately define the interaction weights measured; these in turn determine how each node of the network (a plant) gets its position in the overall network.

2.6.3 | ERGM design

We fitted ERGM with the structure of the individual-based bipartite network as the response variable, the sum of the link weights as a structural covariate, and the plant and cone traits and neighbourhood attributes of individual plants as node covariates. We use the full network to fit the best possible model based on AIC criteria. For this, hierarchical models were built by adding the different groups of variables or factors (area factor, general plant variables and cone quality variables). The best model for the general network is the one that was also used to evaluate the effect of node attributes on the specific networks of each area. Therefore, we finally fitted the same model for the general network and, separately, for the three per-stand networks, adding neighbourhood attributes (specific to each area) as an additional node variable. In order to examine the relative importance of each group of variables (neighbourhood attributes, individual plant traits and cone quality traits) in our models, we calculated the combined effect accounted for by each variable group, relative to the summed value of the estimates. The computation of effects variance partitioning and of goodness-of-fit model estimates are not yet implemented for bipartite weighted ERGM (Kolaczyk & Csárdi, 2014), and we did not estimate them. We use the relative sizes of estimates (and the summed estimate for variable groups) as a proxy of the variable relevance in the model (Arroyo-Correa et al., 2021), and to discern between effects due to link configuration and effects given by node attributes.

3 | RESULTS

3.1 | Predispersal seed–pulp predators

We found the same assemblage composition of seven predispersal seed–pulp predators species in the three study stands (Figure 2). We quantified their importance through two components of the interaction, frequency of occurrence and prevalence. In these terms, the most prevalent interaction was that of *C. chloris* with the plants at the colonization front, interacting with 91% of the plants (Figure 3a). However, considering the 105 plants surveyed, the most widespread predators were invertebrate species (Table S3). Overall, in terms of frequency of occurrence of the interaction, *C. chloris* was the most frequent consumer of *J. phoenicea* seeds, specifically in the colonization front (Figure 3a, Table S3). We counted a total of 7458 cones in seed-traps, preyed upon by *C. chloris*, resulting in 1865 estimated interaction
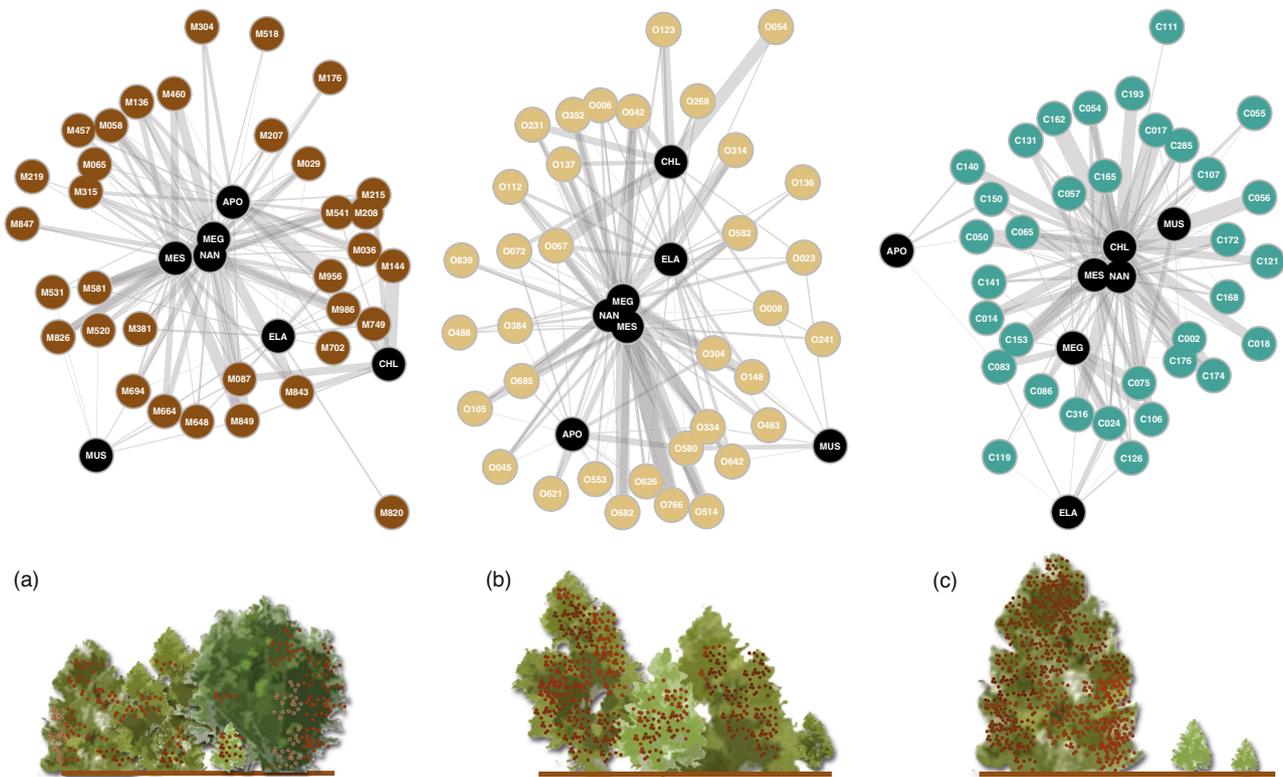
FIGURE 2 Weighted bipartite networks of the three stands representing the focal plants of *Juniperus phoenicea* in each stand (coloured nodes) and the predispersal seed–pulp predator species (black nodes). Each pairwise plant–animal interaction is represented by a grey link whose thickness varies according to its frequency of occurrence. Node labels identify each focal plant. Animal species codes: APO - *Apodemus sylvaticus*, MUS - *Mus spretus*, CHL - *Chloris chloris*, MES - *Mesophleps oxycedrella*, ELA - *Elachista* sp., NAN - *Nanodiscus transversus*, MEG - *Megastigmus amicorum*. Bottom, illustrative representation of the three stands along the regeneration gradient, from the most mature stand (MAR; a), to the intermediate stand (OJI; b), and ending at the colonization front stand (COL; c). In addition, some differences between stands, such as neighbourhood density, plant size or fecundity, are represented.

events. *Chloris chloris* interactions were much more frequent (and also spread between plants) at the colonization front than in the intermediate and mature stands (Figure 3a). From the 7905 collected and dissected cones we found 2175 unique pairwise interactions between juniper cones and invertebrate species. Except for the case of *C. chloris* at the colonization front, invertebrates were more important in terms of interaction intensity and prevalence (Figure 3a). Finally, rodents (*A. sylvaticus* and *M. spretus*) were the least frequent group (Figure 3a; Table S3). We quantified a total of 154 potential rodent-focal plant interaction events, 36% sampled by live traps and 64% by camera traps.

3.2 | Individual-based, antagonistic interaction networks of *J. phoenicea*

The three stand-based networks were small and their structure differed from stand to stand (Figure 2). Hamming distances indicated that the networks of mature (MAR) and intermediate (OJI) stands were more similar to each other than compared to the colonization front (COL) network. The minimum number of link substitutions required to change one network into the other was 3760 between COL-OJI, 3780 between COL-MAR and 2636 for OJI-MAR.

At the node level, the spread with which the strength of interactions between individual plants was distributed differed between stands. As a result, fewer plants at COL, compared to MAR and OJI, showed antagonistic interaction strength values >0.20 (COL = 8, MAR = 12, OJI = 14, Figure 3b). The node strength of animal species varied greatly between the three networks (Figure 4a). *Chloris chloris* had a high importance in the COL area, with a reduced importance of the rest of the species in comparison to MAR and OJI, where invertebrate species were dominant. The wasp *M. amicorum* and the moth *M. oxycedrella* show a peak in OJI although they were also relevant in MAR.

The three estimated network descriptors (wC, wNODF and M) showed marked, almost linear, trends along the landscape gradient (Figure 4b), with significant differences among them. Weighted connectance (wC) increased strongly from MAR to OJI and to COL, when approaching the colonization front, showing a linear trend (Figure 4b, Table S4). The same pattern was also found for weighted nestedness (wNODF) which was significant for the three networks (in comparison with randomly built networks), and also with highly significant differences between the three sites (Figure 4b). In contrast, modularity decreases when approaching the colonization front (Figure 4b). For both wC and wNODF, the MAR and OJI measurements were closer to each other than the COL values. We did not detect any clear pattern
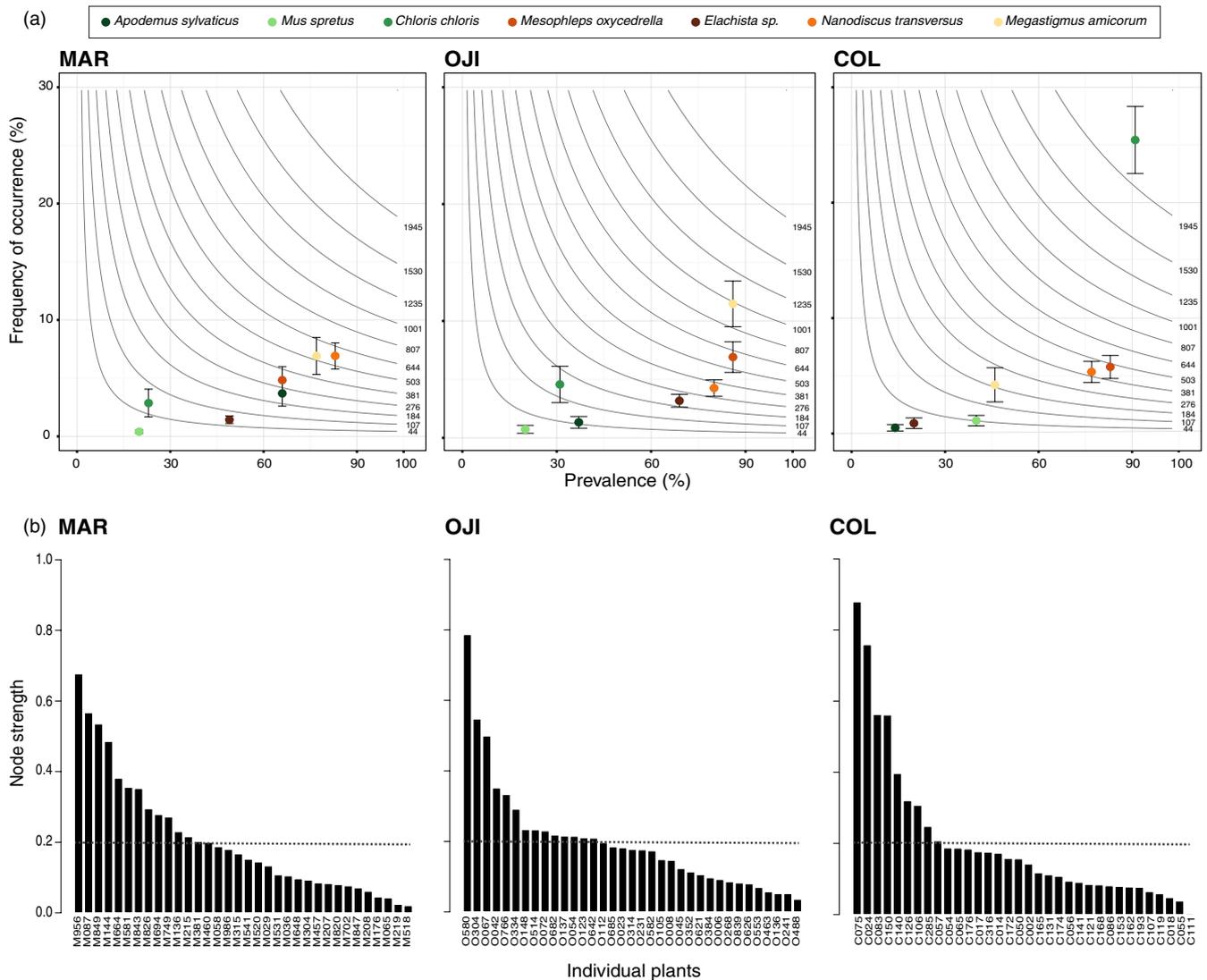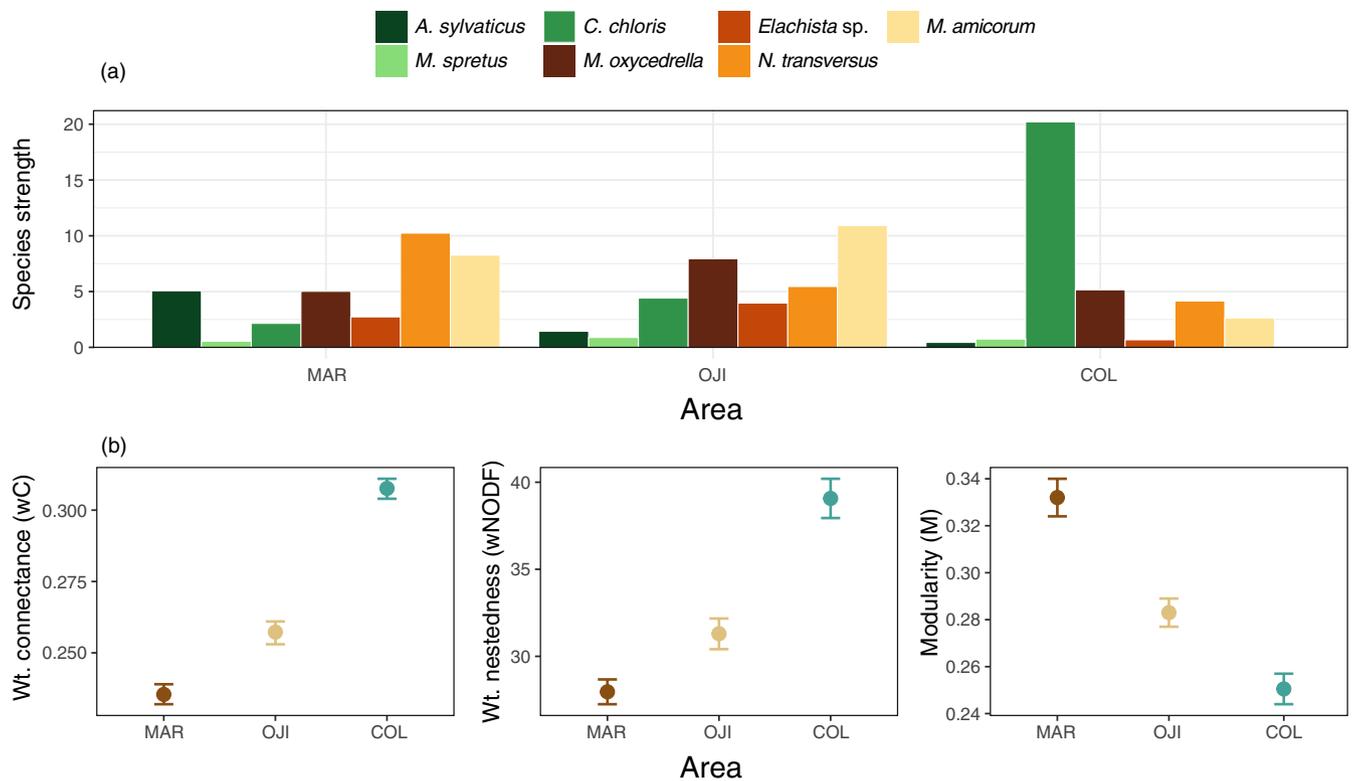
FIGURE 3 (a) Role of predispersal seed–pulp predator species in terms of frequency of occurrence in our sampling (lines show ±1 *SE*), and prevalence (percentage of plants with at least one interaction recorded). The isolines (and their values) represent the product of both components and can be used to illustrate the magnitude of the differences between species roles. (b) Rankings of plant individual strengths (plant codes along the *x* axis) in each study area (most mature stand, MAR, intermediate stand, OJI and colonization front, COL). Dotted lines illustrate a reference threshold set at 0.2 to highlight the number of plants with node strength above or below it in each network.

in the number of modules across the colonization gradient (MAR = 3, OJI = 5, COL = 4; Figure S7). The seed-predator *M. amicorum* and the pulp-predator *M. oxycedrella* belong to the same module in the three networks. In all three networks, *C. chloris* formed a single module or was accompanied by other vertebrates, but never shared with invertebrate species. All network metrics were significantly different from those calculated by null models; their observed values, and their detailed confidence intervals can be found in (Table S4).

3.3 | Plant characteristics

Linear discriminant analysis showed that individual plant and cone traits are good predictors for specific area classification, indicating significant differences in plant characteristics among areas. The two first discriminant functions assign correctly each plant to its stand in 70.47% of the cases. This means that plants within stands tend to be more similar to each other in terms of traits in comparison with plants from the other stands. The significant independent variables according to Wilks' lambda, were plant level variables (plant height and cone crop size) and cone level traits (seed mass and number of seeds per cone; Table S5). The first discriminant function (LD1) accounted for 83.57% of variance, discriminating individual plants of the colonization front (COL) from the rest of individuals (Figure S8). This first function is characterized by the effect of plant height and plant fecundity, with the younger plants from COL being taller and with larger cone crop sizes. Cone traits also discriminated plants from COL, with more seeds per cone and the heaviest seeds. The second discriminant function (LD2) accounted for the remaining 16.43% of trait variance, contributing

FIGURE 4 Metrics of the three individual-based interaction networks of individual *Juniperus phoenicea* and their predispersal seed–pulp predators in the three stands studied; MAR, mature stand; OJI, intermediate maturity stand and COL, the colonization front. (a) Relative importance of animal species in each network, estimated using the species strength metric. (b) Structural metrics at network level in the three stands.

TABLE 1 Summary of general Exponential Random Graph Models (ERGMs, all study stands pooled) together with a schematic summary of the results of the ERGM models in each stand (most mature stand, MAR; intermediate stand, OJI; and colonization front, COL). The model estimates the effects of individual features on the weighted network structure. The 'sum' effect can be interpreted as the effect of link weight's distribution on the configuration of the observed network. The right-hand side of the table shows the direction of the effect: (+) increasing or (−) decreasing the logged number of interactions. If the effect of the variable is significant the symbol appears in bold, and 0 indicates there is no direction of the effect.

	General			MAR	OJI	COL
	Estimate $\pm$ SE	z value	p value	Effect		
Sum	1.525 $\pm$ 0.01	82.418	**<0.001**			
General plant traits						
Plant diameter[1]	−0.063 $\pm$ 0.02	−2.717	**0.006**	−	−	+
Plant height	0.062 $\pm$ 0.02	2.580	**0.009**	0	+	0
Plant crop size	0.184 $\pm$ 0.02	8.165	**<0.001**	+	+	+
Cone traits						
Cone diameter	0.109 $\pm$ 0.02	3.753	**<0.001**	0	+	0
No. seeds/cone	0.165 $\pm$ 0.02	6.517	**<0.001**	+	+	+
Seed viability	−0.117 $\pm$ 0.02	−5.715	**<0.001**	−	0	−
One-seed mass	0.037 $\pm$ 0.03	1.330	0.183	−	0	+
Neighbourhood attributes						
Juniper neighbourhood crop size				−	−	+
Juniper neighbourhood density				+	−	0

slightly to separation between MAR and OJI in terms of the relation between the number of seeds and their per-seed weight. According to the second discriminant function, OJI plants had

more seeds per cone than the MAR plants with fewer but heavier seeds per cone. Overall, plants of the youngest stand (COL) were the ones that differed the most in their individual traits, being the

plants of the intermediate stand (OJI) and the mature stand (MAR) much more similar to each other (Figure S8).

3.4 | Drivers of network topology

3.4.1 | General ERGM

From all the fitted models, the best ERGM model was the one that included three general plant attributes and four cone quality traits. We found a strong and positive effect of 'sum' in the fitted ERGM (Table 1). Thus, the total interaction frequency between focal plants and predators influences the probability of detecting this specific network configuration. However, individual plant and cone traits (node attributes) were also significant predictors shaping the observed network structure (Table 1). For example, our general model indicated that the odds of establishing more interactions increases with cone diameter. Thus, a one-standard deviation increase in this predictor variable is expected to result in an increase in interaction odds by a factor of $\exp(0.109) = 1.115$, or nearly 11% (Table 1). At cone level, the more important network topology driver was the number of seeds per cone, increasing the interaction odds by a factor of $\exp(0.165) = 1.179$ or nearly 18% of increase. Surprisingly, seed viability showed a negative effect on link establishment chances, decreasing interaction odds by a factor of $\exp(0.117) = 1.12$ or −12%. We did not find an effect of one-seed mass. We found that odds of interaction between focal plants and predators increased with individual crop size by a factor of $\exp(0.184) = 1.202$ (*c*. 20% increase; Table 1). Plant diameter showed an opposite effect, decreasing link establishment odds by a factor of $\exp(0.063) = 1.065$, or nearly −6.5%. Plant height showed a similar effect on interaction chances, but consistently increasing the interaction odds.

3.4.2 | ERGM per stand

We found that the predictive potential of individual plant traits together with neighbourhood context decreased notably in COL (Figure 5). The topology of the colonization front network was less driven in terms of the combined effect of plant-cone traits and neighbourhood attributes (MAR = 53.30%, OJI = 50.98%, COL = 37.52%, Figure 5). When splitting the effect of explanatory variables between individual traits and neighbourhood attributes, we found that the neighbourhood variables were less important drivers of network topologies (Figure 5). In the colonization area network, the role of neighbourhood variables was marginal for explaining the observed network topology. The importance of variables at the plant level and at the cone level did not remain constant between networks. While cone quality traits were much more important explaining the topology in MAR and COL, in OJI we detected the inverse pattern (Figure 5). Individual plant traits and neighbourhood effects on network topologies were not consistent between the three stands (Table 1; Figure S9). Yet individual crop size had a positive effect in interaction odds between focal plants and predator species in the three populations. Considering traits at the cone quality level, the
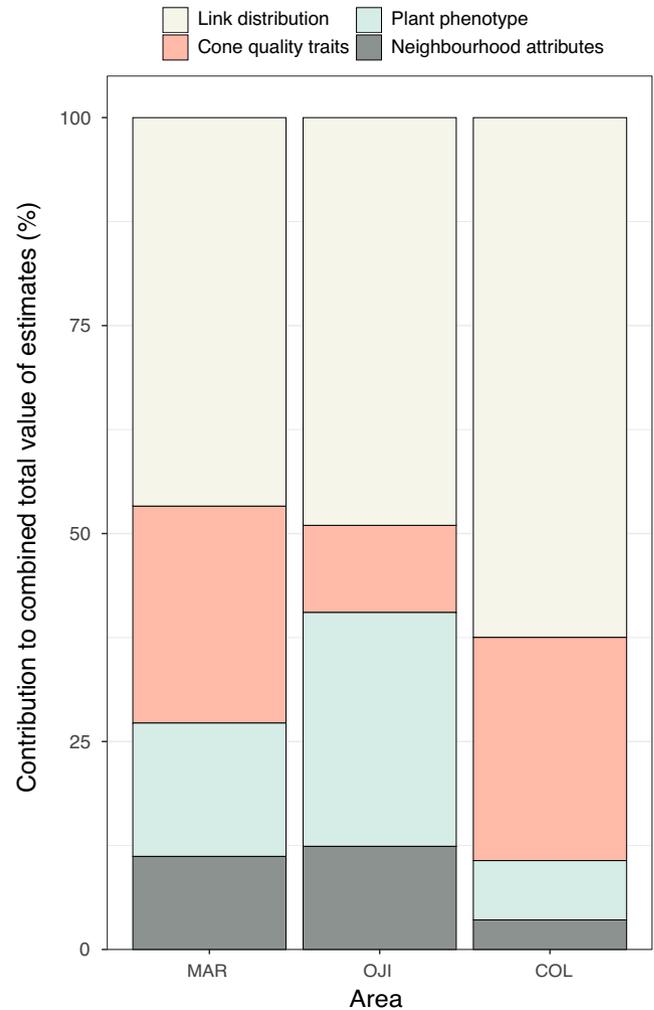
FIGURE 5 Contribution to combined total value of estimates of the main variable groups included in the ERGM's models. Each bar represents the same ERGM model fitted for the network of each stand respectively. The colours indicate the % of the total value of estimates accounted for by each variable group (e.g. in COL the neighbourhood metrics lose relevance compared to their role in MAR and OJI). Link distribution is the 'sum' parameter importance estimated in each ERGM and is interpreted as how much the model predicts that the interaction frequency between focal plants and antagonists influences the probability of detecting this specific network configuration.

number of seeds per cone was the most robust node variable, with a positive and significant effect in COL and MAR and a positive but not significant trend in OJI. Likewise, seed viability had a negative effect on the three networks (significant in COL and MAR), which means that the property of having a higher percentage of well-developed seeds reduces interaction odds with predators in the three study stands.

4 | DISCUSSION

Unravelling ecological interactions at the highest possible resolution (e.g. among individuals, within populations) and their imprint at

higher levels of ecological complexity (e.g. multi-species interaction networks) represents a new challenge (Guimarães, 2020). Plant–animal antagonistic interactions have been frequently studied at the species level during regeneration processes (Redmond et al., 2019; Villa-Galaviz et al., 2012). Nevertheless, to our knowledge, this is the first study addressing the reconfiguration and topological drivers of individual-based antagonistic networks that provides a detailed description of their variation along environmental gradients. Despite using a three-location replicated design, some limitations persist for generalizations about how biotic interactions at the expansion front may impose constraints applicable to other systems. Our sampling of individual plants at each of the study areas, however, was spatially stratified so as to encompass a broad variety of contexts, as well as temporally replicated by studying two reproductive seasons.

In agreement with our hypothesis, individual traits and neighbourhood context acted as drivers of individual network topology patterns. However, we did not find a sustained pattern for the driving role of individual and neighbourhood context across colonization stages, probably due to species role turnover and individual plant traits variability. Our results indicate a positive relationship between the maturity of the stand and the relevance of individual traits determining final network topology, besides high predispersal predation in the colonization front. Overall, our findings suggest that *J. phoenicea* antagonistic interaction networks were driven by individual traits and neighbourhood context. Despite the fact that some groups of antagonists dilute their effects towards the colonization front, this is not the case for granivorous birds for which we found strong predispersal seed-predation pressure in the front area. Consequently, the intensity and stand distribution of predispersal predation pressure suggest that the colonization process is not promoted by a substantial antagonistic release in recently established areas.

4.1 | Individual-based, antagonistic interaction network of *J. phoenicea*

We found a small and functionally diverse assembly composed by the most representative seed–pulp predator groups: insects, mammals and birds. In addition to the seven species presented here, we have also detected the presence in the area of the mite *Trisetacus quadrisectus* consuming cone pulp in the study area, although not on the sampled focal plants. The fact that different areas in the expansion gradient have identical assemblages helps us to disentangle the context-dependent effects over the individual network topology patterns. *Chloris chloris* was the most important predispersal predator, and although it was not specifically analysed, it was the one that caused the greatest loss of propagules. At the colonization front *C. chloris* dominated the interactions, with a central role in the antagonistic network, explaining an important part of the differences between networks in addition to the effect of network topology drivers in this area. We think that the dispersal potential of *C. chloris* along with their preferences for high, productive and isolated trees (distinctive in colonization front; Figure S8; Table S5) were the

main reasons for this trend. Regarding the invertebrate assemblage, the specific interactions found had been previously described by past studies (see Materials and Methods). Our results indicate that their interactions in general were well-established in mature and intermediate-maturity areas, dominating the antagonistic networks, a contrasting situation with the *C. chloris*-dominated interactions in the colonization front. This pattern was probably related to the fact that these species, closely linked to *J. phoenicea*, required a longer time to establish stable and important populations. Rodents were the least abundant group with low predispersal seed–pulp predation pressure throughout the study area.

The larger spread of interactions detected in the mature and intermediate stands compared to the higher concentration in a few plants at the colonization front may be a sign of the shorter interaction history in these new stands. A reduced subset of the plants appears to accumulate most interactions at the colonization front, with a larger fraction of plants showing reduced interaction strengths with the antagonists and, according to the ERGM results, this appears driven largely by size and fecundity hierarchies and cone characteristics (Weiner & Solbrig, 1984). These heterogeneous interaction patterns between stands generated general structural changes detectable by the topological network descriptors.

Despite the fact that the interaction assemblage was identical across sites, our analysis revealed different topological patterns, meaning that these differences must have been driven from a smaller scale: the individual-based interaction modes. The heterogeneous patterns of species roles between stands were in part due to consistent variation of plant traits between stands, as revealed by results of the discriminant analysis. The colonization front is formed by scattered, large and productive plants mixed with younger, recently established individuals, probably due to intraspecific competitive release in these new environments or a more heterogeneous age structure following punctuated episodes of establishment. In contrast, plants of the intermediate and mature stands were more similar in their phenotypes.

Overall, we found a higher connectance of these individual-based networks compared with other antagonistic, species-based interaction networks (e.g. Park et al., 2018). This finding was probably related to the fact that the individual-based resolution of the data results in more evenly distributed interactions due to the virtual deletion of forbidden links in the matrix. Thus, interactions with most antagonistic partners, both vertebrates and invertebrates, had >40% prevalence at any studied site. The higher connectance at the colonization front may emerge from the overall higher prevalence and resulting strength of the major antagonistic interactions in this stand. Regarding nestedness, the three networks were moderately nested. Downscaling to the individual level is expected to dissolve this pattern, as interspecific variability in the mode of interaction is assumed to be greater than intraspecific variation. It is clear to us that *C. chloris*' role in network structure greatly determined this pattern. In analogy with super-generalist species in species-based interaction networks, *C. chloris* interacted intensively with all the plant nodes (Figure S7), acting as a super-generalized partner for most individual junipers in the colonization front. We also

found high values for modularity, an expected result for antagonistic networks (Cagnolo et al., 2011) and also when downscaling to the individual level (Dupont et al., 2014; Tur et al., 2015). The decreasing trend of modularity towards the colonization gradient could be promoted by two processes: (1) the generalization of *C. chloris* and high prevalence of their interaction reduced the possible modules and their intensity at the colonization front and; (2) plants' traits heterogeneity of mature stands favoured the appearance of modules due to a higher specificity of the interactions (Figure S10). The modularity analysis also reveals a truly checkerspot pattern in the overall antagonistic interaction strength across sites: distinct groups of individual junipers showed up at the three sites in terms of their sharing of interaction partners. These modules never include both vertebrates (especially *C. chloris*) and invertebrates or, if including just invertebrates, almost invariably they contain a seed predator (*M. amicorum*) and a pulp consumer (*M. oxycedrella*). The better representation of invertebrates in the mature and intermediate stand together with the dominance of *C. chloris* at the colonization front is probably responsible for the greater dissimilarity of the youngest network regarding the two more mature stands, as detected by the higher Hamming distances.

4.2 | Drivers of network topology

In the general ERGM, individual crop size was the main driver of network architecture. In seed dispersal, the number of fruits is the best supported and understood individual driver of variation in interactions (Schupp et al., 2019); more seeds are preyed upon as more cones are produced. This production cost could be profitable since the resource is so abundant that a large part of seeds produced can escape from seed predators. This huge cone production strategy could be explained under a predator-satiation hypothesis (Janzen, 1971; Linhart et al., 2014), yet framed here at the individual level. We think that the increase in interactions with plant height may be related to the improved visibility and attractiveness of taller trees to some bird species (Perea et al., 2014), and flying invertebrates (moths and wasps) increasing their encounter probabilities during flight and, therefore, increasing predation probabilities upon cones. Ultimately, this might reflect the pervasive effects of size hierarchies in populations of long-lived plants (Weiner & Solbrig, 1984) determining also interaction strength hierarchies. Regarding the diameter of the plant, we find a negative effect on the number of node interactions. In our study area these larger diameters are typical of old plants, irregularly branched, with lower fecundity, smaller cones, etc., and therefore less attractive to predators. As the per-stand results indicate, this negative effect is seen in mature and intermediate stands, where this plant physiognomy is prevalent. At the cone scale, both cone diameter and number of seeds increased network interactions, probably because of their greater attractiveness in terms of pulp (pulp eaters) and seed (seed predators) of these individuals. We expected that plants with a higher proportion of filled seeds would establish more interactions because predators actively choose them (Fuentes & Schupp, 1998), but we found the opposite pattern, in concordance with previous studies with similar juniper

interactions (García, 1998). Two hypotheses might explain this result, although as each encompasses different animal groups, both may be valid: (1) for *C. chloris*, probably they need to peck more cones on more inviable plants than on plants with more full seeds, where they find the full seeds rapidly and; (2) for the invertebrates, some plant species induce more frequent seed abortion when detecting insect-damaged fruits or indirectly by ovipositing insects introducing fungi that can cause abortion (Sallabanks & Courtney, 1992). Our results of interactions with predispersal seed predators drivers are consistent with previous literature (Hulme & Benckman, 2002; Janzen, 1971; Kolb et al., 2007; Sallabanks & Courtney, 1992), although their effect on the topology of emergent and complex networks (e.g. combining vertebrates and invertebrates) had not been previously explored.

Networks from each stand showed variations in the sign and the significance of predictive traits, in some cases differing between stands. This result is consistent with the findings of Miguel et al. (2018), where the effects of predictors varied between study areas. Here we only detect a consistent trend in network topologies for plant fecundity and number of seeds per cone, both of which had a positive effect on linkage establishment. The combined estimate (summed effects) of the variables studied showed a marked drop in the colonization front, most likely linked to an expected decrease in the neighbourhood effect in this newly formed stand. This lower combined estimate for the pooled effects of variables suggests a reduced predictability of interaction build-up in this stand compared to the intermediate and mature stands. We suggest that the more mature remnants had longer 'interaction histories' compared to the colonization front, where individual junipers might be farther from stabilizing their interaction modes. At the more mature stands, with probably more than hundreds of years of interaction history, neighbourhood effects and plant characteristics drive the likelihood of link formation for individual plants. In contrast, in the colonization front, probably with <40 years of interaction history, only a few plants form a central subset in the network core, with interactions building up according to variability in fecundity and cone traits. These results may evidence the stabilization time of plant–animal interactions in plant expansion scenarios in terms of species, interaction network structures and trait drivers of these interactions.

In the present work we did not focus on the consequences of antagonism for individual plant fitness and thus its contribution to limit the expansion processes. The fact that at the colonization front the spread of antagonistic load is found to be concentrated in a reduced subset of plants, together with the lower importance of invertebrates in this stand, may suggest a release of pressure by predispersal antagonists, favouring fast plant range expansion. However, our results evidence a turnover of antagonistic agents, with the widely ranging, granivorous birds being the main driver of topological network trends. Moreover, functionally, this interaction is likely to result in a much higher seed loss at the colonization front. The trend of these juniper populations in recent years, with a rapid expansion (García et al., 2014) does not support the idea that *C. chloris* might limit expansion either. To fully understand the relationship of plant–animal interactions and rapid expansion it is essential to analyse seed dispersal by frugivores in the system. Our results

suggest that compensation by mutualistic seed dispersers at the colonization fronts (e.g. Holthuijzen & Sharik, 1985; Escribano-Avila et al., 2014) and/or effective release from antagonists in certain masting years that favour expansion waves (Linhart et al., 2014) may help understanding these rapid processes of plant range expansion. Furthermore, a similar analysis of the drivers of seed dispersal interactions may be key to assess how animal preference processes exert opposing or confluent selection pressures explaining changes in phenotypes and genotypes along these gradients. Future research addressing variations in the structure of seed dispersal networks, their ecological drivers and their functional consequences in range expansion scenarios will be key to a holistic understanding of the role of ecological interactions in plant range shifts.

AUTHORS' CONTRIBUTIONS

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CONFLICT OF INTEREST

The authors declare no conflict of interest with the content of this work.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and analysis code are available at Zenodo https://doi.org/10.5281/zenodo.6583228 (Isla, Jacome-Flores, Pareja, et al., 2022) and GitHub https://github.com/PJordano-Lab/Juniperus_antagonists_2022, and datasets are also available in Dryad Digital Repository https://doi.org/10.5061/dryad.0rxwdbs38 (Isla, Jácome-Flores, Pareja et al., 2022).

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