

# The role of invasive species in the network of the Mediterranean ecosystem dominated by sclerophyllous vegetation of central Chile

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# Abstract

The ecosystem dominated by sclerophyllous vegetation in central Chile has been defined as a biodiversity hotspot due to a combination of high levels of endemism and threats, such as biological invasions. Understanding how embedded these invasive species are within the community provides relevant information for decision-makers to conserve this ecosystem efficiently. For this purpose, a network of the sclerophyllous vegetation was constructed based on a bibliographic review of the distribution and diet of species, as well as an evaluation of its topological properties. Additionally, to identify the key invasive species within the network, centrality metrics and *in silico* extinction analysis were employed. The network comprises 252 species and 798 trophic interactions, with 63% basal, 33% intermediate, and 4% higher trophic levels. The European rabbit was consistently the invasive species with the highest centrality indices, followed by dogs, rats, mice and Californian quail. The *in silico* rabbit eradication analysis primarily resulted in the relief of herbivore pressure on several native and endemic plants (e.g., *Neltuma chilensis*, *Convolvulus chilensis*), which could regenerate in their absence and serve as resources for native herbivores, thereby reducing competition pressure. However, it reduced the dietary range of some native and threatened predators (e.g., *Galictis cuja*, *Leopardus guigna*). Managing invasive species is a priority for preserving the ecosystem dominated by sclerophyllous vegetation in central Chile. Therefore, it is necessary to conduct experimental exclusion studies and monitoring programs to assess the impact of invaders on the regeneration ecosystem and the most vulnerable species.

## Introduction

The Chilean Mediterranean-type ecoregion, one of the five Mediterranean zones worldwide, is characterized by strong seasonality, with dry summers, wet winters, and a latitudinal precipitation gradient (Lionello et al. 2006). Located between the Atacama Desert and temperate forests, it is dominated by sclerophyllous forests and shrublands (Luebert and Pliscoff 2017; Garfias et al. 2018; Cartes-Rodríguez et al. 2022). These ecosystems provide key services such as soil and water regulation, carbon storage, biodiversity maintenance, and cultural values (Gangas 2015; Smith-Ramírez et al. 2023). The region is also a global biodiversity hotspot, harboring nearly half of Chile's vascular plant endemics but facing severe threats from land-use change, invasive species, wildfires, and a prolonged megadrought (Arroyo and Cavieres 1997; Myers et al. 2000; Schulz et al. 2011; Alaniz et al. 2016; Miranda et al. 2017; Garreaud et al. 2017, 2020; Martinez-Harms et al. 2021). These pressures have reduced cover, structure, and composition, with exotic herbivores identified as major barriers to ecological succession and natural regeneration (Holmgren 2002; Noonan et al. 2021).

To date, Chile records 1,119 exotic species, many invasive due to their wide distribution and ecological impacts (Jaksic and Castro 2016; PNUD 2017). The Mediterranean ecoregion hosts the highest number of invasives (Jones et al. 1996), particularly herbivorous mammals such as livestock and lagomorphs (European rabbit and hare), which strongly affect resource distribution and habitat dynamics (Gálvez-Bravo et al. 2011; PNUD 2017). Livestock, for instance, has strongly contributed to the expansion of

savannas dominated by *Vachellia caven* in central-southern Chile, especially in valleys where livestock grazing is greater, which has reduced the abundance of native woody plants such as *Neltuma chilensis*, chiefly because *V. caven* seeds survive and germinate more successfully after ingestion by livestock (Fuentes et al. 1989; Holmgren 2002). Similarly, the endemic *Beilschmiedia miersii* (Vulnerable, IUCN) suffers from fruit predation, seedling herbivory, and trampling by cattle, horses, and goats, in addition to seedling predation by European rabbits (*Oryctolagus cuniculus*) in open scrublands (Henríquez and Simonetti 2001; Becerra et al. 2004; Morales et al. 2015; de Kok 2021). The endemic palm *Jubaea chilensis*, also threatened, has experienced marked population declines due to seed and seedling predation by invasive herbivores such as *Rattus rattus* and *O. cuniculus*, particularly affecting its regeneration (Wara 2007; Fleury et al. 2015; Cordero et al. 2021).

Moreover, European rabbits generate greater mortality of native seedlings of other typical species of the sclerophyllous forest, such as *Quillaja saponaria*, *Schinus latifolius*, and *Lithraea caustica* because they have larger feeding ranges than native rodents such as *Octodon degus* that only consume seedlings found up to five meters from their burrows (Simonetti and Fuentes 1983; Fuentes et al. 1983); making it difficult to establish woody seedlings in open areas (Holmgren et al. 2000; Holmgren 2002). Consequently, herbivory by invasive species may limit the ecological succession and even restoration efforts by preventing the establishment of woody plants.

Recovering and preserving biodiversity in these ecosystems is essential, and restoration provides an opportunity to address invasive species (Guo et al. 2018). Passive and assisted strategies can promote forest recovery, with the latter is required where degradation prevents natural regeneration (Rey-Benayas et al. 2008). Although livestock management (e.g., regenerative grazing) and invasive herbivore control may facilitate native biodiversity recovery (Myers et al. 2000), management actions may have unexpected impacts, especially indirect effects on nontarget species mediated by the network structure of the community. Barbar and Lambertucci (2023) recently demonstrated that lagomorphs subsidize predators both in native (Spain) and exotic ranges (Australia, Argentina). This pattern is also evident in Chile, where native predators such as the Black-chested eagle (*Geranoaetus melanoleucus*), Harris hawk (*Parabuteo unicinctus*), and Culpeo fox (*Lycalopex culpaeus*) shown an increase in the consumption of European rabbits during the last decades (Jiménez and Jaksic 1989; Jaksic 2001; Figueroa and González-Acuña 2006; Pavez et al. 2010; Lobos et al. 2020).

In Chile, network studies in north-central and southern regions show that the European rabbit is highly connected within communities that include predators, competitors, and plant producers—encompassing endemic, native, and exotic species (Gübelin et al. 2023; Mann-Vollrath et al. 2024). These findings highlight the difficulty of predicting the impacts of managing invasive species with a long history in ecosystems, particularly when their level of integration and current ecological roles remain unclear (Prior et al. 2018; Crystal-Ornelas and Lockwood 2020). Therefore, invasive species management must be evaluated using practical tools before it has an impact on the ecosystem.

Network analysis provides a holistic framework to evaluate invasive species, as it integrates multiple effects simultaneously and helps prioritize management according to species' impacts, pressure, and community invasibility (Frost et al. 2019). Further, it includes information about bottom-up and top-down effects and if an invasive species is central in a network and interacts with other highly connected species to establish if drastic abundance changes on invasive species can affect the community (Lees and Bell 2008; Ings et al. 2009; Barbar et al. 2016; Frost et al. 2019). Thus, this paper aims to analyze the network of the Mediterranean-type ecosystem in central Chile, characterized by sclerophyllous vegetation (both forest or scrub), and to identify the role of invasive species, their primary interactions, and potential ecological mechanisms, thereby proposing recommendations for their management.

## Methods

### Study area

The study area is situated within the Mediterranean-type ecoregion of central Chile (31–37°S), specifically between 31°S and 37°S, spanning the regions from Coquimbo to Biobío and ranging from the coast up to 2200 MASL (Luebert and Plischoff 2017). This area is characterized by a pluviseasonal Mediterranean-type climate, with winter precipitation and hot-dry summers (Fig. 1), with precipitation that increases both southwards and from the Andes to the Coastal range (Luebert and Plischoff 2017). The vegetation is dominated by sclerophyllous formations—scrub and forest—composed of hard-leaved evergreen trees and shrubs, with species composition varying by latitude and elevation (Luebert and Plischoff 2017). Forests in more humid coastal areas include hygrophilous species such as *Drimys winteri* and *Beilschmiedia miersii*, while Andean ranges are dominated by *Lithraea caustica*, *Quillaja saponaria*, and *Cryptocarya alba*. The entire region has been heavily altered by anthropogenic pressures, resulting in open scrubs with numerous exotic herbaceous plants and xerophytic woody species such as *Baccharis linearis* and *Vachellia caven* (Luebert and Plischoff 2017). This ecoregion concentrates 66% of Chile's population and the largest urban areas (INE, 2018), and its landscapes are dominated by agriculture, forestry plantations, livestock, and expanding urban areas (Nahuelhual et al. 2012; Rojas et al. 2013). Only eight protected areas within the National System of Protected Wild Areas (SNASPE) safeguard native biodiversity (Fig. 1).

### Literature review

The literature review included documents in English and Spanish (papers, books, theses, governmental and museum reports, and personal communications). Sources were searched in Web of Science, Google Scholar, and the repository of the Pontificia Universidad Católica de Chile (repositorio.uc.cl), covering 1978–2024. All possible trophic interactions were compiled, whether persistent or transitory, using keyword combinations (e.g., diet, prey, trophic ecology, feeding, central Chile, sclerophyllous forest, sclerophyllous scrub) with the scientific names of potential predators and prey. References were included regardless of quantitative diet information, and when data were unavailable at the species level,

information was recorded at the Order or Family level. Given the scarcity of diet studies in the area, we also considered species feeding on surrounding vegetation types within comparable latitudinal and altitudinal ranges. For plants, only species occurring in sclerophyllous forests and scrub (Luebert and Pliscoff 2017) were included. Terrestrial arthropods and mollusks were considered basal resources due to the absence of dietary data. Each species was then classified by origin (introduced, native, endemic) (MMA 2019) and, when applicable, by conservation status following the IUCN Red List (IUCN 2023).

## **Trophic network, keystone invasive species and *in silico* extinction analysis**

To construct the trophic network of the Chilean Mediterranean ecosystem dominated by sclerophyllous vegetation (hereafter referred to as the Chilean Mediterranean ecosystem), we considered three trophic levels: top predators; intermediate consumers (macropredators, omnivores, and herbivores); and basal species (resources or species without a diet). Structural attributes were evaluated, including species richness, number of links, link density, the proportion of basal, intermediate and top species, connectance, generality, connectivity, and vulnerability, following standard definitions (Dunne 2009; Santana et al. 2013). All metrics were calculated in R v.4.3.3, and network visualization was performed in Network3D (Williams 2010), using standardized connectivity to highlight the relative importance of each species.

To evaluate the relative importance of invasive species in the network as drivers of ecosystem deterioration, we calculated four centrality metrics: (1) degree centrality, the number of trophic interactions of a node; (2) closeness centrality, reflecting the average distance of a species to all others; (3) betweenness centrality, which quantifies the frequency of a species on the shortest paths between others; and (4) eigenvector centrality, which considers the influence of a species and that of its interacting partners (Estrada and Bodin 2008; Delmas et al. 2019). Metrics were computed with the “NetworkX” package in Python (Hagberg et al. 2008). To identify invasive species with the highest centrality, rankings were established for each metric and then summed to produce an overall ranking.

A *in silico* network extinction simulation for the invasive species with the highest centrality was employed to understand the short-term mechanisms in a possible scenario of management, using the “igraph” package in R version 4.3.3 (Csárdi et al. 2023). All interactions were assumed to contribute equally (network based on presence and absence), where the node corresponding to the introduced species with the highest centrality index from the network was removed to quantify the effect. After the *in silico* extinction analysis, the percentage of prey that a predator lost and the percentage of resources that were released by the extinction analysis were quantified (Ávila-Thieme et al. 2023). To identify the species that could be indirectly influenced by the eradication of the most centrally invasive species (e.g., relaxation of interspecific competition), the species that fed on the same resources as the introduced species were identified. A predator-prey subnetwork was generated, considering the resources

consumed by the introduced species and its other consumers. The result was visualized using Network3D software (Williams 2010).

## Results

### Literature review

Twenty-one predator species were identified within the Chilean Mediterranean ecosystem. Of these, 12 correspond to top predators, including birds of prey, carrion birds, and carnivorous mammals. Among birds of prey and carrion birds, native species include *Athene cunicularia* (Burrowing Owl), *Bubo magellanicus* (Magellanic Owl), *Elanus leucurus* (White-tailed Kite), *Falco femoralis* (Aplomado Falcon), *Geranoaetus melanoleucus* (Black-chested Buzzard-Eagle), *G. polyosoma* (Variable Hawk), *Parabuteo unicinctus* (Harris Hawk), *Strix rufipes* (Rufous-legged Owl), *Tyto alba* (Barn Owl), and *Vultur gryphus* (Andean Condor). In addition, two mammalian top predators were identified: *Puma concolor* (Puma) and the introduced *Canis lupus familiaris* (domestic dog).

Regarding intermediate species (mesopredators, omnivores, and herbivores), among mesopredators, eight native species were identified: birds of prey *Falco sparverius* (American Kestrel), *Glaucidium nanum* (Austral Pygmy Owl), *Milvago chimango* (Chimango caracara) and carnivorous mammals *Leopardus guigna* (Kodkod or Chilean cat), *Galictus cuja* (Lesser grison), *Lycalopex griseus* (Chilla fox), and *L. culpaeus* (Culpeo fox), and *Conepatus chinga* (Molina's hog-nosed skunk); while two endemic species were the reptiles *Philodryas chamissonis* (Chilean Long-tailed snake) and *Callopiastes maculatus* (Spotted False monitor). Twenty-three omnivorous species were also recorded, including native and endemic birds (e.g., *Ochetorhynchus melanurus*, *Turdus falcklandii*), endemic lizards (e.g., *Liolaemus nitidus*, *L. tenuis*), introduced rodents (e.g., *Rattus norvegicus*, *R. rattus*), and the endemic amphibian *Rhinella arunco*. At broader taxonomic levels, the genus *Liolaemus*, the family Icteridae, and the orders Chiroptera, Galliformes, and Squamata were also incorporated into the omnivore category. Thirty-nine herbivorous species were identified, including native, endemic, and introduced birds (e.g., *Diuca diuca*, *Nothoprocta perdicaria*, *Callipepla californica*), native, endemic, and introduced small mammals (e.g., *Abrothrix longipilis*, *Chelemys megalonyx*, *Oryctolagus cuniculus*), and native and domestic large mammals (e.g., *Lama guanicoe*, *Equus caballus*). Additionally, the genera *Abrothrix*, *Octodon*, and *Phyllotis*; the families Troglodytidae and Tyrannidae; and the order Passeriformes were included as herbivores.

Fifty-four arthropod taxa were identified as basal species at different taxonomic levels, including phylum, class (e.g., Insecta), order (e.g., Diptera, Araneae), family (e.g., Elateridae, Formicidae), and genus (e.g., *Agrotis*, *Edrabius*), as well as endemic and native species such as *Acanthinodera cummingi* and *Calosoma vagans*. In addition, one introduced mollusk was recorded at the species level (*Cornu aspersum*). Finally, 72 plant species were identified as native, endemic, or introduced (e.g., *Ephedra chilensis*, *Lithraea caustica*, *Eucalyptus globulus*). At higher taxonomic levels, 20 genera (e.g., *Senecio*, *Prunus*), three families (Asteraceae, Fabaceae, Poaceae), and five plant components (e.g., seeds, fruits) were also considered.

# Trophic network, keystone invasive species, and in silico extinction analysis

The trophic network of the Chilean Mediterranean ecosystem (Fig. 2) comprised 252 species (nodes), of which 63% were basal (plants, arthropods, mollusks), 33% intermediate (herbivores, omnivores, mesopredators), and 4% top predators (raptors, carrion birds, carnivorous mammals). A total of 798 trophic interactions were identified, with a connectance of 0.01, indicating that only a small fraction of potential links was realized. Generality and vulnerability showed greater variability in prey number than in predator number (SD = 2.06 and 1.24, respectively). Connectivity values ranged from 0.16 to 6.95, with most highly connected species being native, although several exotics also ranked among the top 40 (e.g., *Canis lupus familiaris*, *Rattus rattus*, *Mus musculus*, *Callipepla californica*, *Oryctolagus cuniculus*). The highest connected species were the native owl *Glaucidium nanum* (6.95), followed by the native owl *Athene cunicularia*, and the exotic lagomorph *O. cuniculus* (6.0), and the native canid *Lycalopex culpaeus* (5.84). The network as a whole was composed mostly of native (53%) and endemic (25%) species, while 22% were invasive (refer to Table S1 for species origin details).

The introduced species with the highest degree centrality was *Oryctolagus cuniculus* (European rabbit, 0.15), with 39 interactions, followed by *Callipepla californica* (California quail) and *Canis lupus familiaris* (dog), both with 18 interactions. The latter was also the species with the highest closeness centrality (0.44), followed by *O. cuniculus* (0.42) and *Rattus rattus* (Black rat, 0.39), indicating that these species were the closest to the rest of the species. In a similar manner to the degree centrality level, betweenness centrality in *O. cuniculus* (0.12) was the species with the highest value, followed by *C. lupus familiaris* (0.08). Finally, regarding the eigenvector, the species with the highest value was *O. cuniculus* (0.18), followed by *C. lupus familiaris* (0.15) and *R. rattus* (0.14), indicating that these exotic species were highly influential in the network (Fig. 3). Species were ranked according to their centrality values of the four-centrality metrics, and *O. cuniculus* was the top-ranked species (Table 1). The European rabbit node had many interactions with other species which were also highly connected (e.g., birds of prey and foxes), and it was a key connector in this network.

**A. B. C. D.**

Table 1

Introduced species with greater centrality according to the number of direct interactions, centrality metrics and their ranking in ascending order. Bold letters indicate the highest values in each metric. See Table S2 for full centrality values.

| Species                       | N° Links  | Degree      | Closeness   | Betweenness | Eigenvector | Ranking |
|-------------------------------|-----------|-------------|-------------|-------------|-------------|---------|
| <b>Oryctolagus cuniculus</b>  | <b>39</b> | <b>0.15</b> | 0.42        | <b>0.12</b> | <b>0.18</b> | 1       |
| <i>Canis lupus familiaris</i> | 18        | 0.07        | <b>0.44</b> | 0.07        | 0.15        | 2       |
| <i>Rattus rattus</i>          | 16        | 0.06        | 0.39        | 0.01        | 0.14        | 3       |
| <i>Mus musculus</i>           | 21        | 0.06        | 0.39        | 0.02        | 0.12        | 3       |
| <i>Callipepla californica</i> | 18        | 0.08        | 0.37        | 0.05        | 0.07        | 5       |

Rabbits consumed 23 of the 110 plant species in the network (six native, two exotic, and 15 endemic). These plants shared between one and 11 consumers (Fig. 4, colored bars). The European rabbit played a crucial role in the persistence of several species primarily consumed by them (Fig. 4, black bars). For example, simulations indicated that rabbit removal would cause the complete loss of all consumers for eight plant species, including the native *Neltuma chilensis* and the endemic *Alstroemeria zoellneri*. Several other species (e.g., *Cryptocarya alba*, *Quillaja saponaria*) would lose about half of their consumers, while others (e.g., *Schinus molle*, *Vachellia caven*) would experience smaller reductions. Full details of affected species are provided in Table S3.

The European rabbit was identified as a potential competitor of different herbivores, including large native mammals (*Lama guanicoe*) and exotic mammals (e.g., *Bos taurus*, *Capra hircus*, *Equus caballus*), small endemic mammals (*Abrocoma bennetti*) and native mammals (*Abrothrix longipilis*, *A. olivacea*, *Octodon bridgesi*, *O. degus*, *Oligoryzomys longicaudatus*, and *Phyllotis darwini*), native passerine birds (e.g., *Diuca diuca*, *Mimus thenca*, *Turdus falcklandii*), and native omnivores (*L. culpaeus* and *L. griseus*) and an exotic omnivore (*C. lupus familiaris*) (Fig. 5).

The European rabbit was consumed by 15 of the 21 predators in the network (71%) (Fig. 6). Predator diets were heterogeneous (7–37 prey items), and no species specialized exclusively on rabbits. The *in silico* extinction analysis showed that rabbit removal would reduce predator diets by 2.7–14.3%, with the highest losses in *Puma concolor*, *Leopardus guigna*, *Galictis cuja*, and *Geranoaetus melanoleucus*. Most predators, including owls, foxes, and raptors, lost < 10% of their prey. Full dietary breadths and prey loss percentages are provided in Table S4.

## Discussion

The Chilean Mediterranean ecosystem has been heavily fragmented by anthropic disturbances (e.g. species' introduction) with severe consequences for regeneration and conservation (Schulz et al. 2011; PNUD 2017; Garfias et al. 2018; Jaksic and Castro 2021). Because invasives are long established and

integrated, effective management requires understanding their ecological roles to guide biodiversity recovery. Our results highlight the conservation value of this ecosystem: 78% of species in the network are native or endemic, underscoring their importance as a biodiversity reservoir (Kaiser-Bunbury and Blüthgen 2015). Conversely, 22% are introduced—both a symptom and a driver of degradation (MacDougall and Turkington 2005)—showing how exotics can become functionally embedded in native communities.

Structurally, the network is dominated by basal nodes (63%), mainly primary producers that underpin ecological stability and socio-ecological services (Chapin et al. 2011). Plants connect basal processes to apex predators and the resilience of ecosystems via seed dispersal, soil retention, and microclimatic regulation (Bonilla and Johnson 2012; Banfield et al. 2018; Smith-Ramírez et al. 2023). Intermediate nodes (32%) maintain key processes such as seed dispersal and prey control but are also where exotic species most disrupt native dynamics through functional replacement or displacement (Lopez-Calleja 1995; Figueroa et al. 2002; Reid and Armesto 2011; Miranda et al. 2019; Marchante et al. 2021).

Centrality analyses shows that a few invasive species have a disproportionately large effect on the network structure. The European rabbit was identified as the most influential introduced species, followed by dogs, commensal rodents and California quail. Together, these species represent distinct mechanisms by which invasions reshape the network:

1. **Herbivory:** Rabbits inhibit the regeneration of herbaceous and woody species, impeding the progress of succession and natural recovery (Fuentes et al. 1983; Holmgren 2002; Meserve et al. 2011; Becerra et al. 2018; Gómez-Fernández et al. 2023; Correa-Cuadros et al. 2023). Controlling these species, in addition to excluding livestock, can alleviate the recruitment limitations of native and endemic species.
2. **Competition:** Introduced granivorous and generalist species (e.g., quail, commensal rodents, rabbits) compete with native species for resources or indirectly limit regeneration, altering the niches of native taxa (Torres-Contreras et al. 1994; Jaksic 1998, p. 199; Holmgren 2002; Jaksic et al. 2002, p. 2016; González Acuña et al. 2013; Banks et al. 2015; Jaksic and Castro 2016; Gómez-Fernández et al. 2023; Andrews et al. 2023).
3. **Trophic subsidy.** Rabbits now constitute a substantial part of predator diets, generating dependence between carnivores and raptors (e.g., puma, Lesser grison, Kodkod, Black-chested eagle) (Jaksic et al. 1981; Ebersperger et al. 1991; Correa and Roa 2005; Pavez et al. 2010; Lobos et al. 2020). It has also been reported in other parts where introduced lagomorphs are an essential subsidy for native predators (Barbar and Lambertucci 2018, 2023). Complicating control, rabbit reduction may benefit native vegetation and herbivores but may temporarily reduce predator diets.
4. **Disease vectors.** Although dogs had lower standardized connectivity, their high closeness centrality reflects rapid network-wide effects. They displace native predators and transmit diseases, especially near protected-area edges (Banks and Bryant 2007; Vanak and Gompper 2009; Gompper 2014; Silva-Rodríguez et al. 2023). Commensal rodents also ranked high in closeness/eigenvector centrality, consistent with broad interactions and pathogen sharing in disturbed habitats (Lobos et

al. 2005; Silva-Rodríguez et al. 2010; Banks et al. 2015; Jaksic and Castro 2016; Llanos-Soto et al. 2019; Torres-Pérez et al. 2019). Maintaining intact sclerophyllous habitats is thus key to buffering their ecological and epidemiological impacts.

Scenario analyses suggest that reducing rabbits (> 40%) can release resources for native small mammals (Lurgi et al. 2018). In central Chile, the megadrought since 2010 has altered vegetation and resource phenology, reshaping small-mammal dynamics and predator diets (e.g., *Octodon degus* declines coinciding with greater rabbit use; Pavez et al. 2010; Garreaud et al. 2017, 2020). Thus, rabbit control combined with vegetation recovery could improve habitat for native rodents and help rebalance predator–prey relations (Courchamp et al. 2000; Padilla and Pugnaire 2006; Cuevas and Quesne 2006).

However, these outcomes remain hypothetical, underscoring the urgent need for field experiments to quantify rabbit impacts. Given the rabbit's centrality, integrated management—including targeted reduction, exclosures, browse protection, and livestock regulation—offers the best potential benefits, provided it is paired with multitrophic monitoring and adaptive thresholds to prevent unintended effects on predators (Courchamp et al. 2003; Palmer et al. 2016).

Although our analysis highlights dogs, commensal rodents, and California quail as influential invaders in the network, their management requires more nuanced consideration. For dogs, strategies such as promoting responsible ownership and reducing their presence in conservation areas have been suggested. For commensal rodents, maintaining habitat integrity and sanitation is likely to be important. Regarding California quail, interventions should first assess the degree of resource overlap with native granivores. Further studies are needed to evaluate the feasibility and effectiveness of these actions in the Chilean Mediterranean ecosystem.

In sum, the Chilean Mediterranean ecosystem, dominated by sclerophyllous vegetation, is rich in native and endemic species but functionally reshaped by a few introduced species, primarily the European rabbit. Network analysis identifies rabbits as a keystone invader with different impacts. The release of herbivorous pressure corresponds to the most important mechanism triggered by the hypothetical eradication of rabbits, yet their precise role in plant regeneration remains uncertain. Field experiments are therefore essential to disentangle rabbit effects from those of other herbivores and to inform adaptive, multi-trophic management strategies that can restore resilience in these landscapes.

## Declarations

### Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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## Author contributions

All authors read and approved the final version of this manuscript. Patricia Gübelin: Conceptualization, methodology, formal analysis, investigation, data curation, visualization, writing – original draft, writing – review & editing. Jennifer Paola Correa-Cuadros: Conceptualization, methodology, formal analysis, supervision, writing – review & editing, validation. M. Isidora Ávila-Thieme: Conceptualization, methodology, formal analysis, writing – review & editing, validation. Carlos Riquelme: Data curation, investigation. Sebastián Ramírez-Baeza: Data curation, investigation, Writing – review & editing. Melanie Duclos: Data curation, investigation, Writing – review & editing, validation. Enrique Silva-Aranguiz: Data curation, Investigation. Pablo Becerra: Funding acquisition, writing – review & editing, validation. Fabián M. Jaksic: Funding acquisition, writing – review & editing, validation.

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## Data availability

The datasets generated and analyzed during the current study are available in the [Sclerophyllous forest\_food\_web] repository, [<https://github.com/IsidoraAvilaThieme>].

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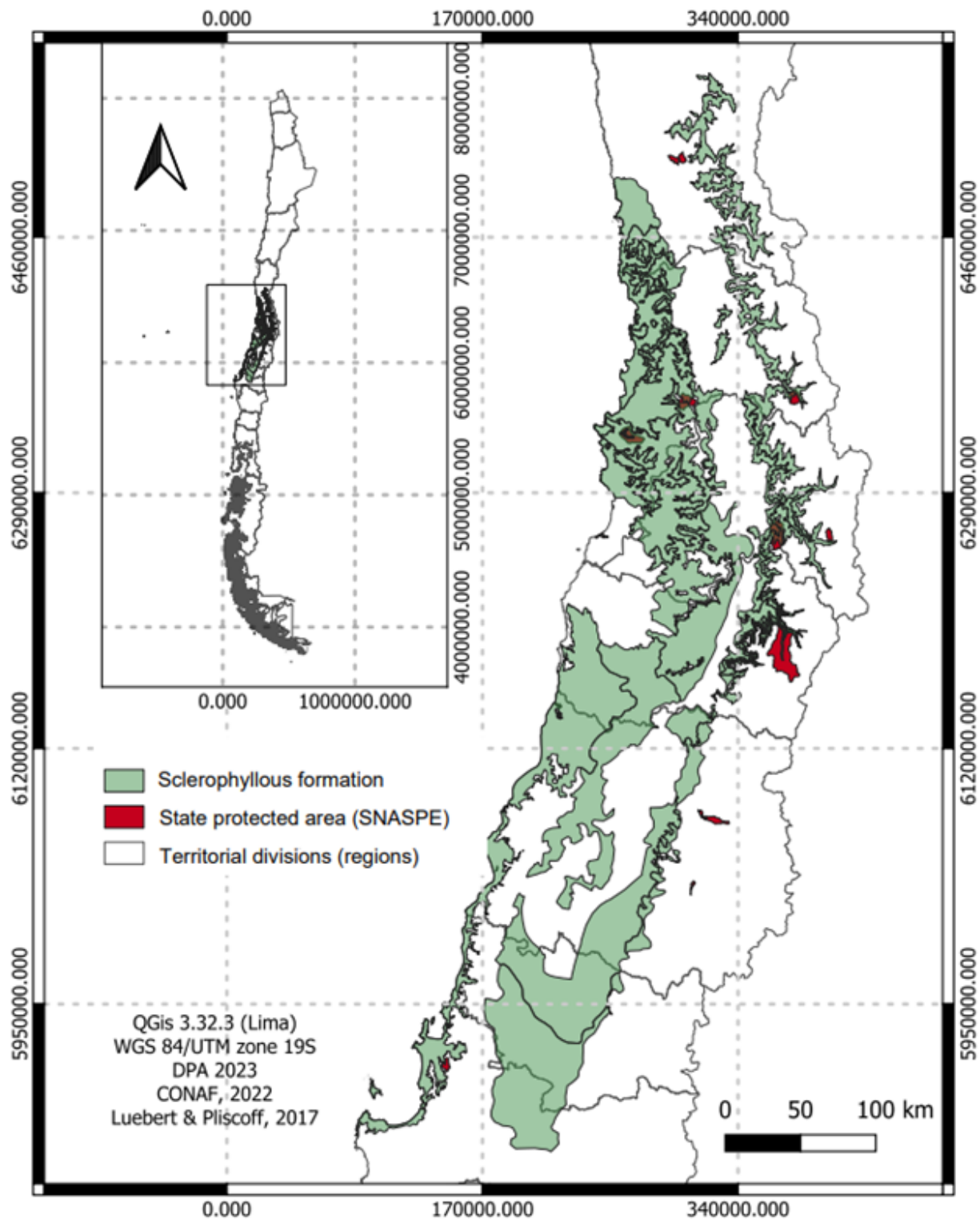
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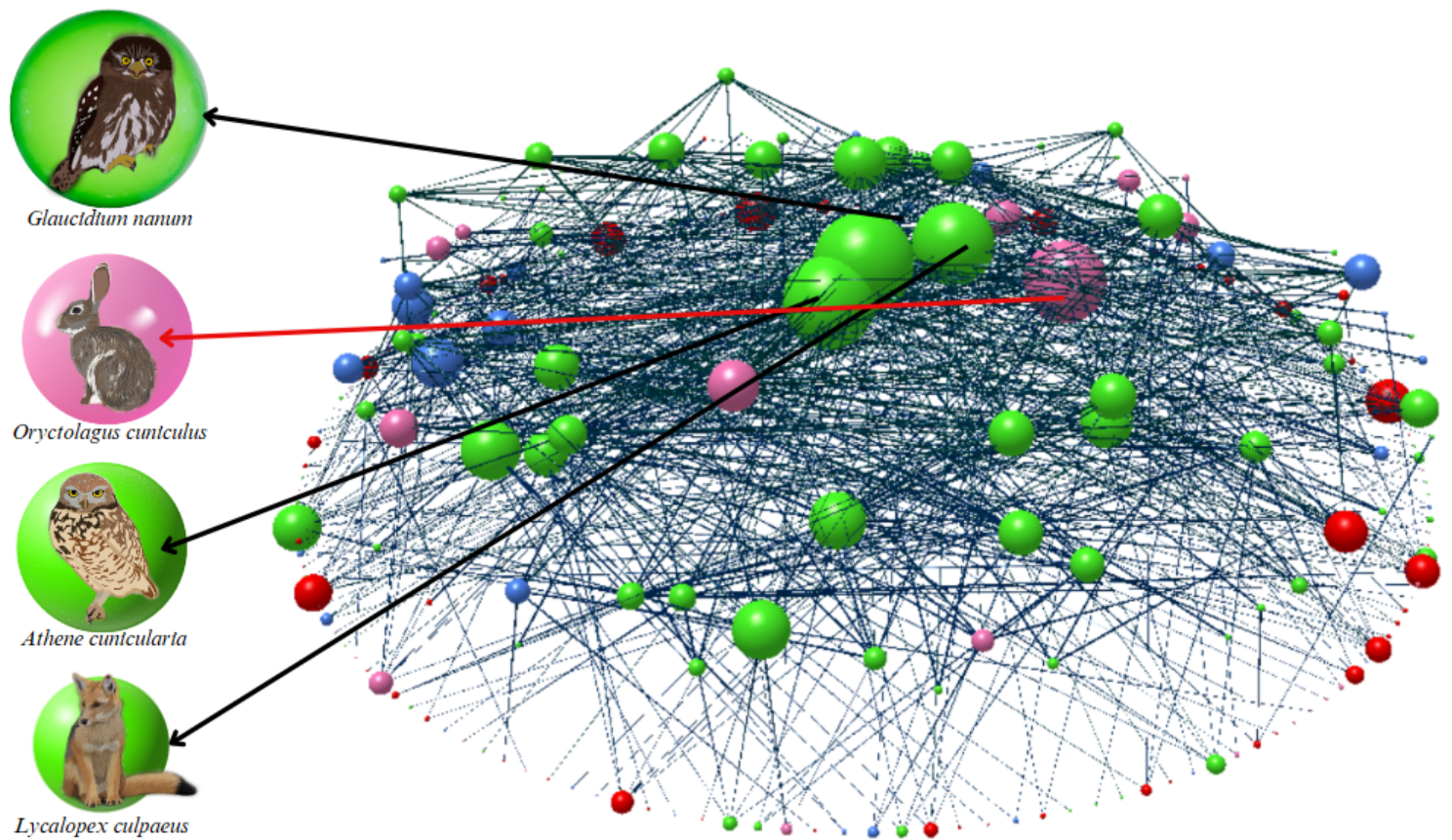
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## Figures



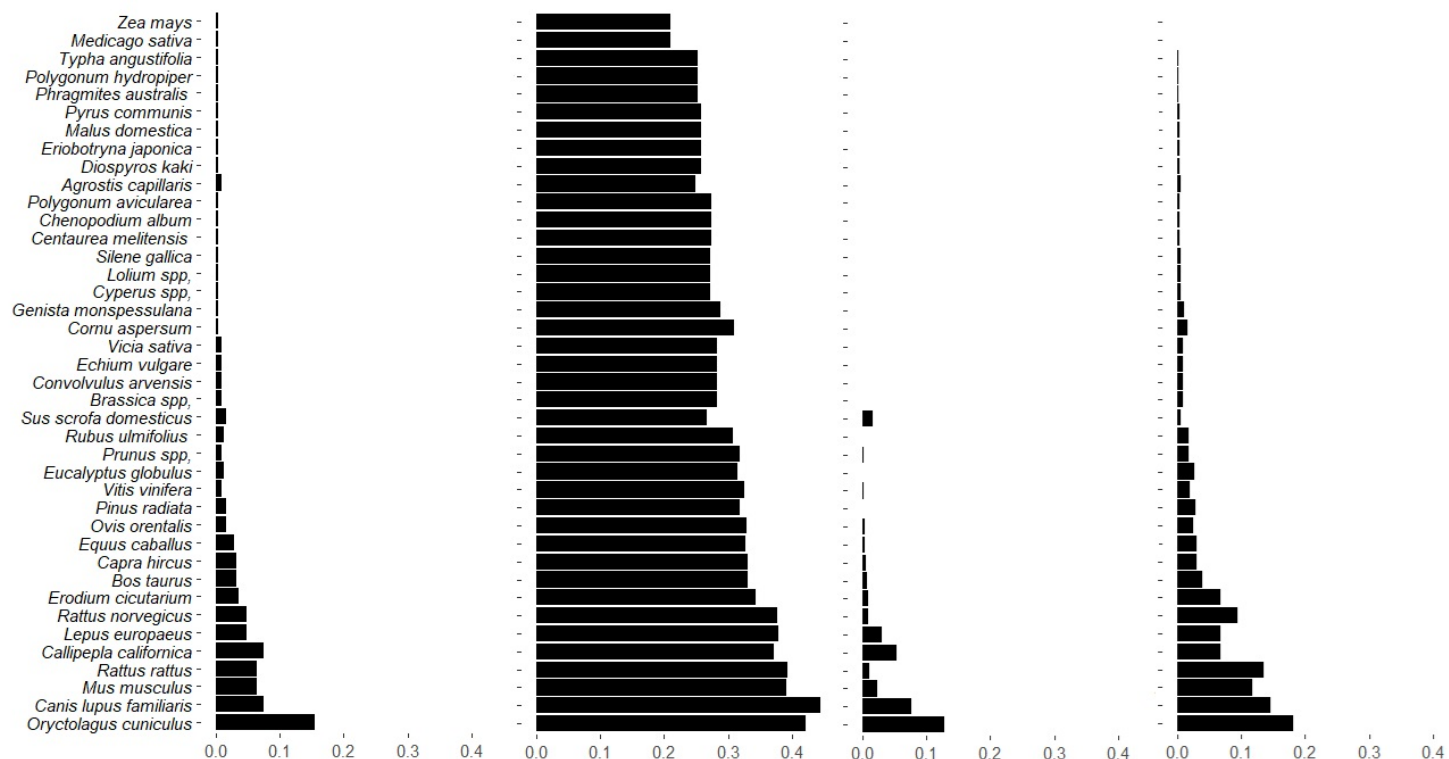
**Figure 1**

Map illustrating the study area corresponding to sclerophyllous vegetation within the Chilean Mediterranean-type region and its protected areas (parks, reserves, and national monuments). The green area represents the potential occurrence of this vegetation, according to Luebert and Plischoff (2017).



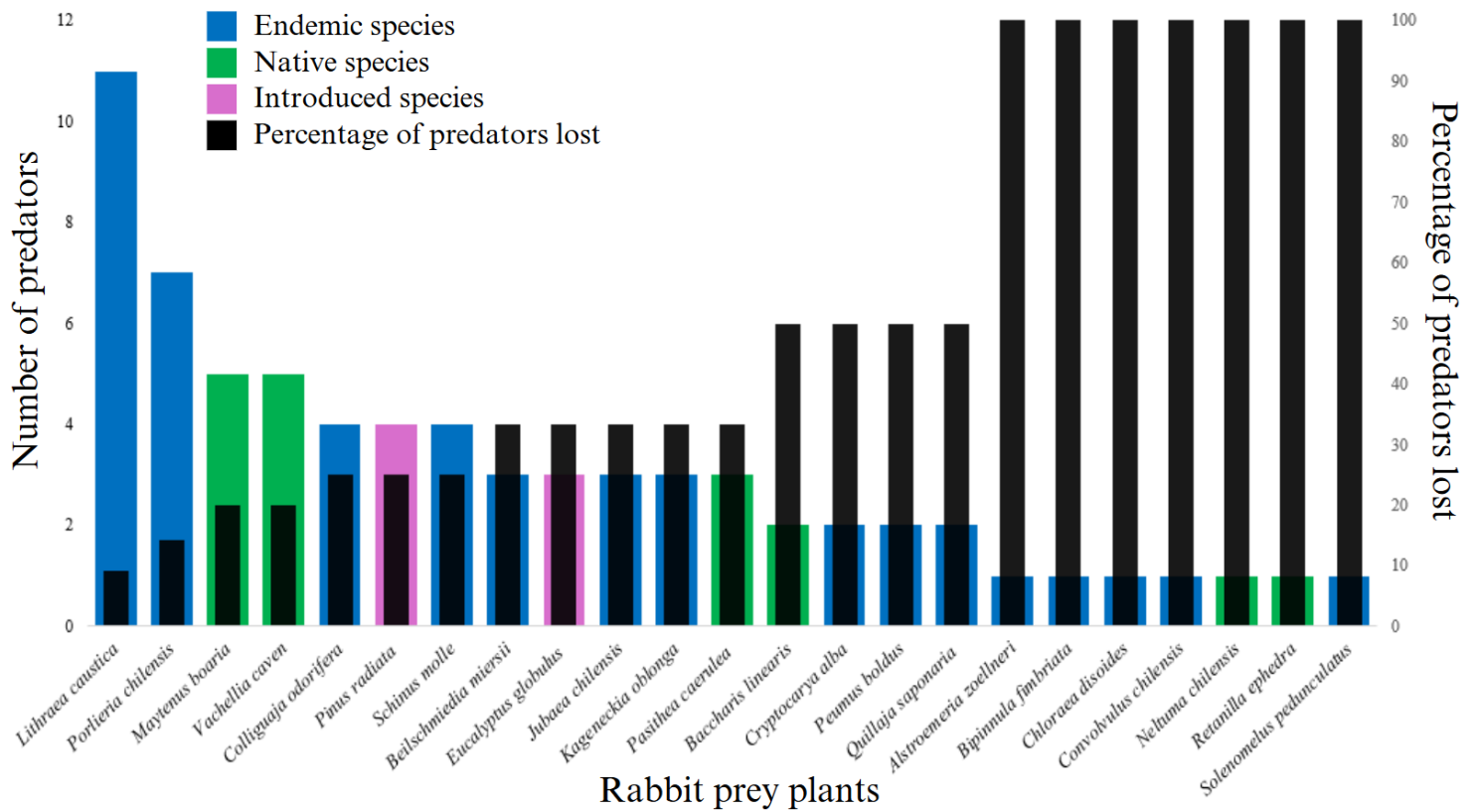
**Figure 2**

Network visualization of the Chilean Mediterranean ecosystem dominated by sclerophyllous vegetation. The nodes (spheres) represent species ( $n = 252$ ), and dark blue lines represent links of trophic interactions (798). The size of nodes represents their connectivity values. The colors indicate the origin of the nodes: pink for introduced species, sky blue for endemic species, green for native species, and red for very general nodes (e.g., Genus, Family) whose origin could not be identified. The four nodes with the greatest connectivity values stand out in decreasing order.



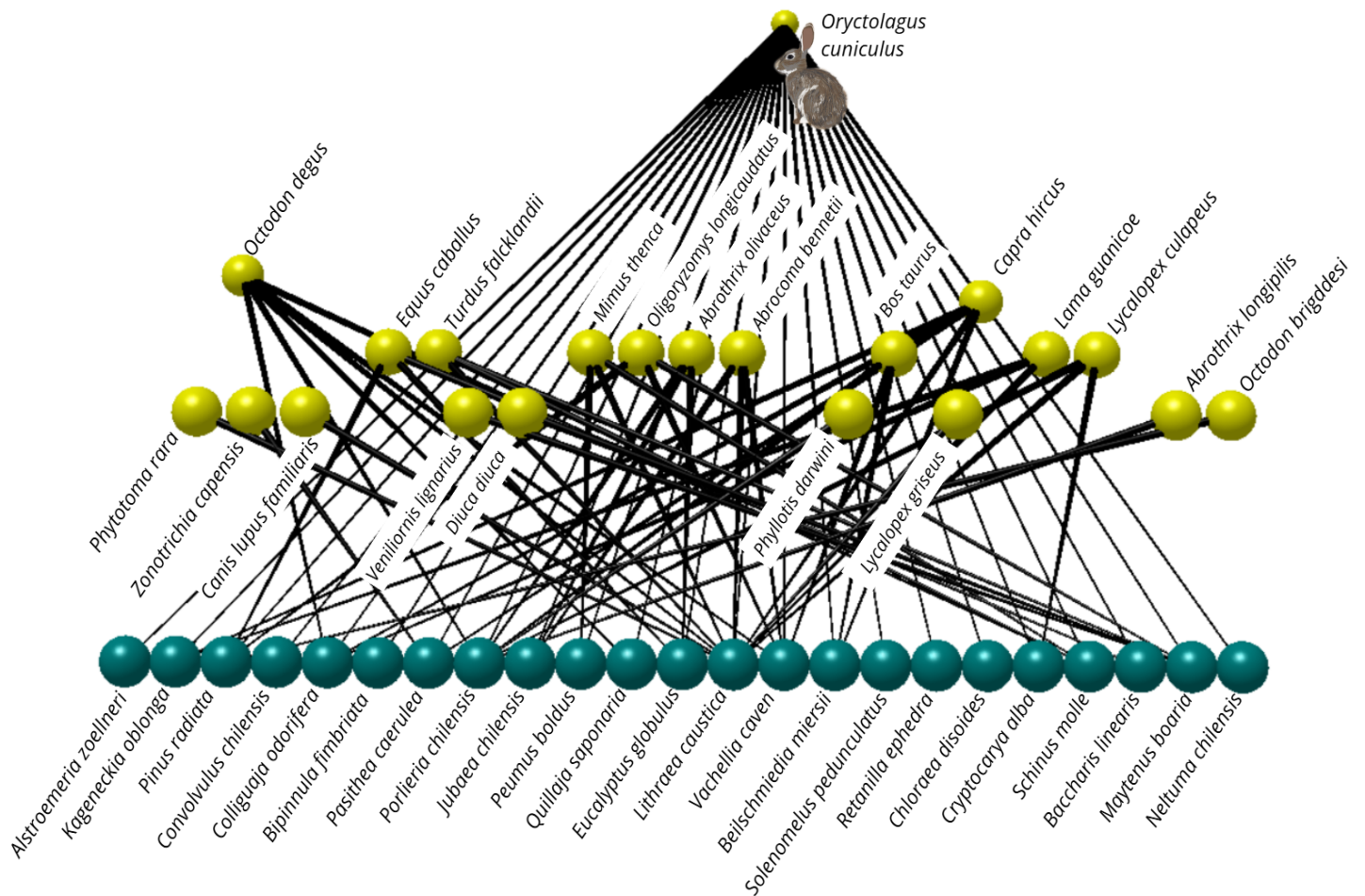
**Figure 3**

Relative importance of the introduced species in the network based on centrality measures. The ranges of (A) degree, (B) closeness, (C) betweenness, and (D) eigenvector are represented on the x-axis. The y-axis shows the introduced species. We ranked species based on four centrality measures, all of which indicated that *O. cuniculus* had consistently greater centrality (Table 1; for detailed values see Table S2).



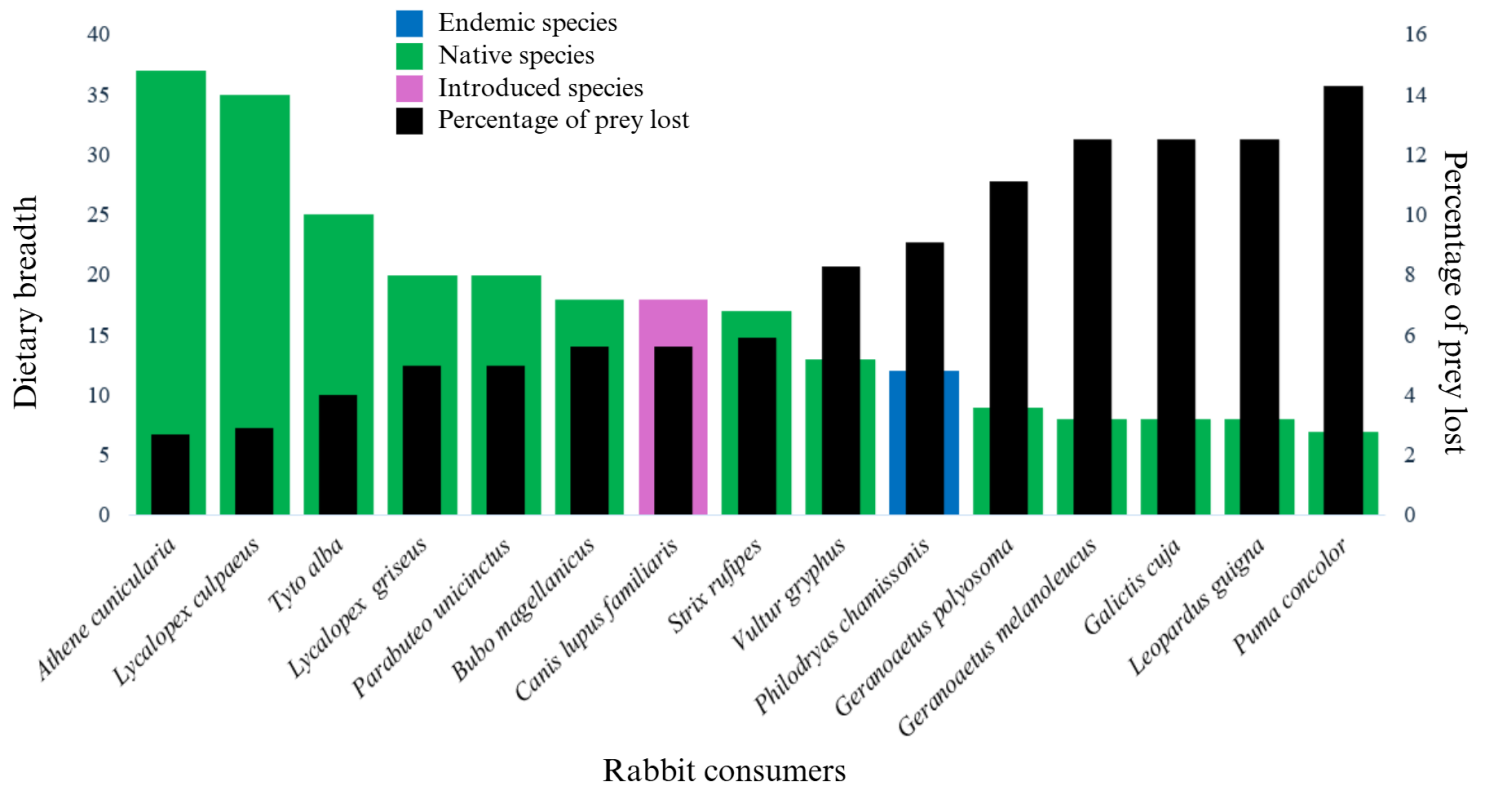
**Figure 4**

Relative importance of the European rabbit for the plants it consumes and for other consumers within the Chilean Mediterranean network. Bar colors indicate the origin of each plant species. Black bars represent the percentage of consumers lost for each plant following the removal of the rabbit node.



**Figure 5**

Diagram of competitive interactions between European rabbits and other species by plant consumption within the Chilean Mediterranean network. The green nodes represent plants, and the yellow nodes represent their consumers.



**Figure 6**

Relative importance of the European rabbit for predators within the Chilean Mediterranean network. Bars represent the dietary breadth of predator species, with colors indicating their origin. Black bars represent the percentage of prey items lost from the diet of each predator species following the removal of the rabbit node.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

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