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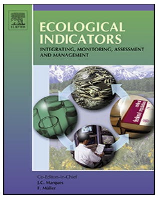

Review

Testing the keystone plant resource role of a flagship subtropical tree species (*Araucaria angustifolia*) in the Brazilian Atlantic Forest

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ABSTRACT

Ecological attributes enable the identification of Keystone Plant Resources (KPRs), including their community-wide contribution to vertebrate consumers, which are often highly threatened in terrestrial ecosystems. KPRs have been defined by intersecting four ecological attributes that influence local communities of vertebrate frugivores: temporal redundancy (TR); degree of consumer specificity (CS); reliability (RR); and resource abundance (RA). The conifer *Araucaria angustifolia* (Bert.) O. Kuntze (Araucaria) is the main arborescent component of Araucaria Forests, within the subtropical Atlantic Forest of South America. The large Araucaria seeds (*pinhão*) are heavily consumed by local faunas, and consequently could be automatically defined as a KPR. However, no previous studies have conceptually assessed the *pinhão* as a KPR based on their ecological attributes and trophic interactions with vertebrates. Using empirical data and a comprehensive literature review, we examine the degree to which Araucaria trees can be formally defined as a KPR within the subtropical Atlantic Forest. Our results show for the first time that Araucaria is a KPR according to both its ecological attributes and community-wide importance. Araucaria cones exhibited low temporal redundancy, low consumer specificity, high resource reliability and high resource abundance, structuring the associated vertebrate consumers spatio-temporally. Our insights contribute to understanding the implications of historical Araucaria population declines through logging and deforestation, as well as ongoing vertebrate defaunation. Both of these processes can lead to changes in baseline ecological process (e.g. seed dispersal *versus* seed predation), forest regeneration, community reassembly, and potential evolutionary consequences such as seed downsizing.

1. Introduction

The milestone "keystone" term is often vaguely applied in ecology and conservation. We thus provide a brief glossary of concepts that refer to the "keystone" terminology. The keystone species (KS) term was originally coined by Paine (1969) and first applied to a keystone predator in rocky intertidal zones (Paine, 1969). Keystone species form populations whose underlying presence is critical in maintaining local community organization and diversity, and are exceptionally high-importance species compared to other community components (Paine, 1969). Keystone plant resources (KPRs) encompass one of the main classes of keystone species and are defined as plant species that seasonally produce critical trophic resources (Peres, 2000). Cultural keystone species (CKS) are defined as a species — or resources — with strong sociocultural identity, generally with implications to the subsistence for local peoples (Garibaldi and Turner, 2004), such as non-timber forest products (NTFPs) (Peres et al., 2003; Guariguata et al., 2017). The concept of "culturally important species" (CIS) has recently been amplified to include many other subsistence resources on which landscape-scale conservation related to a strong cultural heritage can be focused (de Freitas et al., 2019).

To some extent, these criteria also serve to describe the notion of foundation species, which are defined as species (or groups of functionally similar taxa) that numerically dominate an assemblage in overall abundance (usually biomass). They also determine the diversity of associated taxa through non-trophic interactions, modulating nutrients and energy fluxes at multiple control points in the ecosystem (Ellison, 2019). Ecologically, a keystone species also exerts a

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disproportionately large effect on its environment compared to its abundance or population biomass (Paine, 1969), thereby maintaining community stability through trophic interactions (Paine, 1969; Bond, 1993). Keystone species (KS) have therefore been identified via a combination of observational and experimental approaches, including natural history, historical reconstructions, comparative studies and both field and mesocosm experiments (Power et al., 1996). Species that play keystone roles in communities and ecosystems interact intensively with both native organisms and newcomer species (Power et al., 1996). The strength of ecological interactions involving a KS is disproportionally greater in terms of community foodwebs (Kricher, 2011).

From an ecosystem functioning perspective, even some weak interactors may also play important roles by magnifying the spatiotemporal variation in community structure (Paine, 1992; Berlow, 1999; Berlow et al., 1999). This issue raises reciprocal adaptation and coevolutionary dynamics, shaping the adaptive peaks of pairs of interacting species, from weak to strong interactors (Guimarães et al., 2017). The KS concept can therefore be extended to plant species associated with critical resource availability (i.e. flowers, floral nectar, fruits, and seeds) for consumers during periods of severe food scarcity (Whitmore, 1990; Peres, 2000; Kricher, 2011). In most terrestrial ecosystems worldwide, keystone plants provide pivotal trophic resources during periods of seasonal scarcity, which has been used as a key ecological attribute to identify keystone plant resources (KPRs) and assess their relative contribution to vertebrate assemblages (Peres, 2000).

In defining KPRs, candidate species have been assessed by Peres (2000) who defines four intersecting ecological attributes governing their community or assemblage-wide importance to primary consumers: (1) resource temporal redundancy, (2) degree of consumer specificity, (3) resource reliability, and (4) resource abundance (Peres, 2000). Resource temporal redundancy (TR) is the degree to which the availability of a potential KPR synchronizes with the combined pool of alternative food resources used by the overall consumer assemblage (i.e. providing critical resources during periods of scarcity). The degree of consumer specificity (CS) is an inverse function of the percentage of consumer species in a local vertebrate assemblage (e.g. all sympatric bird and mammal species including > 50% of fruit in their diet) known to exploit a putative KPR. Resource reliability (RR) is the probability of a KPR predictably becoming available every year to sustain vertebrate consumers at a given site, and in the case of low-redundancy resources, through annual periods of scarcity. Resource abundance (RA) is the crude abundance or biomass of a potential KPR at a given site, which could be based on the patch density and size (e.g. crown volume) of a given resource.

From a consumer perspective, keystone plants should produce highly reliable (RR) and low-redundancy seasonal or year-round resources (RA) that are harvested by a large proportion (CS) of coexisting primary consumers (Peres, 2000). These ecological traits (e.g. RR, RA, and CS) are also related to high levels of plant diversity in tropical forests. For example, comparing sister clades across several independent lineages show that species traits (e.g. dispersal type and growth form) increases the diversity of fleshy-fruited understory plants in tropical forests (Smith, 2001). The Neotropical realm represents the world's greatest expression in the number and morphological design of fleshy-fruiting plant species (Howe, 1993; Smith, 2001) but these species generally exhibit high spatial turnover (Mendoza et al., 2016). The proportion of species bearing fleshy-fruits dispersed by vertebrates can reach up to 90% in many neotropical plant communities (Howe, 1984; Almeida-Neto et al., 2008; Galetti et al., 2011). Neotropical mammal and bird assemblages also show high rates of species turnover (Melo et al., 2009; Bogoni et al., 2017), high levels of taxonomic and functional diversity at local to regional scales (Ojeda, 2013; González-Maya et al., 2017), and provide several key regulatory roles in ecosystem functioning (Lacher et al., 2019).

In tropical forests, plant resources comprise most of the net ecosystem productivity harvested by the widest spectrum of consumers, thereby underpinning the trophic structure of any given site according to consumer traits (Terborgh, 1986; Peres, 2000). The seeds of most neotropical plant species are ingested and dispersed by birds and mammals (Howe and Smallwood, 1982; Pizo et al., 1995). Fruit and seed removal generates important feedbacks to plant fitness that have implications for long-term forest composition and dynamics (Terborgh, 1992; Barraclough, 2015). However, wholesale human degradation of tropical ecosystems worldwide severely hampers ecological feedback processes (Ceballos et al., 2017). Population co-declines or co-extinctions can lead to a simplification of mutualistic interaction networks that may result in community reassembly (Guimarães et al., 2017), and habitat patch size affects the structure of fruit-frugivore networks (Bomfim et al., 2018).

The ecological consequences of depleting or otherwise extirpating different types of KPRs from tropical forests remain poorly understood since the earliest applications of this concept (Howe, 1977; Gilbert, 1980; Peres, 2000). Yet selective removal of KPRs — for example, via selective logging and fire-induced tree mortality — can result in dramatic reductions in forest carrying capacity for generalist frugivores and seed predators (Howe and Westley, 1988, Whitmore, 1990), which comprise the bulk of the vertebrate biomass in Paleotropical (Gautier-Hion et al., 1985) and Neotropical forests (Terborgh, 1983; Peres, 1999).

Within the subtropical province of the Atlantic Forest, *Araucaria angustifolia* (Bert.) O. Kuntze (Araucaria) trees comprise the main component of mixed ombrophilous forests (FOM), also known as Araucaria forests (Rambo, 1951; Mattos, 2011). Humans managed araucaria forests since Pre-Columbian times, with human activities driving forest expansion since the late Pleistocene. For instance, some ethnic groups (Kaingang and Xokleng) cultivated *Pinhão* for food and religious rituals (Reis et al., 2014). This may be related to high levels of environmental resilience and seed productivity of Araucaria trees (Reis et al., 2014; Robinson et al., 2018). However, Araucaria forests succumbed to extensive timber overexploitation in the 20th century, which was aggravated by conversion to agriculture and expansion of urban areas (Ribeiro et al., 2009; Mattos, 2011). This led to the extirpation of Araucaria trees in much of their former FOM range, so that relictual forest remnants now cover only ~15% of the original Araucaria domain (Ribeiro et al., 2009; Rezende et al., 2018).

Several studies have shown that the vertebrate fauna associated with Araucaria forests is heavily dependent on Araucaria trees (e.g. Kindell, 1996; Solórzano-Filho, 1995; Lamberts, 2003; Iob and Vieira, 2008). This association has led to *pinhão* being widely considered as a keystone resource. However, a seasonal boom in pinhão production and its association with a fraction of the vertebrate fauna do not necessarily ensure that Araucaria can be defined as a de facto KPR. For example, it is paramount to examine the consumer specificity (i.e., CS: what fraction of all vertebrates consume pinhão), which are the alternatives resources for vertebrate frugivores/granivores and how much these resources overlap with the fruiting phenology of Araucaria (i.e. TR). To adequately assess the potential of Araucaria as a KPR within the subtropical Atlantic Forest of South America requires further examination of the ecology of *Araucaria angustifolia*. On the basis of empirical data and a comprehensive literature review, we seek to identify whether Araucaria trees operate as a KPR by quantitatively assessing their ecological attributes and contribution to vertebrate consumers. We hypothesize that Araucaria trees meet all four criteria that characterize a KPR (*sensu* Peres, 2000). These include low temporal redundancy compared to alternative fruit/seed resources, low consumer specificity with seeds consumed by a wide spectrum of vertebrate species, temporal resource reliability due to nearly continuous seed production and high per capita resource abundance. We further hypothesize that *pinhão* comprises a critical seasonal resource in subtropical forests that are otherwise low-productivity in terms of fleshy-fruits, thereby playing an important regulatory role in structuring vertebrate assemblages in space and time. Further, based on the (pre)historical interaction between Araucaria and humans, we discuss the importance of pinhão use and how the overexploitation of this resource can affect the mammal occupancy and forest regeneration, with a view of enhancing this ecological research agenda.

2. Methods

2.1. Brief review on the natural history of Araucaria angustifolia

Araucaria trees are the iconic symbol of South American Mixed Ombrophilous vegetation, the so-called "Araucaria Forest". *A. angustifolia* (Araucariaceae) is the only species of this genus in Brazil (Rambo, 1951; 1954). Araucaria is rare Andean element in the subtropical Atlantic Forest, together with two species of *Podocarpus* (Rambo, 1951; Reitz and Klein, 1966). The Araucaria distribution is limited to the quadrilateral formed by parallels 19°15' and 31°30'S and through the meridians 41°30' and 54°30'W (Reitz et al., 1988). Araucaria populations are mainly concentrated in Southern Brazil (states of Paraná, Santa Catarina, and Rio Grande do Sul) with relict patches in southeastern Brazil (São Paulo, Minas Gerais, and Espírito Santo) (Backes, 1999). Araucaria Forests were managed by pre-Columbian Amerindians, with some geographic refugia since the late Pleistocene attributed to human dispersal (Reis et al., 2014; Robinson et al., 2018). Since the European conquest of southern Brazil, this forest type and its emblematic tree species rapidly succumbed to selective logging, deforestation, and agricultural frontier expansion (Ribeiro et al., 2009; Mattos, 2011).

Araucaria is a wind-pollinated dioecious conifer, exhibiting a reproductive cycle spanning from two to four years (Shimoya, 1962; Mantovani et al., 2004). The female strobilus (*pinha* or cone) is comprised of viable seeds (hereafter, *pinhão*) with high nutritional value consisting mainly of carbohydrates (Rogge-Renner et al., 2013), non-viable seeds (*chochos*) and sterile straws (Burlingame, 1914; Mattos, 2011). Cones mature between April and June, each of which producing from 10 to 150 mature *pinhões* (Reitz et al., 1988). Although Araucaria phenological cycles are partly asynchronous, cone development begins from August to January and *pinhão* maturation occurs from February to December (Mattos, 2011). Peak seed production occurs from March until August (autumn-winter of the southern hemisphere) depending on botanical varieties (Adan et al., 2016; Tagliari and Peroni, 2018).

Annual phases of seeds maturation overlap with low precipitation and low temperatures in the coldest areas of southern Brazil. *Pinhão* production is typically highest during this period, ranging from 106.6 kg/ha^{-1} to 427.0 kg/ha^{-1} (Solórzano-Filho, 1995; Mantovani et al., 2004; Bogoni et al., 2020). Density of Araucaria females range from 9.4 to 49.6 indiv./ha^{-1} (Paludo et al., 2009; Bogoni et al., 2020). Mature seed biomass is therefore highly variable across spatial gradients because of (i) female tree density; (ii) intrinsic and extrinsic variation in cone productivity; and (iii) extraction pressure by local people (Mattos, 2011). As consequence, variable local productivity of Araucaria Forests influence different consumers, either boosting or suppressing populations of key interactors, such as granivores birds and small mammals (Supporting Information S1). These constraints lead to widespread assumptions about Araucaria as a keystone species (Pereira and Ganade, 2008) from both an ecological (KS and KPR) or sociocultural (CKS) perspective.

2.2. Floristic composition and phenology of alternative resources in Araucaria forests

Araucaria trees dominate the upper stratum of Araucaria Forests. The main plant families forming the middle and lower strata are Myrtaceae and Lauraceae (Rambo, 1951, 1954), a few species of which also dominate the flora in the middle and lower strata (Veloso et al., 1991). These taxa are typically characterized by small fruits (< 1 cm of diameter) (Gressler et al., 2006). *Acca sellowiana* [Berg] Burret (Feijoa) is an exception to the small-fruiting pattern of Myrtaceae trees. Feijoa is native to southern Brazil and northern Uruguay and produces large fruits (> 50 g) (Bogoni et al., 2018a).

Despite the high spatial turnover in floristic composition of Araucaria forests, the main species bearing fleshy-fruits are in the genera *Campomanesia*, *Eugenia*, *Inga*, *Ocotea*, *Nectandra*, *Syagrus* and *Butia* (Gressler et al., 2006; Liebsch and Mikich, 2009; Higuchi et al., 2012; Gasper et al., 2013; Possette et al., 2015), across the overstorey and the understorey forest strata. Species of these genera generally bear small to medium-sized fruits (< 15 g) that ripen from December to February, the southern hemisphere summer (Liebsch and Mikich, 2009; Gressler et al., 2006). The arborescent palm *Syagrus romanzoffiana* (Cham.) Glassman is an exception but rarely co-occurs with Araucaria. *Syagrus* palms exhibit a peak fruiting period ranging from March to September that partially overlaps that of Araucaria (Henderson et al., 1995; Genini et al., 2009).

2.3. Is Araucaria a keystone resource?

2.3.1. Criterion 1: Temporal redundancy (TR)

Using search engines (i.e. Scopus, Web of Science, Scielo and Google Scholar), we performed a systematic literature search combining the terms "*Araucaria Forest** (or Mixed Ombrophilous Forest*)" and "*plant(s)* (or *tree(s)*) *phenology**". We also used non-indexed references (e.g., books, MSc and PhD thesis), unpublished data, and personal observations on the reproductive phenology of *Araucaria*. In doing so, we obtained the year-round fruit production cycle of each main plant species (i.e. over 100 species representing 64 genera) within Araucaria Forests and calculated TR based on a ratio describing the temporal overlap of *Pinhão* availability and all other alternative plant resources (i.e., mainly fruits and seeds from other plant species) throughout the Araucaria *pinhão* period. This ratio was obtained by the following equation:

$$TR = \frac{\sum (Mpi^{th-esima}_{species})}{\sum nt_{species}\text{x}12}/10$$

where: $Mp\ i^{th\text{-}esima}{}_{species}$: monthly presence of each species fruits/seeds along the year (i.e., 351); $nt_{species}$: total number of species (i.e., 104) multiplied by 12 months; the value is corrected based on a scale 1–10 (i.e., max. TR value according to Peres (2000)).

2.3.2. Criterion 2: Consumer specificity (CS)

To define CS, we performed a systematic literature search using the terms "*Araucaria**" and "*seed predation**", or "*seed dispersal**" or "*seed consume**" or "*pinhão predation**" or "*pinhão dispersal**" to identify the potential vertebrate assemblages of *pinhão* consumers and non-consumers. We completed the dataset using unindexed references and unpublished data derived from both interview and camera-trapping data obtained in Southern Brazilian highlands from 2016 to 2017. Due to scarce data availability, we also include data from the "gray literature", including PhD and MSc dissertations. Based on Bello et al. (2017) and Paglia et al. (2012) we classified the diet of all mammal and bird species as either frugivores or non-frugivores (i.e. > 50% and < 50% of fruits consumed, respectively (following Peres, 2000). We then calculated the proportional number of frugivore/granivore species averaged across the nine vertebrate assemblages that are dedicated consumers of *pinhão* (i.e. S_f). Based on this estimate, we then derived a CS value according to the linear relationship between S_f and CS (see Peres, 2000). The CS metric is conceptually similar to that of consumer-resource connectance in foodweb theory (Pimm, 1980), but it ignores the strength of interactions because more detailed data are largely unavailable (Peres, 2000). To further explore the ecological association between vertebrate consumers and *pinhão*, we used a bipartite network to represent the spatial pattern of these interactions across the entire Araucaria Forest domain (Boccaletti et al., 2006).

2.3.3. Criterion 3: Resource reliability (RR)

To define the resource reliability (RR) criterion, we revisited some classic and specialized literature on Araucaria ecology (i.e., Rambo, 1951; 1954;; Reitz and Klein, 1966; Reitz et al., 1988; Mattos, 2011; Adan et al., 2016; Tagliari and Peroni, 2018), unpublished data, and personal observations over many years monitoring the species. However, the RR definition was partially arbitrary given that several Araucaria varieties may co-occur along their distribution gradient, presumably staggering the availability of mature seeds (Coutinho and Dillenburg, 2010). All varieties appear to be highly consistent in their annual *pinhão* productivity.

2.3.4. Criterion 4: Resource abundance (RA)

To define RA, we used published data using search engines and the terms "*Araucaria**" and "*demography**" and unpublished data on female Araucaria tree density (per hectare) obtained from 2015 to 2016 at 7 sites throughout the subtropical Atlantic Forest plateau. Based on this dataset, we obtained the average density of females per km^2. The RA value ranges from 1 (densities equal to or less than 0.01 patch ha^{-1}) to 10 (densities > 2.5 patches ha^{-1}), because it is simply intended to provide a coarse measure of the total amount of a given resource that becomes seasonally available to vertebrates at a given forest (Peres, 2000).

3. Results

To define TR, we obtained data from 16 books, refereed papers, theses, and personal observations that described the phenology and seed/fruit maturation of Araucaria and, following Liebsch and Mikich (2009), another 104 animal-dispersed plant species within the Araucaria Forest domain (Fig. 1; Supporting Information S2). According to literature, the Araucaria trees produce *pinhão* all year-round, depending on the variety (Rambo, 1951, 1954; Adan et al., 2016). At least three of the main Araucaria varieties co-occurs throughout their original distribution (Coutinho and Dillenburg, 2010) under varying abundances (Adan et al., 2016; Tagliari and Peroni, 2018), amounting to the overall *pinhão* productivity over the annual cycle (Fig. 1). However, pinhão availability decreases after peak production, indicating low availability after August and September when only the rarest variety (i.e. *macaco*) is still shedding seeds (Adan et al., 2016, Tagliari and Peroni, 2018). We calculated a temporal redundancy (TR) value of 2.81 based on the overlap between the availability of *pinhão* (considering all varieties) and ripe fruits from all other alternative co-occurring resources throughout the annual cycle.

To calculate CS, we obtained published and unpublished data on vertebrate consumption of *pinhão* in nine areas along the natural distribution of Araucaria Forests (Fig. 2B). Among all birds and mammals, 29 species consume *pinhão* (Fig. 2B), including two exotic species (*Lepus europaeus* and *Sus scrofa*). Based on the diets of all vertebrate species and their patterns of *pinhão* consumption, an average of $S_f = 69.8\%$ (± 17.5 *sd*) of all mammal and birds species across all nine sites were heavily dependent on this resource on at least a seasonal basis. We therefore obtained a very low overall value of CS = 1.0, indicating little or no consumer specificity (see Criterion 2; Table 1). For instance, 1,825 of 2,621 (69.6%) independent camera-trapping records at seven typical Araucaria Forest areas are comprised of species that rely heavily on *pinhão* during throughout the year (Fig. 3; Bogoni et al., 2020).

Despite the yearly and geographic variation in *pinhão* production (Mattos, 2011; Mantovani et al., 2004; Solórzano-Filho, 1995), there are no records in the literature showing a year-round failure in *pinhão* production (Rambo, 1951; 1954;; Reitz and Klein, 1966; Reitz et al., 1988; Mattos, 2011). Consequently, we defined RR as the maximum value (RR = 10; Table 1). Data from eight sites including 10.22 ha of forest inventories showed an average Araucaria density of 2,985 females/km^2 ($\pm$ 1,467 *SD*; ranging from 940 to 4480 females/km^2) (Paludo et al., 2009; Bogoni et al., 2020). Despite this high spatial variation, Araucaria can be considered a hyperabundant tree in forest remnants (Peres, 2000; Bogoni et al., 2020) again supporting the maximum RA value.

4. Discussion

Foodweb connectedness has a strong tradition in ecology (Paine, 1980), and ecological webs serve as a backbone for many modern theoretical developments in community ecology (Zhao et al., 2016). As such, we revisited a quantitative definition of KPRs (Peres, 2000) to assess if Araucaria accounts for all attributes of the KPR definition, retaining much connectedness in its ecological network. Based on available studies and empirical data, our results show that *pinhão* comprises a typical KPR in subtropical Atlantic Forests because they clearly comply with all four ecological criteria in the KPR definition. Araucaria trees are hyper-abundant, provide a high-energy resource during times of food shortage when local climate is least favorable (coldest months), present low specificity in their trophic interactions, produce seeds over a very extended fruiting period, and which account for the chief fruit resource in Araucaria Forests considering all angiosperms and gymnosperms. Furthermore, our results are consistent with other empirical studies indicating that Araucaria trees operate as an underpinning species, because they generate the appropriate biophysical condition for the establishment of heterospecifics via facilitation (Duarte et al., 2006; Barbizan-Sühs et al., 2018). Araucaria trees therefore modulate critical ecological and ecosystem processes (e.g., subcanopy structure, vertebrate assembly, and carbon sequestration), buffering resource scarcity in an otherwise highly seasonal environment due to their abundant and widely distributed seed crops. They also yield an important resource for human seed harvesting and as such have a long history as a culturally important species.

According to Peres (2000), from a vertebrate perspective, keystone plant resources are those producing highly reliable (RR > 5), low-redundancy (TR < 5) resources that are consumed by a large spectrum of the vertebrate assemblage with which they coexist (CS < 5). In this study, all of these metrics were well within these proposed ranges (TR = 2.81; RR = 10; CS = 1.00), thereby clearly qualifying Araucaria trees as a prime Keystone Plant Resource for the bird and mammal fauna. Resource abundance can also be used to further narrow the definition of a KPR, but in any case, this attribute is seen as secondary to the redundancy, reliability, and specificity of any given resource (Diaz-Martin et al., 2014), because temporally stable resource availability is far more important than an ephemeral boom in fruit/seed production (Peres, 2000). In most cases, values assigned to a point scale can only be approximately estimated due to scarce information on the composition of the overall frugivore assemblage, consumer-resource matrix, and patterns of fruiting phenology for the entire plant community (Peres, 2000). In any case, however, our results show a high RA value, which corroborates the final criterion of the KPR definition. Supplementary information from future studies conducted at the same sites could be used to boost the accuracy of these scoring procedures, particularly in highly diverse neotropical forests (Peres, 2000).

Hence, different plant species have highly divergent importance values in maintaining ecosystem functions (e.g. biomass stock and energy flows) in communities (Paine, 1980; Jordán, 2009). Generally, there is a density-dependent effect in quantitatively defining the degree to which a resource is a "strong interactor per unit biomass density" in exerting a critical role in foodweb structure (Power et al., 1996). Quantitative frameworks seek to identify the unusual importance or influence of a KS from a conservation ecology perspective (Jordán, 2009). Within biological communities, KPSs occupy a central role in forging many links across the fabric of interaction networks (Jordán, 2009). Under this perspective, some underlying patterns and processes on the role of Araucaria trees within Araucaria Forests has been poorly understood. For instance, quantitatively identifying the strongest interactors based on known biomass density of vertebrates in remaining

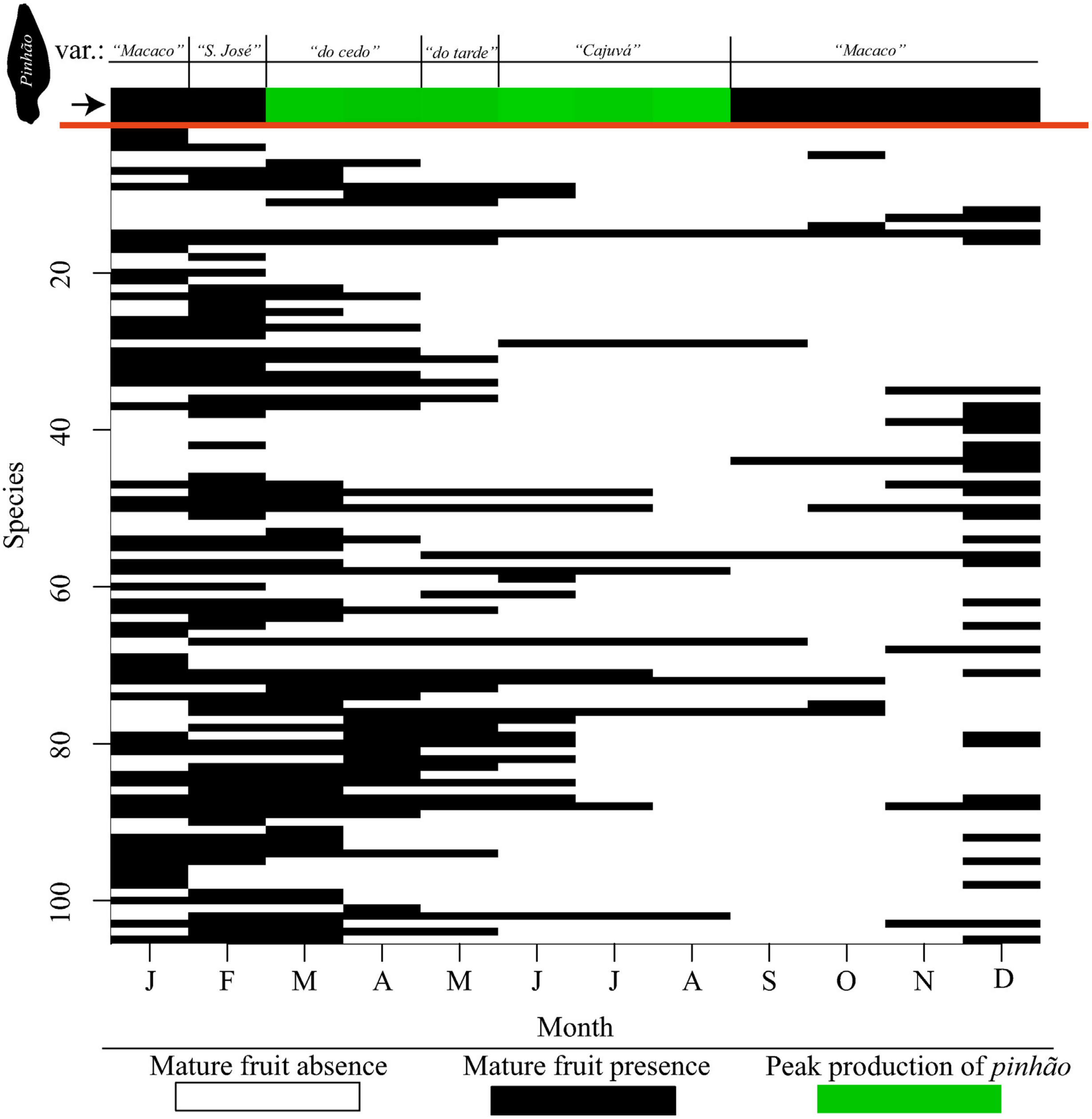

Fig. 1. Reproductive phenology of fruit and seed production (including the *pinhão*) of the main tree species bearing fleshy fruits in Araucaria Forests according to data from the literature and our own personal observations. Araucaria phenology is based on Rambo (1951 (1954); Reitz and Klein (1966); Reitz et al. (1988); Mantovani et al. (2004); Coutinho and Dillenburg (2010); Mattos (2011); Adan et al. (2016); Tagliari and Peroni (2018); J.A. Bogoni, pers. obs. Known Araucaria varieties are: (i) "*Macaco*": *A. angustifolia* var. *indehicens*; (ii) "*S. José*": *A. angustifolia* var. *sancti joseph*; (iii) "*do cedo*" and "*do tarde*": *A. angustifolia* var. *angustifolia*; and (iv) "*Cajuvá*": *A. angustifolia* var. *caiova*. Despite constant changes, other eight varieties are reported in literature, without description of *pinhão* maturation (see Adan et al. (2016)). Phenology of other animal-dispersed species is based on Liebsch and Mikich (2009) (see species checklist in Supporting Information S2).

Araucaria Forest patches is hindered by virtually nonexistent information, particularly based on field studies carried out at meaningful spatial scales.

However, some studies could shed light on the relative strength of Araucaria-animal interactions. Qualitative evidence amassed from these studies show that small- to medium-sized rodents (e.g. Cricetidae, *Coendou* sp. and agoutis [*Dasyprocta* sp.]), Azure-jay (*Cyanocorax caeruleus*), Plush-crested jay (*C. chrysops*), and some parrots (Psittacidae) are the principal interactors (Iob and Vieira, 2008). However, these interactions have not been adequately assessed under a quantitative framework at several sites containing different vertebrate assemblages. Addressing this gap in empirical evidence could help identify the strongest Araucaria interactors, both as seed predators and seed dispersal agents. From both a consumer and resource viewpoints, identifying key consumers is essential to understand the geographic variation in interaction strength across gradients of disturbance, productivity, biophysical features, and abundance of other resource and consumer species (Power et al., 1996). It is possible to better understand how local context affects the strength of species interactions and predict thresholds of community importance of different resource species, particularly in terms of their community-wide importance to vertebrate frugivores (Peres, 2000).

Based on our systematic review, we identified some candidate species that can be considered as strong interactors with Araucaria, such as cricetid rodents, brocket deer, capybaras, coatis and agoutis. Yet, *pinhão* is widely consumed across the vertebrate assemblage (low

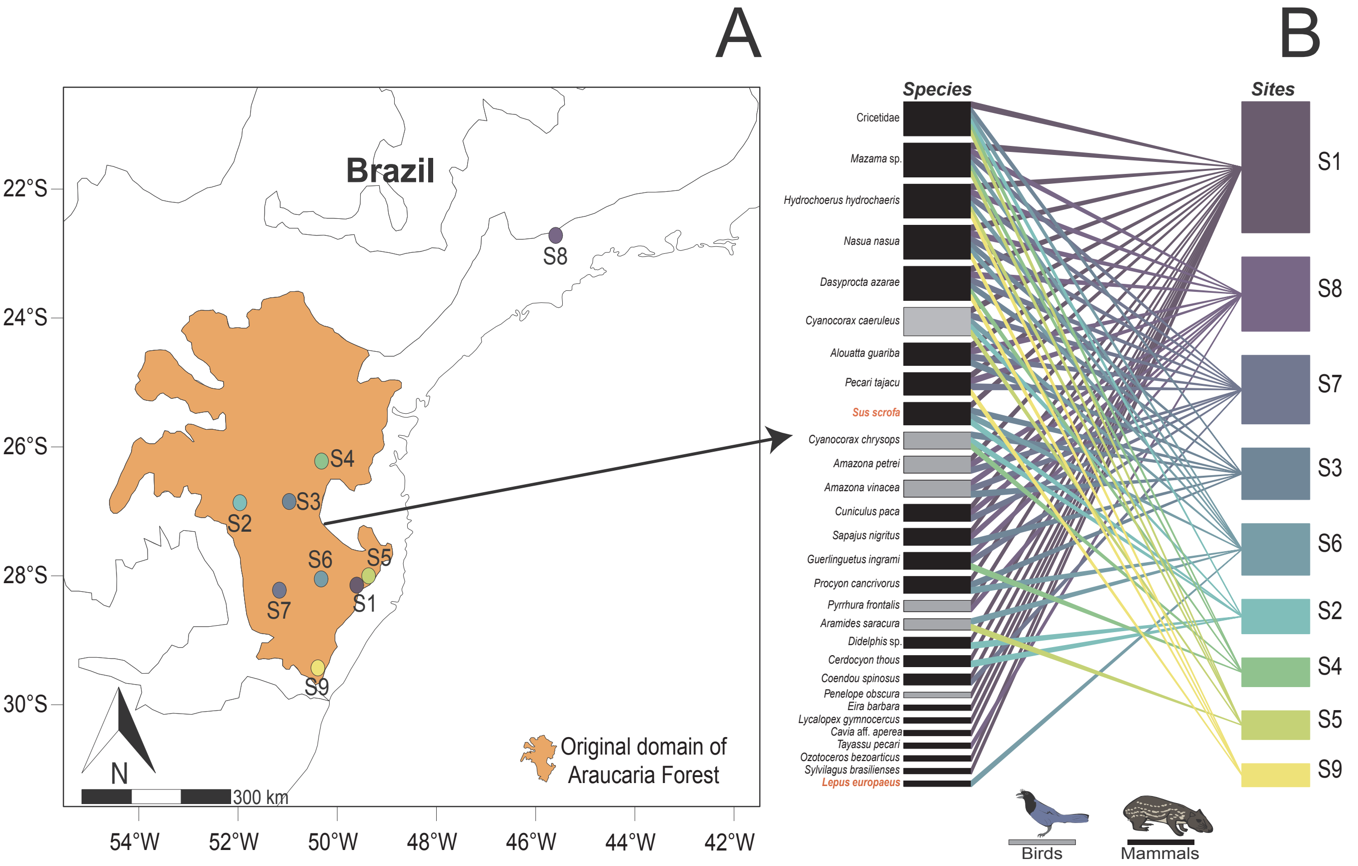

Fig. 2. Araucaria Forest domain in subtropical southern and southeastern Brazil and the geographic distribution of study sites addressing plant-animal interactions[1] between *Aracauria* trees and vertebrate consumers (A), which were used to construct the interaction network topology (B). Data sources are available in Table 1. [1] Sourced from: Solórzano-Filho (1995); Kindell (1996); Lamberts (2003); Batista (2015); Schüssler (2014); and Bogoni et al. 2020.

CS value) indicating that it is at least a fallback if not a staple resource for most coexisting homeotherms. Our data shows that more than two thirds of all species typically recorded in Araucaria Forest patches rely heavily on *pinhão* for at least part of the annual calendar. This pattern of generality shows that this resource is shared across several species, and when *pinhão* is unavailable, other alternative food resources (e.g. Feijoa) become seasonally important (Bogoni et al., 2018a). *Pinhão* is also consumed opportunistically by browsers and grazers, such as brocket-deer and capybara, and carnivores with exhibiting generalist diet (e.g. crab-eating fox and crab-eating raccoon). Our results for the CS criterion showed that Araucaria typically maintains a large and well-connected interaction network, potentially comprising over 29 vertebrate species. The classic 'keystone species' concept coined by Paine (1969) implies that a KS has a disproportionately large effect on its community compared to its population abundance or biomass. However, we acknowledge that Araucaria trees are partly at odds with this assumption. Araucaria exerts a large effect on its environment via its extensive network but is the dominant tree species in the few remnant forest patches of southern Brazilian highlands.

It is expected that ecosystem processes are controlled by the high Araucaria dominance and biomass in supplying resources to vertebrate consumers and co-dependent species (Bogoni et al., 2020). Empirical evidence reveals that this dominance does not exclude subordinate species which are also strongly involved in determining ecosystem functions (Grime, 1998). For instance, there are at least five plant species (4.8%; *Rubus sellowii*, *Smilax campestris*, *Aureliana tomentosa*, *Solanum acerosum* and *Duranta vestita*) across the Araucaria forest domain that can supply resources to homeotherm vertebrates during peak production of *pinhão,* and many Myrtaceae and Lauraceae trees sustain consumer demands during months of low *pinhão* availability (Liebsch and Mikich, 2009). Moreover, due to the spatial-scale-dependence of co-occurring varieties and divergent abundances among them, the RR and RA criteria can vary across the natural distribution of Araucaria, thereby meriting long-term studies to understand the structural role of Araucaria across their gradient. For example, two years of monitoring revealed high variation in seed production (68.7%) across seven typical

Table 1
Ecological attributes and community-wide importance for vertebrate consumers of Araucaria seeds (*pinhão*) and their conceptual definition as a Keystone Plant Resource (KPR) *sensu* Peres (2000). Where: TR: temporal redundancy; CS: consumer specificity; RR: resource reliability; RA: resource abundance; L: Low; and VH: Very High.

Attribute	Estimated score	Level	Sources
TR	2.81	L	Rambo (1951); (1954;); Reitz and Klein (1966); Reitz et al. (1988); Mantovani et al. (2004); Liebsch and Mikich (2009); Adan et al. (2016); Tagliari and Peroni (2018); J.A. Bogoni personal observations.
CS	1.00	L	Solórzano-Filho (1995); Kindell (1996); Lamberts (2003); Batista (2015); Schüssler (2014); Bogoni et al. (2020).
RR	10.0	VH	Rambo (1951); (1954;); Reitz and Klein (1966); Reitz et al. (1988); Mattos (2011), Adan et al. (2016); Tagliari and Peroni (2018).
RA	10.0	VH	Paludo et al. (2009); Bogoni et al. (2020).

Fig. 3. (A) Azure jay (*Cyanocorax caeruleus*), (B) gray brocket deer (*Mazama gouazoubira*); (C) Cricetidae rodents; and (D) Coati (*Nasua nasua*) recorded using camera-traps while feeding on *pinhão* within Araucaria Forest patches located at 1,549 m.a.s.L. within the Santa Barbara plateau of São Joaquim National Park, Santa Catarina, Brazil (28°09′S, 49°30′W).

areas of Araucaria forest (Bogoni et al., 2020).

Understanding the structuring roles of foundation species based on the commonness and magnitude of non-trophic facilitative and mutualistic interactions also presents a challenge in ecology (Ellison, 2019). Foundation species ameliorate abiotic stressors and play central roles in species coexistence, whereas their loss from a non-trophic plant-plant interaction networks may lead to cascading co-extinctions of associated species (Ellison, 2019). This general phenomenon is also observed in Araucaria forests. Beyond their trophic importance to vertebrates, Araucaria trees contribute to increasing community-wide sapling species richness and abundance, and in assembling plant community composition underneath their broad crowns, thereby providing a non-trophic contribution to landscape diversity in upper-montane regions (Duarte et al., 2006; Barbizan-Sühs et al., 2018).

In addition to existing evidence in the literature, our results also showed that Araucaria trees achieve a strong KPR role due to their intra-population asynchronous fruit production (high RR value), while consistently reaching peak seed production during times of scarcest resource availability over the cold, high-elevation subtropical winter. This reduces their temporal redundancy (low TR value) in relation to other less abundant tree species bearing fleshy fruits within the Araucaria domain. Araucaria populations are widely variable in their fruit productivity in space and time, which is strongly associated with climatic conditions and species varieties (Mattos, 2011). Yet, their seed crops is a highly reliable abundant resource (high RA value) within remaining Araucaria forest patches. The persistence of Araucaria trees in southern Brazil is primarily due to their ecological attributes, some of which used here in their KPR classification. Araucaria is widely recognized to exhibit high phenotypic plasticity, including several features that contribute to their success (Coutinho and Dillenburg, 2010). For example, Araucaria is (i) a pioneer species that can become established in adverse environmental conditions; and (ii) typically exhibits high longevity (Backes, 1999; Dillenburg et al., 2009; Barbizan-Sühs et al., 2018) with many centenarian individuals having survived the Araucaria-logging economic cycle of southern Brazilian from late 1910s to the early 1990s. Araucaria Forests comprise the most threatened vegetation formation of the Atlantic Forest biome (Ribeiro et al., 2009). The dramatic historical reduction of Araucaria Forests isolated their populations inducing many detrimental ecological and genetic consequences for this species (Ribeiro et al., 2009; Lacerda, 2016) and its interactors (Iob and Vieira, 2008). Despite the unprecedented historical reduction of Araucaria population sizes by timber extraction and forest conversion to agriculture, this species retained a strong relationship with human populations harvesting their highly edible seeds since the late Pleistocene to modern times (Adan et al., 2016; Robinson et al., 2018).

The massive modern retraction of Araucaria forests reversed their pre-historical expansion induced by past paleoindian populations through human seed dispersal (Reis et al., 2014, 2018; Robinson et al., 2018). In addition, several ethnovarieties of *Araucaria* are distinguished and described by contemporary local people throughout the Araucaria Forest domain (Adan et al., 2016). This is strong evidence of the continued human influence on Araucaria trees, suggesting a deliberate or inadvertent domestication process across their distribution (Reis et al., 2018). This cultural process, which accounts for the multiple use and management of Araucaria by local communities, their specific local ethnobotany and terminology, and their role in narratives and symbolism in southern Brazil, ensures that they can be classified as a cultural keystone species (CKS) (Garibaldi and Turner, 2004). Despite this symbolic appeal and the importance of *pinhão* to local economies, recruitment rates of natural Araucaria populations are low (Paludo et al., 2009; Bogoni et al., 2020). It is therefore ironic that the concept of non-timber forest products (NTPFs) often excludes the structurally most important components of forest stands (Lawrence, 2003). These NTFPs are harvested across the tropics by millions of people, contributing to both international and domestic markets and supplying rural households with both much needed income and subsistence resources (Peres et al., 2003; Guariguata et al., 2017). However, the *pinhão* trade in Southern Brazil deserves further studies to assess the harvesting sustainability. The overexploitation of this NTFP presumably results in chronic detrimental impacts to both the associated vertebrate fauna and Araucaria recruitment, leading to negative effects for all ecological processes and ecosystem functioning of this historically reduced forest type of the southern plateaus.

As Araucaria populations retracted since the European conquest of southern Brazil, vertebrate biotas across the Atlantic Forest biome and its vegetation types experienced an unprecedented process of defaunation (Canale et al., 2012; Bogoni et al., 2018b). Defaunation disrupts several ecosystem process, including seed dispersal, phytodemographic dynamics and maintenance of carbon stocks (Peres et al., 2016). Moreover, defaunation leads to inflated rates of seed predation in the Atlantic Forest (Galetti et al., 2015). Our results show that only three vertebrate species (i.e. jays and agoutis) are widely known to regularly disperse *pinhão* from an overall pool of 29 interactors. The vast majority of Araucaria consumers are indeed consistent seed predators (Iob and Vieira, 2008). We highlight that nonrandom changes in mammal diversity and population density can disrupt the dispersal dynamics of *pinhão*, severely compromising the patterns of Araucaria regeneration across the southern Brazilian highlands.

Insights from this systematic review enable us to conclude that *Araucaria angustifolia* clearly qualifies as a Keystone Species (KS), a Keystone Plant Resource (KPR), and a Cultural Keystone Species (CKS). We provide clear evidence that rules out any arbitrary or ambiguous definition of Araucaria as a KPR, given the KPR ecological criteria proposed by Peres (2000). The hypotheses posed here were therefore vindicated as *pinhão* exhibits low temporal redundancy, low consumer specificity, high resource reliability and high resource abundance, thereby fundamentally underpinning vertebrate community structure in space and time. Conservation prospects for healthy persistence of Araucaria forest ecosystems and Araucaria population depend on retaining all consumer interactors — from the strongest to the weakest — and rely on smart public policy and fiscal incentives that can effectively protect the last Araucaria Forest patches and their components. A large body of theoretical and empirical evidence points to the contemporary retraction of Araucaria Forests, a concomitant process of selective vertebrate defaunation, and the systematic failure in forest regeneration due to a seed dispersal bottleneck. This is perhaps leading to evolutionary changes that are gradually reducing the size of *pinhão* to accommodate the smaller-bodied residual fauna of dispersal agents. This is a topic that merits further empirical investigation.

Declaration of Competing Interest

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106778.

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