Predicting dynamic trajectories of a protected plant community under contrasting conservation regimes: Insights from data-based modelling

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ABSTRACT

Data-based modelling of the dynamic behaviour of ecological communities is a big challenge in systems ecology and conservation biology. Implementing such models to forecast future scenarios is key for supporting decision-making in ecological reserves, given the multiple disturbances threatening their future. Using demographic and dynamic data for three tree (or tree-like) species from the Pedregal de San Ángel Ecological Reserve (Mexico City, Mexico), we constructed a family of dynamical models (using systems of ordinary differential equations) to reconstruct their dynamic interactions. The first two models considered two native species (*Pittocaulon praecox* and *Buddleja cordata*), with either antagonistic or cooperative interactions between them. These species have been considered ecosystem engineers playing different roles in the system and determining several community attributes. These models predict the transition from a stable steady state dominated by *P. praecox* (as reported in the 1950s) to the current community whose structure is apparently shifting to an alternative stable state dominated by *B. cordata*. The second pair of models additionally incorporate the invasive tree *Eucalyptus camaldulensis*, which exerts negative effects on all native plant species. The prediction of these models is an *E. camaldulensis*-dominated state with the exclusion of the native species from the reserve, provided this invasive species follows current population growth trends, without external intervention to check this process. Bifurcation analysis of this latter model allowed us to rationally design optimal intervention strategies that could potentially divert the trajectory from converging to an *E. camaldulensis*-only configuration into the stable coexistence of the native species. For the two-species and three-species models we made two versions, one with only competitive interactions and another one including a facilitation interaction between *B. cordata* and *P. praecox*. This analysis shows that facilitation is a requirement to achieve stable coexistence between the two native species, even in the presence of *E. camaldulensis*. The models constructed here, which integrate multiple data sources, help clarify conflicting empirical information regarding potential ecological mechanisms, and allow making predictions for strengthening the future management and *E. camaldulensis* control programs before its effects irreversibly modify the functioning and biodiversity of the biotic community protected in the reserve.

1. Introduction

As the human footprint on Earth deepens (Williams et al., 2020), good management of nature reserves becomes increasingly important as an instrument to prevent losses in our planet's biological legacy (Suding and Hobbs, 2009; Venter et al., 2016; Schuwirth et al., 2019). Uncertainty about the efficacy of nature protection areas arises from the difficulty to ensure the continuity of the biota and the overall ecosystem health in them (Shrestha et al., 2021). Integrating information on the past, present, and future dynamics of protected areas allows assessing

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the possibility to achieve such continuity, or identifying system shifts towards unknown new states. This information constitutes an important decision-making tool, allowing to adjust or improve current management of a protected area based on sound knowledge on species dynamics in the community (Schuwirth et al., 2019). Identifying the roles of those species contributing the most to community structure and functioning should enable the prediction of future scenarios for protected areas based on quantitative ecological relationships (Suding and Hobbs, 2009). Mathematical modelling is very useful to this end; computing (*in silico*) experiments are an attractive option vis-à-vis field experiments, as they allow searching for optimized solutions to ecological problems rapidly and cheaply (Borenstein, 2012). For example, invasive species management, a key topic in conservation biology, could strongly benefit from this approach.

Invasions of nature reserves by exotic and non-exotic species may gradually lead to communities that have little in common with the original ones. To examine this possibility, the alternative stable states theory offers an adequate theoretical framework (Petraitis, 2013). The notion of alternative stable states can be traced back to Lewontin's (1969) discussion of community structural stability, followed closely by the seminal papers of Holling (1973), May (1973) and Noy-Meir (1975) on the existence of alternative attracting equilibrium points. These early ideas prompted a rapidly growing field of research, in which the current debate largely focuses on the issue of ecosystem stability in the event of disturbances. Central to this topic is the concept of ecological resilience, defined as the magnitude of a disturbance required to trigger a transition into a qualitatively different stable state (Holling, 1973; Peterson et al., 1998; Gunderson, 2000; Petraitis and Sudgeon, 1999; Suding and Hobbs, 2009). Each of these stable states is associated with a different basin of attraction (Scheffer and Carpenter, 2003; Suding and Hobbs, 2009; Angeler and Allen, 2016). Often, big changes observed in ecosystems are associated to transitions from one alternative stable state to another (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Petraitis and Sudgeon, 2004; Rietkerk et al., 2004; van Nes and Scheffer, 2007; Norström et al., 2009). Crossing the boundaries between the basins of attraction of alternative steady states is possible when disturbances are strong enough to push the trajectories beyond the critical threshold (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Guttal and Jayaprakash, 2008; Petraitis, 2013; Angeler and Allen, 2016). The stability of stable steady states is roughly associated to feedback loops that maintain and sustain the system's functionality (Angeler and Allen, 2016). A bifurcation of a dynamical system has been defined as a topological change in the phase space that results from smooth changes in a bifurcation parameter (Andersen et al., 2009). Saddle node bifurcations, in which a stable steady state disappears when it collapses with an unstable branch (Guttal and Jayaprakash, 2008; Dakos et al., 2012; Nazarimehr et al., 2018) are amongst the most common ecologically relevant bifurcations (saddle node bifurcations are also known as thresholds; Scheffer et al., 2009; Petraitis and Hoffman, 2010; Kéfi et al., 2014; Angeler and Allen, 2016).

Some earlier modelling exercises of alternative stable states have focused on the effects of invasive species on ecological communities (Morton et al., 1996; Wearne and Morgan, 2006; Firn et al., 2010; Nicholls et al., 2011; Faist and Beals 2017). From a theoretical perspective, Morton et al. (1996) showed that exotic species that are absent from the regional species pool can trigger more complex feedbacks and, consequently, changes in community assembly; in these cases, the models analysed with numerical integrations proved to be more appropriate and reliable. Similarly, an experimental study in Lake Ontario, Canada, found that an invasive mussel species was capable of causing deep modifications in the structure of the main communities of the system (Nicholls et al., 2011).

Here, we integrate field data and mathematical modelling into an alternative stable states framework to study the possible long-term configurations of a terrestrial system in the presence or absence of an invasive species. We focus on a nature protection area, the Pedregal de

San Ángel Ecological Reserve (hereafter SAR), located on the National Autonomous University of Mexico (Universidad Nacional Autónoma de México; UNAM) main campus. Vegetation in SAR is a xerophytic scrub, given its arid condition due to incipient soil development (Rzedowski, 1954; Cano-Santana and Meave, 1996). A recent account of SAR's vascular flora comprises 373 vascular plant species (Castillo-Argüero et al., 2004, 2009), amongst which some 10 are trees and the remaining comprise an array of smaller growth forms. Amongst these trees, two Eucalypt species are prominent (*Eucalyptus camaldulensis* and *E. globulus*; Myrtaceae), and the Peruvian peppertree or *Pirul* (*Schinus molle*; Anacardiaceae). Despite the protection status of the area, *E. camaldulensis* has displayed an invasive behaviour that compromises the integrity of SAR and its biota.

Backed up by a wealth of field data on the plant community protected in SAR, currently two potential future dynamic scenarios are being debated for this community. First, based on the relentless urbanization around SAR and probably in association with increased air pollution, some authors have noted the increasing prevalence of the short tree *Buddleja cordata* (Scrophulariaceae). Soberón-M. et al. (1991) predicted the future dominance of this species in the community and several authors have reported an increasing abundance of it in SAR (e.g., Hernández Islas, 1984; Cano-Santana, 1994; Flores Vázquez, 2004). On this basis, we formulated the "*B. cordata* dominance hypothesis", the first one to be tested in our study, which states that the fate of this community would be a *Buddleja cordata*-dominated system.

A second hypothesis derives from the conspicuous presence of Eucalypts in SAR. The potential ecological effects of the introduction of *E. camaldulensis* to this area half a century ago have been amply documented, including impacts on community structure and diversity, through competitive effects and allelopathic interference (Segura-Burciaga, 2009; Espinosa-García, 1996; Segura-Burciaga and Meave, 2001). Thus, Eucalypts are likely to trigger feedback loops potentially leading to catastrophic, qualitative changes in this community's future dynamics. Hence, the "*E. camaldulensis* dominance hypothesis" foresees a future scenario for this community characterized by the dominance of this invasive species.

Based on this background, we asked in which direction this plant community is shifting, and what are the potential effects of the entry of invasive species to the community. To answer these questions, we analysed the dynamics of the plant community present in SAR to test the two aforementioned hypotheses. We did this by modelling the dynamics of this plant community to predict future scenarios for this natural protected area. Our mechanistic mathematical models are dynamical representations of key ecological interactions between the focal species that drive the establishment of stable plant communities. To the extent that it was possible, we derived the ecological mechanisms from empirical observations. To deal with conflicting or missing observations, we constructed a family of mathematical models, representing either the *B. cordata* dominance (type I models) or the *E. camaldulensis* dominance (type II models) hypothesis and assessed their plausibility (or explanatory capacity) by measuring their ability to reproduce field observations (i.e., by minimizing a cost function). The rationale behind this modelling approach is that it allows assessing the most plausible ecological interactions between the tree species given empirical data limitations (Schuwirth et al., 2019). We expect that this modelling-based study will prove useful in making informed decisions to manage this ecological reserve, and that this approach will eventually become widespread to promote sounder management of natural protected areas.

2. Materials and methods

2.1. Selection of focal species

Pittocaulon praecox (Cav.) Rob. & Brettell (common name, *Palo Loco*). This species is a large, dichotomously branched, succulent shrub, usually < 4 m tall but occasionally higher, allowing its classification as

arborescent or tree-like. The selection of this species was based on its past dominance in the community (Rzedowski, 1954). Despite evidence indicating that the population of this species is still growing (Rodríguez de la Vega, 2003; Pérez Ishiwara, 2011), it seems on its way to becoming a relatively unimportant community component, with a lesser contribution to community structure.

Buddleja cordata Kunth (common name, *Tepozán*). This species is a very frequent, short tree commonly growing in disturbed areas of temperate forests and xerophytic scrub vegetation in the central highlands of Mexico (Mendoza Hernández, 2003). Trees of this species are evergreen (Meave et al., 1994) despite a continuous foliage turnover in their crowns, thus they cast a deep shade even in the harsh dry springtime typical of Mexico City. This suggests that the concept of ecosystem engineer (Jones et al., 1994) is suitable for this species, as arguably it is a key modulator of resources and of abiotic factors, impacting the plant community structure and function in its vicinity.

Eucalyptus camaldulensis Dehnh. (common name, *Eucalipto* or Eucalypt). The selection of this species (incorrectly reported as *Eucalyptus resinifera* Sm. in previous studies in this area; e.g. Segura-Burciaga and Meave, 2001) was based on its high abundance in certain areas of SAR, particularly bordering the inner roads of the University campus and the main city roads that cross it, and because of the suspected impact it is having on this ecosystem (Segura-Burciaga, 2009; Acosta-Arreola, 2015). The abundant information on this species also warrants its recognition as an ecosystem engineer. Normally attaining a much larger height than any other native tree species, Eucalypts dominate the upper stratum, reducing light intensity under their crowns (Segura-Burciaga, 2009). In SAR, the experimental remotion of Eucalypts resulted in higher species richness compared to control plots covered with eucalypt crowns (Segura-Burciaga and Meave, 2001), likely because of volatile allelopathic compounds released by Eucalypts (Espinosa-García, 1996). The thick litter layer that often accumulates around Eucalypt trees decomposes very slowly, apparently deterring seed germination of other species (Segura-Burciaga and Martínez-Ramos, 1994), and increasing fire risk in the dry season. The high Eucalypt growth rates, combined with the lack of native predators and competitors capable of regulating its population, render this species a threat for the future functioning of the entire ecosystem. Three demographic studies covering the 1951–2009 period revealed a rapid growth of the *E. camaldulensis* population over this period, despite the launching of a control program that operated from 1994 to 2001 during which several thousands of individuals were downed (Segura-Burciaga, 2009; Acosta-Arreola, 2015).

2.2. Sources of empirical data

The starting point for the construction of the models was a thorough review of different sources, including grey literature, to search for morphological and ecological information on the focal species. This search produced 23 studies with relevant information, including 13 academic theses and dissertations, five book chapters, and five articles in specialized journals based on research conducted in this community between 1954 and 2015, whose references are provided in the following paragraphs.

Quantitative information sources were of two kinds. The first group comprised empirical descriptions of the ecological interactions involving the model's variables and was used for the construction of the reaction network and hence the mathematical model (Rzedowski 1954; Hernández Islas, 1984; Soberón-M. et al., 1991; Segura-Burciaga and Martínez-Ramos, 1994; Segura-Burciaga, 1995; Cano-Santana and Meave, 1996; Olvera Carrillo, 2001; Segura-Burciaga and Meave, 2001; Mendoza Hernández, 2002, 2003; Rodríguez de la Vega, 2003; Flores Vázquez, 2004; Camacho Altamirano, 2007; Antonio-Garcés et al., 2009; Castillo-Argüero et al., 2009; Valverde and Chávez, 2009; Martí-nez-Orea et al., 2012; Mendoza-Hernández et al., 2013; Santillán Carvantes, 2013). The second group included longitudinal demographic

monitoring of the densities of the three species and were used for parameterizing the mathematical model. Data for the calibration of the kinetic relationships between the two native species were retrieved from Cano-Santana (1994), who reported demographic data (density) and ecosystem-level information, including biomass production for *B. cordata* and *P. praecox* from 1990 to 1992. The increasing trend of *B. cordata* dominance in the community is supported by abundant qualitative and quantitative evidence (Soberón-M. et al., 1991; Cano-Santana, 1994; Cano-Santana and Meave, 1996; Mendoza Hernández, 2002, 2003; Flores Vázquez, 2004; Camacho Altamirano, 2007; Antonio-Garcés et al., 2009; Cano-Santana et al., 2006; Castillo-Argüero et al., 2009; Valverde and Chávez, 2009; Martínez-Orea et al., 2010).

A further set of sources provided information on the Eucalypt's ecology. Demographic information stems mainly from Segura-Burciaga (1995; 2009), Segura-Burciaga and Martínez-Ramos (1994), and Segura-Burciaga and Meave (2001), and was supplemented with a demographic study of this species (Acosta-Arreola, 2015). Interestingly, only five of these studies include demographic matrix modelling: Segura-Burciaga (1995) for *E. camaldulensis*, Mendoza Hernández (2002) and Flores Vázquez (2004) for *B. cordata*, and Rodríguez de la Vega (2003) and Pérez Ishiwara (2011) for *P. praecox*. All these studies confirmed the growing populational trends for these species. In addition, we gathered information from seed bank and post-fire colonization studies that confirmed the increasing dominance of *B. cordata* in SAR (Hernández Islas, 1984; Martínez Mateos, 2001; Mendoza Hernández, 2002; Martínez-Orea et al., 2010, 2012).

2.3. Construction of the mathematical models

We constructed a family of four mechanistic mathematical models representing the dynamic interactions between the two native species and one invasive species. These four systems of coupled ordinary differential equations (ODEs) represent the positive (A) and negative (B) dynamic interplay between the two ecosystem engineers in SAR (namely *B. cordata* and *P. praecox*), both in the absence (I) and presence (II) of the invasive *E. camaldulensis*.

First, we explored the dynamic consequences of both positive and negative interactions between *B. cordata* and *P. praecox* to clarify contradicting empirical evidence regarding these two possible interactions: negative regulation by competition and positive regulation by cooperation between them. We constructed spatially homogeneous and deterministic models based on ODEs. These models assumed that resources and space are limited; therefore, we refer to our model variables as "eco-dimers", i.e., integrated units of space (S) inhabited by a given tree. Because our model variables are trees or tree-like plants, we define an eco-dimer as the plants' crown area projected onto the soil, and hence it has units of area/tree cover. Model construction also assumed total space/resources in SAR to be constant (parameter TS) so that, using conservation equations, the free space can always be represented as an algebraic function (i.e., the constant total space minus the sum of the eco-dimers).

In each model, the dynamic variables are given by the three (or two) species of trees, i.e. $\vec{x} = [PS, BS, ES]$ with entries of $\vec{x}$ corresponding to the space in SAR occupied by *Pittocaulon praecox* (PS), *Buddleja cordata* (BS), and *Eucalyptus camaldulensis* (ES), respectively. Our model also implicitly includes the *Free Space* (FS) variable representing the area of SAR not occupied by any of the tree species. The *Total Space* (TS) is given by the algebraic relation $FS = TS - (PS + BS + ES)$ or, equivalently, $TS = FS + PS + BS + ES$. For each species we assumed that growth (or occupation of space) is a first order process linearly dependant on the free space, with parameter α_{x_i}. Death of individuals of any species is also a first order process that leads to the liberation of space with parameter β_{x_i}.

In models A (negative regulatory interactions, i.e. competition) we assumed that *PS* growth is inhibited by *BS*, representing the asymmetric

competition for resources where *B. cordata* is the aggressive competitor. Support for this negative regulatory interaction derives from field observations by Valverde and Chávez (2009) suggesting the existence of regions of SAR strongly dominated by *B. cordata,* where the canopy is relatively closed, and having a poorly lit lower stratum. We assumed a competitive effect for nutrients, water, soil and light. Nonetheless, there is also increasing evidence that facilitation is a key driver of community assembly in high-diversity systems (Callaway, 1995; Bruno et al., 2003; Valiente-Banuet and Verdú, 2007). Hence, we also included positive interactions: in models B (positive regulatory interactions, i.e. cooperation) we assumed that *BS* favours the growth of *PS* through facultative facilitation. Facilitation is a positive interaction from which at least one species benefits without damaging the other. In facilitative interactions the presence of one species modifies the environment, often with benefits for its neighbours (Bruno et al., 2003; Valiente-Banuet and Verdú, 2007; but see Valladares et al., 2008 for a cautionary view).

In the case of *B. cordata*, facilitation could be inferred if individuals of different species were recruited under a nursing *B. cordata* tree more frequently than expected at random (Valiente-Banuet and Verdú, 2007). Olvera Carrillo (2001) hypothesized that *B. cordata* could serve as the nurse for the cactus *Opuntia tomentosa*; although this author failed to demonstrate specificity in the nursing relationship, she showed that shadier, more humid microsites are key to the successful establishment of plant species in this community. Such conditions may be created by stones, cliffs, and even other plant species. In a different sector of the same lava field but outside of SAR, *B. cordata* fails to limit the establishment of new individuals (Ruiz Amaro, 1996), possibly due to nursing effects or microclimatic modifications around *B. cordata* individuals that could lead to increases in *PS*. Mendoza Hernández (2002, 2003) and Mendoza-Hernández et al. (2013) suggested that *B. cordata* has facilitating effects through the accumulation of soil and humidity around it, promoting seed germination of native species, and highlights its facilitating role for typical old-growth forest species like oaks. Rodríguez de la Vega (2003) reported that in 1997, following a massive recruitment event of *P. praecox* that started in 1992, 88% of *P. praecox* seedlings were located under nurse plants in a *B. cordata*-dominated area; moreover, 44.4% of plants growing under nurse plants survived compared to 3.8% survival for seedlings growing under exposed conditions (Rodríguez de la Vega, 2003). Figueroa-Castro et al. (1998) reported a higher production of reproductive structures for *P. praecox* in shadier, more humid microenvironments. This evidence supports the possibility of a positive, facilitating effect of *B. cordata* on *P. praecox* and probably other species too.

In constructing the type II (three-species) models, we further assumed negative effects of *ES* on the two native species, both by inhibiting their growth and inducing their death. These negative effects are mainly related to competition for nutrients, water and light, and the release of allelopathic compounds. In these models, γ represents the negative effects on the reproduction of native species, mainly related to the physico-chemical barrier represented by a litter layer containing allelopathic compounds in Eucalypt-dominated areas, preventing seed germination of native species (Segura-Burciaga, 1995), but also to the potential toxic effects of Eucalypts on the pollinators of native species (Segura-Burciaga, 1995; 2009). Fig. 1 shows the conceptual diagrams for the four models; Table 1 provides a description of model variables,

Table 1

List of variables included in the models, along with their symbols, units of measurement and explanatory comments.

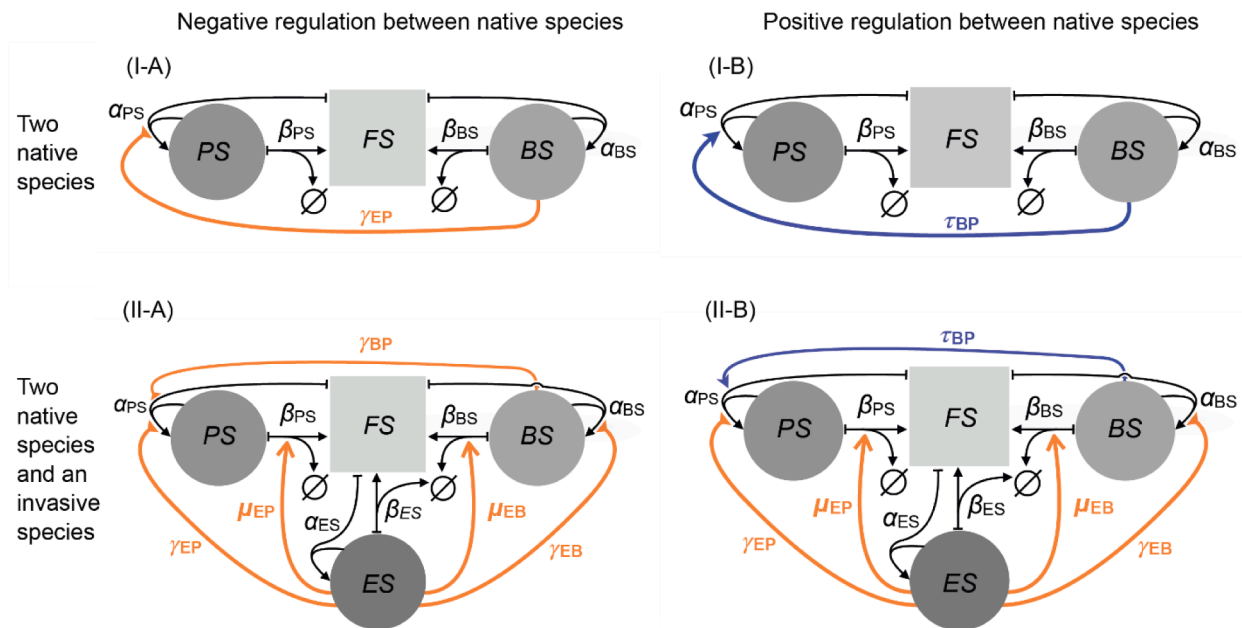| Symbol	Name	Units	Comments
t	Time (independent variable)	years	
FS	Free space	ha	Represented algebraically (conservation equations)
PS	Space occupied by *Pittocaulon praecox*	ha	
BS	Space occupied by *Buddleja cordata*	ha	
ES	Space occupied by *Eucalyptus camaldulensis*	ha	Models II-A and II-B only

Fig. 1. Mathematical models of the interplay between key ecological engineers in the Pedregal de San Ángel Ecological Reserve, Mexico. Type I and type II models represent the positive (Type I-A and Type II-A) and negative (Type I-B and Type II-B) dynamic interplay between *Pittocaulon praecox* (*PS*) and *Buddleja cordata* (*BS*), either in the absence (Type I models) or presence (Type II models) of *Eucalyptus camaldulensis* (*ES*) (in all cases, these acronyms denote the plant-space unit consider an eco-dimer). Circles represent the eco-dimers, and the square represents free space (*FS*). Orange arrows represent negative regulations; blunt end arrows represent inhibitory effects of eco-dimer formation rates, whereas pointed arrows indicate induction of eco-dimer dissociation rates. Blue arrows represent positive regulations (induction of eco-dimer formation). The weight of the interactions is given by the parameter values (Greek letters) defined in Table 4.

and the equations are given in Table 2.

2.4. Construction and standardization of a database with normalized field data of eco-dimer cover

To model growth for the three species we defined the eco-dimer formation as the association of individuals that use free space. Hence, we used units of area (ha) for the three species. The data extracted from the literature were standardized. After the creation of SAR, this nature protection area has undergone changes in dimension due to adjustments in its limits. Nonetheless, we treated the area of SAR as constant from 1954 until 2011 with a value of 146.9 ha, as this was its area during the period when most ecological records were made.

For the Eucalypt, the first cover data point is represented by the number of Eucalypt trees planted in the early 1950s. To obtain further dynamic datapoints we searched the literature for distributional and density data and found data for three additional dates, namely 1990 (Segura-Burciaga and Martínez-Ramos, 1994; Segura-Burciaga, 1995), 1998 (when a Eucalypt control programme was in effect; Segura-Burciaga, 2009) and 2011 (Acosta-Arreola, 2015). Based on the observation that in the area of Eucalypt occurrence 25% of the soil is free from its influence (Segura-Burciaga, 1995), we adjusted its distribution area by 75% to determine its net cover area (Table 3).

Information for *P. praecox* and *B. cordata* was retrieved from Cano-Santana (1994). This author distinguished in the lava field two main terrain units, namely rugged sites (defined by the abundance of cracks and depressions), and flat sites. Then, for these two species he quantified biomass stocks by site type for the years 1990, 1991 and 1992. The author also recognized three vegetation strata (tree, shrub and herb strata); interestingly, despite the arborescent condition of

Table 2

Model equations. Parameters in coloured font represent the effects of the ecological interactions of one species on another. Parameters in orange font imply a negative effect, whereas parameters in blue font represent the facilitation of *B. cordata* on *P. praecox*.

Model	System of equations
I-A	$$\frac{dPS(t)}{dt} = \frac{\alpha_{PS} \cdot PS(t) \cdot FS(t)}{1 + BS(t) \cdot \gamma_{BP}} - \beta_{PS} \cdot PS(t)$$ $$\frac{dBS(t)}{dt} = \alpha_{BS} \cdot BS(t) \cdot FS(t) - \beta_{BS} \cdot BS(t)$$ $$FS(t) = TS(t) - (PS(t) + BS(t))$$
I-B	$$\frac{dPS(t)}{dt} = \alpha_{PS} \cdot PS(t) \cdot FS(t) \cdot (1 + \tau_{BP} \cdot BS(t)) - \beta_{PS} \cdot PS(t)$$ $$\frac{dBS(t)}{dt} = \alpha_{BS} \cdot BS(t) \cdot FS(t) - \beta_{BS} \cdot BS(t)$$ $$FS(t) = TS(t) - (PS(t) + BS(t))$$
II-A	$$\frac{dPS(t)}{dt} = \frac{\alpha_{PS} \cdot PS(t) \cdot FS(t)}{1 + BS(t) \cdot \gamma_{BP} + ES(t) \cdot \gamma_{EP}} - PS(t) \cdot (\beta_{PS} + \mu_{EP} \cdot ES(t))$$ $$\frac{dBS(t)}{dt} = \frac{\alpha_{BS} \cdot BS(t) \cdot FS(t)}{1 + ES(t) \cdot \gamma_{EB}} - BS(t) \cdot (\beta_{BS} + \mu_{EB} \cdot ES(t))$$ $$\frac{dES(t)}{dt} = \alpha_{ES} \cdot ES(t) \cdot FS(t) - \beta_{ES} \cdot ES(t)$$ $$FS(t) = TS(t) - (PS(t) + BS(t) + ES(t))$$
II-B	$$\frac{dPS(t)}{dt} = \frac{\alpha_{PS} \cdot PS(t) \cdot FS(t) \cdot (1 + \tau_{BP} \cdot BS(t))}{1 + ES(t) \cdot \gamma_{EP}} - PS(t) \cdot (\beta_{PS} + \mu_{EP} \cdot ES(t))$$ $$\frac{dBS(t)}{dt} = \frac{\alpha_{BS} \cdot BS(t) \cdot FS(t)}{1 + ES(t) \cdot \gamma_{EB}} - BS(t) \cdot (\beta_{BS} + \mu_{EB} \cdot ES(t))$$ $$\frac{dES(t)}{dt} = \alpha_{ES} \cdot ES(t) \cdot FS(t) - \beta_{ES} \cdot ES(t)$$ $$FS(t) = TS(t) - (PS(t) + BS(t) + ES(t))$$

Table 3
Total cover by species (ha) in different dates for the 1954–2011 period in the Pedregal de San Ángel Ecological Reserve, Mexico City.

Year	*Buddleja cordata*	*Pittocaulon praecox*	*Eucalyptus camaldulensis*
1954	–	–	1.105
1990	15.467	0.078	8.932
1991	16.954	0.086	–
1992	19.187	0.096	–
1998	–	–	6.548
2011	–	–	8.251

P. praecox, this species was associated with the shrub stratum, which also includes a group of medium-sized young *B. cordata* individuals. For these two species and for years 1990 and 1991, there are density records for the two taller strata and for both site types. Data on total density and cover of the tree stratum were also available for 1990, and there were total biomass records for the three years by site type. Given the large substrate heterogeneity in this area (Santibáñez-Andrade et al., 2009), we transformed all records to express them in the same units (ha for area and kg for weight). Reference year for inferring 1991 and 1992 cover was 1990 (Table 3). The resulting database for dynamic eco-dimer values is given in Table 3.

2.5. Optimization of parameter values (derivation of nominal values)

Parameters were estimated through global optimization, by minimizing the cost function that measures the difference between empirical measurements of the eco-dimers and the simulated trajectories of our model variables given a set of parameters, as:

$$Cost(\bar{P}) = \sum_{i=1}^{n} \sum_{k=1}^{m} \left(x_i^{data}(t_k) - x_i^{model}(t_k) \right)^2$$

where $\bar{P}$ is the vector of parameters, $i = 1...n$ the index of the vector of model variables, $k = 1...m$ the time points, $x_i^{data}(t_k)$ and $x_i^{model}(t_k)$ are the measured and simulated datapoints of variable i at time k. Global optimization of the cost function was done with the `GlobalSearch` function in `Matlab R2020a` (The Math Works, Inc., 2020). We did not assess parameter interactions due to the lack of controlled field or laboratory experiments. Resulting nominal model parameters are described in Table 4.

2.6. Stability analysis of the mathematical models

The steady state values and their stability conditions were derived analytically for the four models, as explained in Appendix A. Note that, since this is an analytical procedure, the results do not depend on specific parameter choices, which is very robust (they depend on equation structure only).

2.7. Constructing distributions of the stable community configurations of the two 3-species models

We used a Latin Hypercube method to randomly sample 100,000 parameter sets from an 11-dimensional uniform distribution spanning seven orders of magnitude ($[10^{-5} —10^2]$), analytically computed the steady states and assessed their stability through linearization.

2.8. Estimation of the separatrix for model II-B with nominal parameter values

Model II-B (three species interactions with positive regulation between the two native species) (Fig. 1), with nominal parameter values in Table 3, leads to a bistable dynamical behaviour with one stable steady state (p_1) corresponding to long-term extinction of the two native species with high *E. camaldulensis* cover in SAR, and a second one (p_3)

Table 4
Model parameters.

Symbol	Description	Units	Nominal value
α_{PS}	*PS* reproductive rate	ha^{-1}year^{-1} (ha of *PS*)	0.00110
α_{BS}	*BS* reproductive rate	ha^{-1}year^{-1} (ha of *BS*)	0.00137
α_{ES}	*ES* reproductive rate (models II only)	ha^{-1}year^{-1} (ha of *ES*)	0.00100
β_{PS}	*PS* death rate	year^{-1}	0.29000
β_{BS}	*BS* death rate	year^{-1}	0.07000
β_{ES}	*ES* death rate (models II only)	year^{-1}	0.01000
γ_{BP}	Inhibition of growth of *PS* by *BS* (models A only)	ha^{-1}	0.09950
γ_{EP}	Inhibition of growth of *PS* by *ES* (models II only)	ha^{-1}	0.01000
γ_{EB}	Inhibition of growth of *BS* by *ES* (models II only)	ha^{-1}	0.01000
τ_{BP}	Stimulation of growth of *PS* by *BS* (models B only)	ha^{-1}	0.09950
μ_{EP}	Stimulation of death of *PS* by *ES* (models II only)	ha^{-1}year^{-1}	0.01000
μ_{EB}	Stimulation of death of *BS* by *ES* (models II only)	ha^{-1}year^{-1}	0.01000
TS	Total size of SAR	ha	146.9

corresponding to the opposite scenario, with stable coexistence of the two local species and the local extinction of the invasive tree. There are other equilibria (p_0, p_2, p_4) which are all saddle points and are contained in one or more (invariant) coordinate planes. The equilibrium point p_5, which hereafter will be given special attention, is also a saddle point because while some of its associated eigenvalues have a negative real part (characteristic of stable steady states), one eigenvalue is positive (hence unstable).

A key question emerges here as to how to decide on the asymptotic behaviour ($t \to \infty$) of a solution if we only know the state of the system at present ($t = 0$). Will it converge towards p_1 or p_3? In other words, how to tell which initial conditions lead to p_1 from those that go to p_3 in the general case? The key to this answer lies on a special set of solutions associated with the equilibrium p_5. The basins of attraction of p_1 and p_3 are separated by the stable manifold $W^s(p_5)$ of p_5. The manifold $W^s(p_5)$ is a smooth two-dimensional invariant object consisting of all solutions that tend to p_5 in the long term. All the solutions starting on one side of $W^s(p_5)$ converge to p_1, while all solutions on the other side of $W^s(p_5)$ converge to p_3. This means that $W^s(p_5)$ represents the *separatrix* that divides the phase space $[BS, PS, ES]$ into the basin of attraction of the two stable steady states of the system, p_1 and p_3. In general, it is not possible to derive the global stable manifold $W^s(p_5)$ in a closed formula. Here, $W^s(p_5)$ was computed numerically with the method proposed by Krauskopf and Osinga (2007) as a family of orbit segments which can be obtained as solutions of a suitable boundary value problem (BVP), implemented in the package `Auto`. The two-dimensional manifold is obtained from the output data and the respective portion of the manifold is rendered as a surface from the computed orbit segments with dedicated `Matlab` routines.

2.9. Design of optimal control strategies for E. camaldulensis management

We assumed a current state at the point $q90 = (0.0790\ \text{ha};\ 15.4667\ \text{ha};\ 8.9326\ \text{ha})$, which corresponds to the state of the system as recorded from data in 1990. We first show that $q90$ lies above the separatrix $W^s(p_5)$ and in the basin of attraction of $p1$. In other words, the empirical data from 1990 are on the "undesired" side of the separatrix; in the absence of interventions, the native species will go extinct locally. Hence, as $t \to \infty$ the orbit starting at $q90$ converges to $p1$. The point $qm \approx (0.0785\ \text{ha};\ 16.0792\ \text{ha};\ 4.2897\ \text{ha}) \in W^s(p_5)$ is the nearest point in $W^s(p_5)$ to $q90$. Such minimum distance is approximately 4.7163, which is the minimal distance from the coordinate in 1990 to the separatrix —a first measure of the strength of interventions required to avoid extinction of the local species (i.e., a catastrophe)—. The usefulness of knowing point qm lies on the fact that it indicates a possible way to establish actions aimed to eradicate the *E. camaldulensis* with minimum effort. In this context, the effort is associated with the cost of moving down the state of the system from $q90$ beyond the separatrix $W^s(p_5)$ and into the basin of attraction of $p3$. The shortest path to achieve this is by crossing $W^s(p_5)$ along a straight line from $q90$ through the threshold point qm. Since finding an analytical expression for $W^s(p_5)$ is not possible, it is also impossible to find a formula for the point $qm\ W^s(p_5)$. Therefore, we carried out numerical continuation to obtain the coordinates of qm. First, we calculated an orbit segment as a solution of a two-point BVP implemented and solved in Auto. One of these boundary conditions was defined in a fundamental domain lying on the stable eigenspace of $p5$; this is a standard step in the procedure to obtain a global two-dimensional manifold (Krauskopf and Osinga, 2007; Contreras-Julio et al., 2020). The second boundary condition is located on a sphere centred at $q90$ of radius R. In this way, the computed orbit segment represents a solution in $W^s(p_5)$ whose endpoint at $t = 0$ lies at distance R from $q90$. Once the desired orbit segment $W^s(p_5)$ was obtained, we continued this solution in terms of R (which is now a dummy parameter) until a fold is detected with respect to R. This fold point represents a minimum value of R. Finally, we follow this fold point in R, and the integration time T to trace out a locus of minima for R. This

iterative process revealed the global minimum at for the orbit segment in $W^s(p5)$ with initial conditions at qm.

For the second control strategy, shown in Fig. 6, in which only *E. camaldulensis* is allowed to decrease, to find the other endpoint two further boundary conditions are posed, namely, to force it to lie on the planes $PS = 0.0790 + \varphi_1$ ha and $BS = 15.4667 + \varphi_2$ ha, where φ_1 and are dummy parameters. Once an initial orbit segment of $W^s(p5)$ is obtained, we continue this solution in terms of φ_1 and φ_2 until both $\varphi_1 = \varphi_2 = 0$. This iterative process reveals the coordinates of $qm \in W^s(p_5)$ as the initial point ($t = 0$) of the computed orbit segment obtained as the solution of this BVP.

2.10. Code availability

The code is written in `Matlab` version `R2020a` and in `Fortran` and is stored in the `GitHub` repository `github.com/Eli-saDominguezHuettinger/REPSA_Model`.

3. Results

3.1. Conditions for the long-term stable coexistence of the two native species

The qualitative analysis of the two 2-native species models, one with positive and one with negative interaction between the native species, shows that long-term stable coexistence between them is more likely to occur under a positive interaction regime. For both models, four steady states and their stability can be derived analytically, as shown in Appendix A. The construction of systems of equations starting from the integration of highly heterogeneous sources of information and ecological data allowed us to detect the possible scenarios in the plant community. Overall, for the two models we found analytically three possible stable states: (1) when all species become extinct; (2) when only one species survives, and (3) when two survive and coexist (in model I-B only). In addition, in all three models we found multi-stability under certain parameter conditions.

The extinction of the two native species occurs when the eco-dimer dissociation rate is higher than its formation rate, for both species; that is, if certain conditions change and the value of β increases or the value of α decreases. This may be caused by changes in one or several environmental variables, or because of the appearance of a fulminating pathogen, a ravenous herbivore or an aggressive competitor.

In model 1-A (two competing native species), *B. cordata* is in an advantageous position due to its ability to inhibit *P. praecox*'s growth. Therefore, parameter conditions allowing *P. praecox* to survive while leading to *B. cordata*'s extinction are more limited (it occurs if and only if $\alpha_{BS}\beta_{PS} < \alpha_{PS}\beta_{BS}$) than those necessary for the opposite to be true. This scenario is illustrated in Fig. 2A.

In model I-B (two cooperating native species), *P. praecox* benefits from *B. cordata*'s growth. Hence, the survival of *B. cordata* and the displacement of *P. praecox* become true if and only if $\alpha_{BS}\beta_{PS} > \alpha_{PS}\beta_{BS}$. This shows that stable coexistence between these two native species is more likely to occur under a positive interaction regime, since the parameter conditions for which coexistence is observed are less stringent (i.e., stable coexistence regime is more robust to perturbations in parameters). Such a scenario is exemplified in Fig. 2C. This stable coexistence regime is a direct function of the strength of the positive interaction, i.e., it occurs if parameter τ_{BS} is strong enough, as shown in Fig. 2B. Bi-stability between the two local extension regimes in model I-B is not possible.

3.2. Robustness of the native community to the introduction of an invasive species

The symbolic analysis of the two 3-species models presented in

(A) Model I-A (negative interaction)

(B) Model I-B (positive interaction)
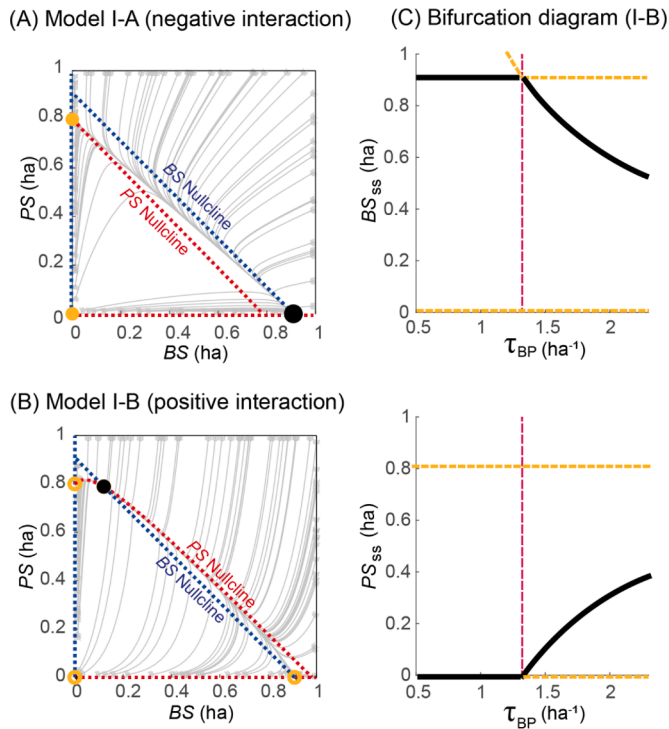

(C) Bifurcation diagram (I-B)

Fig. 2. Qualitative analysis of the 2D native species models assuming negative or positive interactions. **(A)** Representative phase space of model I-A (negative interaction), and **(B)** model I-B (positive interaction), showing stable local extinction of *PS* and stable coexistence, respectively. **(C)** Bifurcation diagram of model I-B with the strength of the positive interaction, τ_{BS}, as a bifurcation parameter, with solid black lines representing stable steady states (denoted by the subscripts "ss") and dotted yellow lines the unstable steady states. Sufficiently strong positive regulatory strengths lead to a stable coexistence of both species. Parameter values are **(A)** $\alpha_{PS} = 1$ ha^{-1}year^{-1}; $\alpha_{BS} = 0.2$ ha^{-1}year^{-1}; $\beta_{BS} = 0.2$ year^{-1}; $\beta_{BS} = 0.1$ year^{-1}; $\gamma_{BP} = 0.1$ ha^{-1}; $TS = 1$ ha; and **(B, C)** $\alpha_{PS} = 1$ ha^{-1}year^{-1}; $\alpha_{BS} = 1.1$ ha^{-1}year^{-1}; $\beta_{PS} = 0.2$ year^{-1}; $\beta_{BS} = 0.1$ year^{-1}; $\tau_{BP} = 10$ ha^{-1}; $TS = 1$ ha.

Appendix A shows that both models (i.e. either with positive or negative interactions between the native species), following qualitatively different dynamic regimes (i.e. stable community configurations), are possible in the long term under certain parameter conditions (illustrated in Fig. 3A): (1) all three tree species go extinct; (2–4) only one of the three species survives; or (5) the stable coexistence of *B. cordata* and *P. praecox* (case 5 in Appendix A). A stable configuration in which *E. camaldulensis* coexists with either one of the other two species is not possible.

The first steady state (all species extinct) is stable if $TS < \min(\beta i / \alpha i)$ for $i = BS; PS, ES$. A *E. camaldulensis*-only point $(0, 0, ES^* > 0, \beta 3 / \alpha 3)$ is stable if ES^* satisfies conditions over parameters 82–85 (II-A) / 60 (II-B) as detailed in the Appendix. A *PS*-only state $(0, PS^* > 0, 0, \beta 2 / \alpha 2)$ is stable if and only if $\alpha 1 \beta 2 < \alpha 2 \beta 1$ and $\alpha 3 \beta 2 < \alpha 2 \beta 3$. A *BS*-only state $(BS^* > 0, 0, 0, \beta 1 / \alpha 1)$ is stable for model II-A if $\alpha 3 \beta 1 < \alpha 1 \beta 3$ and $BS^* > (\alpha 2 \beta 1 - \alpha 1 \beta 2)/\alpha 1 \beta 2 \gamma 2$, and for model II-B if $\alpha 2 \beta 1 < \alpha 1 \beta 2$ and $BS^* < (\alpha 1 \beta 2 - \alpha 2 \beta 1)/\alpha 2 \beta 1 \theta 3$. Finally, the $BS - PS$ stable coexistence point $((\alpha 2 \beta 1 - \alpha 1 \beta 2)/\alpha 1 \beta 2 \gamma 2, PS^*, 0, \beta 1 / \alpha 1)$ is stable for conditions over parameters given in eqs. (61) for model II-A and (66) for model II-B detailed in Appendix A.

To illustrate these conditions over parameters for the two 3-species models, we numerically constructed the probability distributions of the possible community configurations under randomly varied parameter conditions (see details in Methods). We found that bi-stability is very common for both models (69.7% and 72.5% in the cases of models II-A and II-B, respectively), and that model II-A can even display tri-

stability for certain parameters (1%) (Fig. 3B, left).

For the mono-stable scenario occurring in 29.3 and 27.5% of parameter variants for model II-A and II-B, respectively, the proportions of parameters leading to extinction of all species is 2.7 and 2.6%; for a *E. camaldulensis*-only state, 46.8 and 45.3% (Fig. 3C shows an example of this case); for a *B. cordata*-only state, 26.9 and 21.8%; for a *P. praecox*-only state, 23.6 and 26%, and, finally, and most interestingly, stable coexistence between *B. cordata* and *P. praecox* can only take place in model II-B for 4.2% of the parameter variations (Fig. 3B, centre).

As shown in Fig. 3B (right side), for model II-A the only possible bi-stable combinations are a *E. camaldulensis*-only with a *B. cordata*-only state for 90.2% of the cases, or a *B. cordata*-only state with a *P. praecox*-only state in the remaining 9.8% of the bi-stable cases. In turn, while model II-B can also result in bi-stability between a *B. cordata*-only and a *E. camaldulensis*-only state in 43.3% of the cases, and between *E. camaldulensis*-only and *P. praecox*-only in 50.2% of the bi-stable cases, it is interesting that it can also exhibit bi-stability between a *E. camaldulensis*-only stable state and a coexistence state between *B. cordata* and *P. praecox* in the remaining 6.5% of the cases. It is this latter qualitative scenario that we analyse further in terms of intervention strategies. In addition, tri-stability between the three states in which only one of the species prevails can only be exhibited by model II-A (Fig. 3B, bottom-left).

Together, these numerical results confirm the analytically derived community configurations, specifically that *E. camaldulensis* cannot stably coexist with any of the two native tree species.
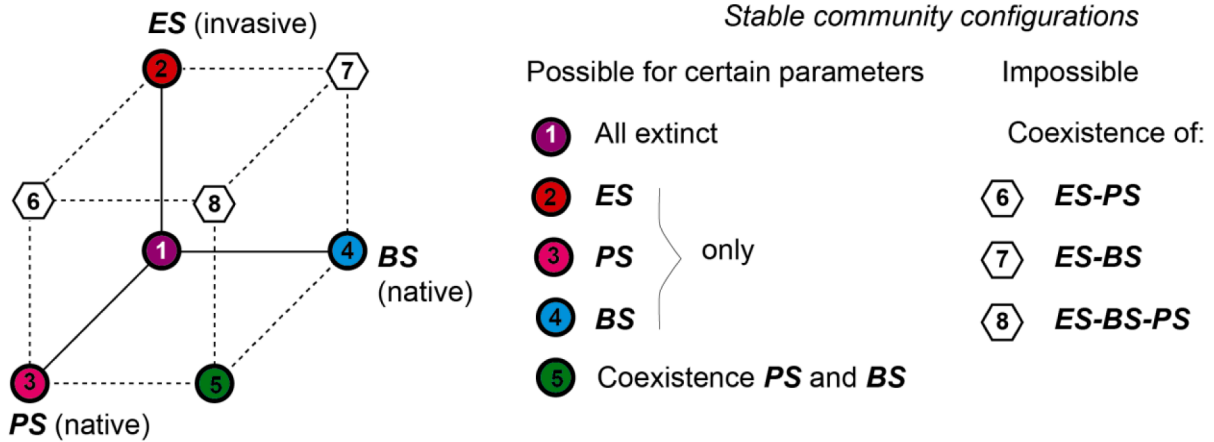
3.3. Catastrophic shifts in SAR: local extinction of the native species in the absence of E. camaldulensis control

Global optimization for model II-B (tree species with positive interactions between the native species) using the field data of Cano-Santana (1994), Segura-Burciaga (1995, 2009), and Acosta-Arreola (2015) resulted in the nominal parameter values given in Table 3, and the dynamic behaviour shown in Fig. 4A. This scenario corresponds to the bi-stability of two qualitatively different regimes; in the long term, either the two native species (*B. cordata* and *P. praecox*) coexist and eventually displace the invasive *E. camaldulensis,* or vice versa. Further, numerical integration of model II-B with optimal parameters shows that, without intervention, the trajectory starting at the 1990 datapoint (the only year for which we have data for all our variables) will eventually converge to the *E. camaldulensis*-only steady state, i.e., it is within the basin of attraction of the *E. camaldulensis*-only steady state (Fig. 4B).

3.4. Mathematical design of optimal strategies for SAR management

Stability and bifurcation analysis suggest that, in the absence of interventions aimed at controlling *E. camaldulensis*, the most likely long-term future scenario of the ecological community is the local extinction of the native communities. Thus, following a similar strategy as in Contreras-Julio et al. (2020), here we design two optimal intervention strategies for SAR through which the dynamical trajectories are re-channelled to converge towards a stable coexistence between *B. cordata* and *P. praecox*. In the first strategy, we assume that the abundance of all the tree species can be modulated (e.g., by planting or felling). While this first strategy retrieves a mathematically optimal solution (Supplementary Figure S1), it is not realistic because *B. cordata* is a very efficient colonizer (Villeda-Hernández, 2010; González-Rebeles G., 2012; Gonzalez Jaramillo, 2018). Thus, we also designed a second, more realistic strategy in which we assume that only the Eucalypt death rate can be reduced (e.g., through felling). In both cases, we assume that the current conditions correspond to the measured state variables in 1990 and computed the minimal intervention effort required to push the state trajectory from one basin of attraction (corresponding to long-term death of the native species) to another (stable coexistence of native species and local extinction of the invasive one).
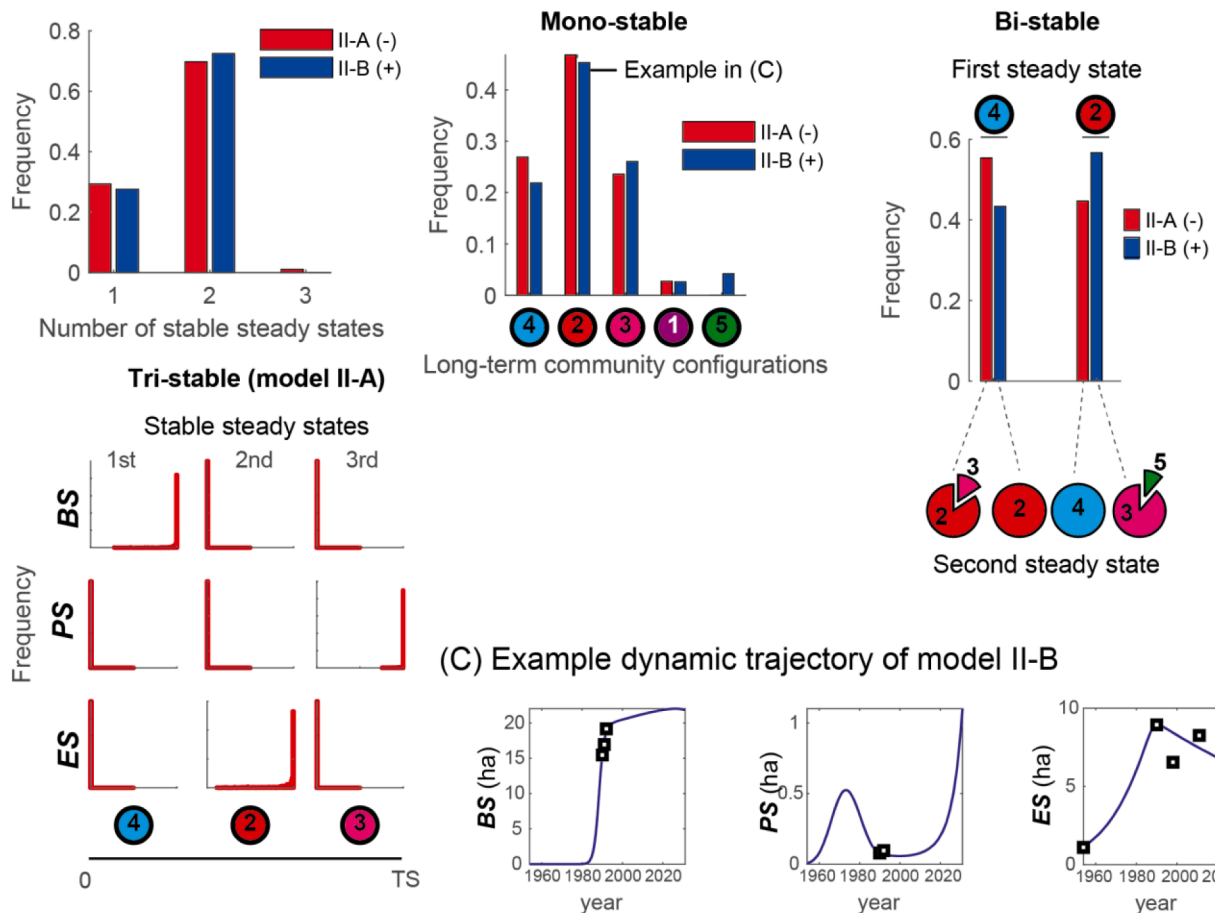
Fig. 3. Possible stable long-term community configurations of the two 3-species models (II-A and II-B). **(A)** Configurations sketched in the 3-species phase space. **(B)** Frequency distributions of number of possible stable steady states and the corresponding possible community configurations for both models. In the bi-stable case, the bars represent the proportions of community configurations of the first steady state, with circles (pie-chart) below them denoting the corresponding configuration(s) of the second steady state. The possible community configurations of the tri-stable case in model II-A are shown by histograms of the three state variables. **(C)** Projection of the empirical data to an example dynamic trajectory for model II-B under a *E. camaldulensis*-only monostable-regime (parameters: α_{PS} = 0.021989 ha^{-1}year^{-1}; α_{BS} = 0.038582 ha^{-1}year^{-1}; α_{ES} = 0.0028517 ha^{-1}year^{-1}; β_{PS} = 0.099878 year^{-1}; β_{BS} = 4.5468 year^{-1}; β_{ES} = 0.3462 year^{-1}; τ_{BP} = 0.1273 ha^{-1}; γ_{EP} = 3.3906 ha^{-1}; γ_{EB} = 0.0001118 ha^{-1}; μ_{EP} = 0.026769 ha^{-1}year^{-1}; μ_{EB} = 9.286e^{-05} ha^{-1}year^{-1}; TS = 146.9 ha). *PS*, space occupied by *Pittocaulon praecox*; *BS*, space occupied by *Buddleia cordata*; *ES*, space occupied by *Eucalyptus camaldulensis*.
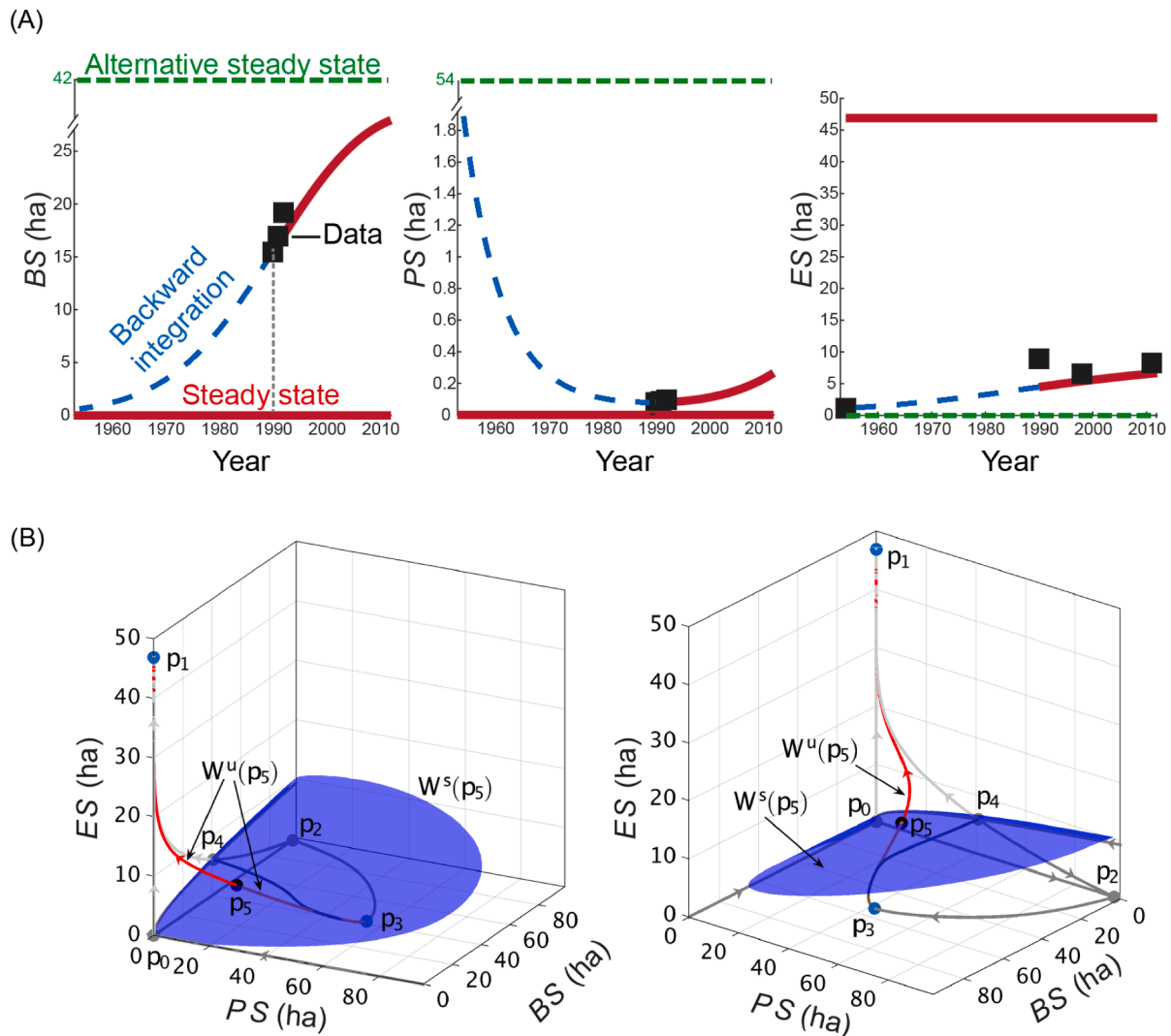
Fig. 4. Model with optimal parameters. Fit of model II-B to data in Table 3 leads to a bi-stable scenario with either a *E. camaldulensis*-only regime (red) or a stable coexistence between *B. cordata* and *P. praecox* in green. The datapoint of 1990 is within the basin of attraction of the *E. camaldulensis*-only regime. Resulting optimal parameters are given in Table 4. **(A)** Dynamic trajectories. **(B)** Phase space representation of the dynamic trajectories showing the boundary separating the set of initial conditions converging to one stable steady state or the other (separatrix) in blue.

That is, we designed an optimal control strategy for the SAR based on the available empirical information and the plausible interventions.

Fig. 5 shows a cross-section of the 3-species space into the 2-native species projection with constant *E. camaldulensis*. Fig. 5A shows a cross section of Σ intersecting $W^s(p_5)$. Σ corresponds to the plane in the $(PS; BS; ES)$-space where $ES = 8.2513$ ha is fixed; this is the recorded value of ES from 2011 data, i.e., the most recent record. Even if the exact values of the other two variables (PS and BS) for 2011 are unknown, it is
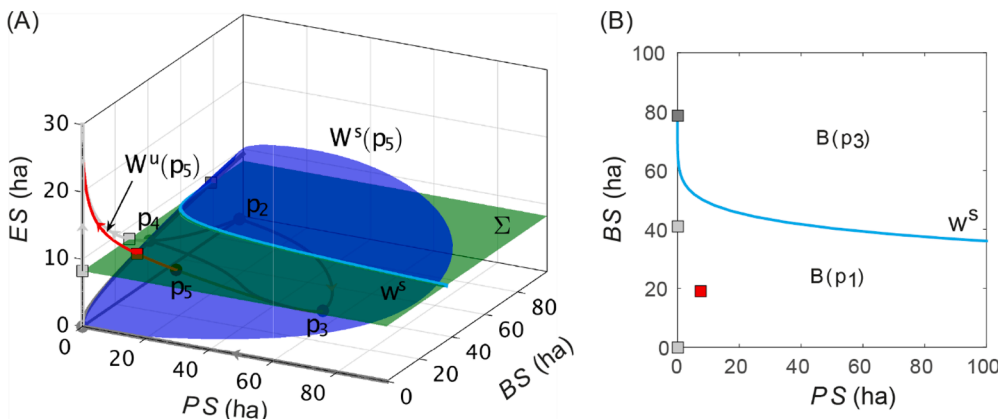

Fig. 5. Cross-section of the 3-species space into the 2-native species projection with constant Eucalyptus. **(A)** Cross section of Σ intersecting $W^s(p_5)$, where Σ corresponds to the plane in the $(PS; BS; ES)$-space, where ES is fixed to its most recent recording (from 2011). **(B)** Projection of the points on Σ on the $(PS; BS)$-plane with $w^s = W^s(p_5) \cap \Sigma$. The region above w^s corresponds to the set of all combinations of $(PS; BS)$ which, for the amount of ES present in 2011, would have allowed long term survival of both native species, and eradication of ES, and vice versa for region $B(p1)$.

still possible to make a sensible prediction about the possible long-term outcome of this ecological interaction. Points on Σ can be parameterized by their projection to the $(PS; BS)$-plane. Fig. 5B shows such representation and how the different intersections of invariant objects and orbits lie on Σ. The set $ws = W^s(p_5) \cap \Sigma$ is a one-dimensional curve rendered in light blue colour. It is bounded on one end by the intersection of the stable manifold of p_4, with Σ which corresponds to a point in the $PS = 0$ plane (dark grey square); the other end of ws lies outside of the plotted range. In Fig. 5D, the region $B(p_3)$ above ws corresponds to those points in Σ lying in the basin of attraction of p_3; any orbit starting in $B(p_3)$ converges to p_3 in forward time. Hence, region $B(p_3)$ is the set of all combinations of $(PS; BS)$ which, for the amount of ES available in 2011, would have allowed the long-term survival of both native species along with the eradication of ES.

In turn, region $B(p_1)$ corresponds to those points in Σ lying within the basin of attraction of p_1. Hence, region $B(p_1)$ is the set of all pairs $(PS; BS)$ which evolve to mutual extinction of PS and BS and colonization by ES. Note that the unstable manifold $W^u(p_5)$ of p_5 (red curve in Fig. 5A) intersects Σ at a point in $B(p_1)$, rendered as a red square in Fig. 5B. Likewise, the two orbits on the plane $PS = 0$ coming from p_0 and p_4, respectively, and converging to p_1 intersect Σ at points in $B(p_1)$ (light grey squares). Note that the long-term outcome of both native species (i.e., survival or extinction) is highly sensitive to variations in BS, but less so to changes in PS, provided PS is large enough. Indeed, the curve ws (i.e., the boundary between $B(p_1)$ and $B(p_3)$) has a small slope for $PS > 20$ ha, so that small variations of BS near —that is, 40 ha $<$

$BS < 50$ ha approximately— may trigger the pair $(PS; BS)$ to shift toward the other basin of attraction by crossing ws up or down. On the other hand, if PS is sufficiently small, say $0 < PS < 5$ ha, and 50 ha $< BS < 80$ ha, it is the other way around: small variations of PS may induce the point $(PS; BS)$ to cross the separatrix ws from one basin to the other. These results provide insight into the best intervention strategy; for example, planting one particular tree species (*B. cordata*) might be much more efficient (cost-effective) than planting the other (*P. praecox*).

The results of the second control strategy (manipulating Eucalypt-only) are shown in Fig. 6. In mathematical terms, this strategy corresponds to following a straight path in the $(PS; BS; ES)$-space while keeping PS and BS constant at 0.08 ha and 15.5 ha, respectively, while only ES is decreased. Once again, knowledge of $W^s(p_5)$ is useful to design an optimal management campaign. It is clear from the definition of the separatrix $W^s(p_5)$ that the minimum number of felled trees is achieved when the point $(PS; BS; ES)$ effectively reaches $W^s(p_5)$. This happens at the point $qm = (0.0790$ ha; 15.4667 ha; 4.0302 ha$) \in W^s(p_5)$. The orbit starting at qm is the first in this strategy that does not converge to p_1 but to p_5; see the blue orbit in Fig. 6A. In this example, this strategy corresponds to decreasing ES from 8.9 ha to (at least) 4.0302 ha. Any value of ES just less than 4.0302 ha will suffice, but the closer to 4.0302 ha, the more cost-effective will be. In the special case that ES is lowered down to exactly 4.0302 ha, the system will evolve to the coexistence equilibrium p_5. However, this asymptotic state is unstable; any generic small perturbation away from p_5 drives the system into the basin of either p_1
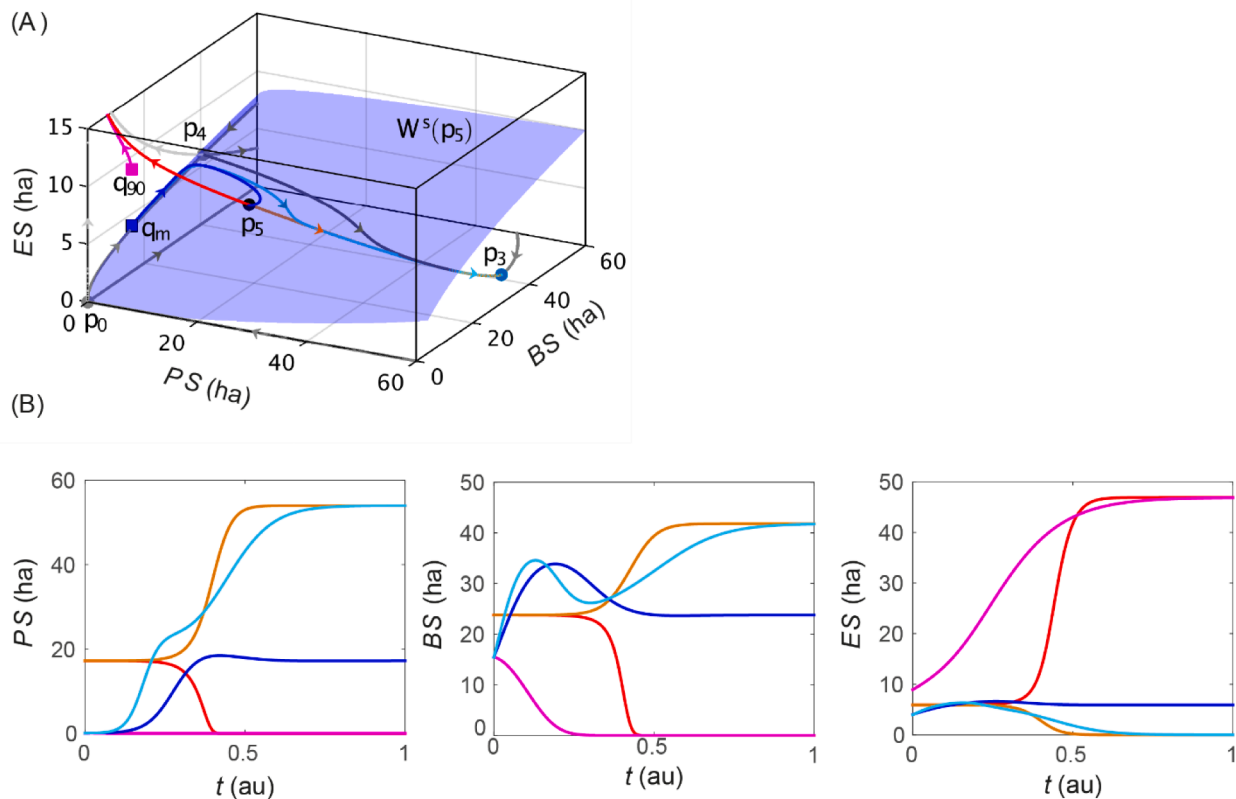

Fig. 6. Optimal *E. camaldulensis* management strategies for a bi-stable regime, assuming that only the Eucalypt cover can be modulated (e.g., by felling). **(A)** shows one phase space projection of the separatrix $W^s(p_5)$ in blue, and **(B)** shows the dynamic evolution of our three model variables. Trajectory from $q90$ (with $t_0=1990$) towards a *E. camaldulensis*-only state (in the absence of interventions) is shown in magenta. The point $qm = (0.0790$ ha; 15.4667 ha; 4.0302 ha$) \in W^s(p_5)$ is the nearest point to $q90$ at the separatrix. The trajectory starting at that point (shown in blue) remains in $W^s(p_5)$. To illustrate the usefulness of this procedure, a cyan orbit is shown in the three panels of **(B)**, whose initial point (not labelled) lies directly below qm in the basin of attraction of p_3. According to this orbit, one might only need a very small (but sufficient) perturbation away from $q90$ to achieve the long-term coexistence of PS and BS along with the elimination of PS (compare the cyan and magenta curves).

or $p3$ (see the blue orbit in panels B). Therefore, to guarantee success in our strategy, one must ensure that $ES < 4.0302$ ha, i.e., the system is driven down to just below qm.

4. Discussion

By using a set of mechanistic mathematical models constructed from, and calibrated with, experimental data, we evaluated the most plausible future community dynamics scenarios in the Pedregal de San Ángel Ecological Reserve; in addition, we gained insight into the effect of perturbation in the form of invasive species (structural perturbations; addition of a variable) and of random parameter variations in reshaping the future configuration of the tree community in this protected area. Our modelling approach was intended to gain insights into the potential consequences of implementing different management regimes with the best scientific tools currently available, as objectively as possible and recognizing both advantages and shortcomings, to ultimately make management recommendations (Schuwirth et al., 2019).

Constructing mechanistic models with ODEs was adequate, given the large amount of information available for this system, although quantitative information on cover was rather limited (Schuwirth et al., 2019). The wealth of information and observations available for SAR clearly point to an increase in *B. cordata* dominance combined with the concomitant reduction of the physiognomic importance of *P. praecox*, along with the generalized structural change in this ecosystem. However, the available information is insufficient to unambiguously determine whether the system has reached stability. To achieve this goal, increasing information resolution would be needed, while attempting that the time coverage of the records is longer than the lifespans of the organisms used for the modelling and considering relevant natural cycles (Suding and Hobbs, 2009; Capon et al., 2015).

Despite the limited temporal resolution of the data, the robustness of models I-B and II-B arises from the integration of all available knowledge on this ecosystem. One important consideration is that our qualitative results are not dependant on specific parameter choices, but rather on the structure of the models, derived in turn from the proposed ecosystem relationships. The two models were analysed symbolically. Moreover, model II-B presented bi-stability, which is uncommon. These characteristics open several possibilities from a mathematical perspective; for example, they allow designing optimal control strategies based on the description of separatrices along with an exhaustive description of the system (independence on parameters choice or "no need for cherry-picking parameters"). Analytical approaches of this kind to detect ecological thresholds and regime shifts have become a matter of urgency due to the rapid increase of human pressure on ecosystems (Andersen et al., 2009).

Predicting future community development has great value for conservation purposes. In SAR, the most limiting factor for plant growth is soil depth (Santibáñez-Andrade et al., 2009; Castellanos Vargas et al., 2017). Being a relatively recent lava field, soil shallowness translates into physiological water deficit (Álvarez et al., 1994; Meave et al., 1994). Through regulation of resource availability and environmental conditions, ecosystem engineers can modify species abundances and the overall interspecific interactions in the habitat (Jones et al., 1994; Suding and Hobbs, 2009; Gaertner et al., 2012). Mendoza Hernández (2002, 2003) and Mendoza-Hernández et al. (2013) concluded that *B. cordata* modifies the microenvironment in its close vicinity and facilitates the recruitment of old-growth community species by accumulating large amounts of soil organic matter, which increases soil fertility and creates safe sites for seed accumulation and germination for other species, offering a larger rooting soil volume and better soil retention.

Our modelling revealed that the native species can develop a more stable coexistence only if facilitation occurs in the community, especially if the dominant element has positive effects on a group of plants that will form part of the ensemble characterizing the new basin of attraction. Likewise, new microhabitats will be created for the successful establishment of typical old-growth community species. Our modelling also suggests that by promoting coexistence, facilitation may also increase community resistance to invasive species compared to relationships based on competition only.

The ecological notion of a world dominated by competition has been ingrained in ecologists since Darwin's times (Bruno et al., 2003). Therefore, the most widespread mathematical models in ecology have attempted to explain community structuring and dynamics based on competition and predation (Clements, 1916; Lotka, 1925; Volterra, 1928; Gause, 1932; Hutchinson, 1961; May and Leonard, 1975; Whittaker and Levin, 1977; Mohd, 2019). Though not necessarily incorrect, this is certainly incomplete (Bruno et al., 2003). Therefore, in model II-B we were interested in incorporating both the positive and negative interactions occurring in nature. Positive interactions are extremely diverse and have been documented in all ecosystems of Earth (Bruno et al., 2003). Although facilitation appears to be more frequent than normally accepted, its role in community structuring has been largely neglected because it is difficult to detect (Lin et al., 2012). We believe that by including positive and negative interactions, model II-B is the most realistic one and has a greater potential to capture and simplify the system's complexity.

Although many coexistence models do not consider facilitation as a structuring interaction of community dynamics, we found that in SAR a fundamental mechanism to explain its high biodiversity is present. Facilitation intensity can vary depending on plants' life stages and environmental changes (Callaway, 1995). In analysing two-species models, Vandermeer (1973) found only two monospecific stable points in some cases, but in another case he found their coexistence with a competitive equilibrium and in yet one further case he found locally stable mutualism. These results depend on the construction of the model and the type of interaction between the species being analysed. Recognizing that both competition and facilitation operate in dynamic environments can help us re-evaluate the importance of cooperation in maintaining the resilience of natural systems and, therefore, of social systems. Ecological theory must incorporate all the research and experimentation that recognizes facilitation as a fundamental driver of ecosystem dynamics by influencing spatial patterns, allowing coexistence and high biodiversity, ultimately driving future community dynamics (Callaway, 1995; Bruno et al., 2003).

In both the 2-native species and 3-species models, we found that coexistence is more likely when a facilitative interaction occurs between the native species. The observed positive interaction between *B. cordata* and *P. praecox* could also be true for many other species occurring in SAR. If facilitation and coexistence modify the structural and functional thresholds changing the basins, then their study becomes imperative in order to thoroughly understand ecosystem dynamics. Our study invites to conducting field experiments aimed at determining whether facilitative interactions occur and how they affect threshold dynamics.

Although our models allowed us to calculate structural properties of the ecological communities giving rise to threshold behaviours, performing experiments is necessary to validate the model predictions (Briske et al., 2005). For example, confirmation that the increase and stabilization of *B. cordata* are modifying ecosystem dynamics can be achieved through experiments to determine the effect of shade, soil and nutrient accumulation, and changes in soils humidity in *B. cordata*'s neighbourhoods (Callaway, 1995), to examine whether this is creating a facilitative effect of some species of the SAR. Experiments comparing species composition and abundance both in the seed bank and in the soil microbiome would be also welcomed (Callaway, 1995; Gaertner et al., 2014) between sites with high and low *B. cordata* density, and with Eucalypts.

Evaluating coexistence and facilitation-derived resistance to biological invasions or pathogen attacks would be also very important. Our model that incorporates *E. camaldulensis* as an invasive species, predicts that, based on its interactions with the dominant components of the community, it has the potential to become dominant, displacing the

native species. Our model, which is an abstract representation of the interactions between native and invasive species, can be generalized through its qualitative or quantitative adjustment, i.e., fine-tuning the regulatory loops between native and invasive species, and adjusting the parameters accordingly. One of them is the African grass *Cenchrus clandestinus*, which in 2009 covered 66 of the 237 ha representing the current area of the reserve (Acosta-Arreola, 2015). Incorporating other invasive species and their interactions into the model would require a thorough literature review to identify the existence and prevalence of three common effects of invasive exotic species when they become established in a community (Gaertner et al., 2012): (1) reduced species richness; (2) changes in seed bank composition, and (3) the modification of interaction networks, mostly seen as decreasing interactions with pollinators or reducing the availability of beneficial soil microorganisms.

Invasive species capable of inducing regime shifts and suppressing native species should be given priority in designing management interventions (Gaertner et al., 2014). Based on our model, it became apparent that implementing a *E. camaldulensis* removal plan for the SAR and the entire UNAM campus is of utmost importance. Once the structural and functional thresholds of a system have been crossed, multiple barriers to restoration emerge, making this process very difficult, if not impossible (Gaertner et al., 2012, 2014). However, it must be noted that removing adult Eucalypt trees may be insufficient; it would also be necessary to ensure that the soil around the removed Eucalypts its favourable for the colonization of *B. cordata*. A similar problem was detected by Wearne and Morgan (2006) in an Australian subalpine community; by modelling this community's dynamics, these researchers revealed the key role of the soil seed bank for the transit of this community toward an alternative state dominated by the invasive species. Future studies should examine the condition of the soil and the seed bank in assessing the success of a control programme of *E. camaldulensis* in SAR.

Firn et al. (2010) proposed a novel strategy to control an invasive grass species through the application of a fertilizer to increase its palatability; as a result of increased consumption of the invasive species by herbivores, native species can outgrow it, thus preventing a shift toward an alternative stable state. It is unlikely, however, that such an approach would be operational in the case of the Eucalypts in SAR because of its lack of natural enemies in this system. This shows the difficulty to generalize control strategies for different biological groups in different ecological contexts and contrasting historical trajectories. The fact that invasive plants are also susceptible to negative effects from other species must not be overlooked. An important factor absent from our model due to lack of information on its role in the SAR is the psyllid *Glycaspis brimblecombei*. This insect of Australian origin, a specific parasite of *Eucalyptus* species, is now present in Mexico City, and there are reports of its strong effects on Eucalypt trees in other protected areas beyond SAR (GODF, 2006). This species could have a regulatory role, potentially curbing the increasing *E. camaldulensis* trajectory projected by our modelling.

All this modelling and the identification of non-linear effects of ecological interactions aims at generating knowledge that is applicable to management plans of nature protection areas. Idealizing ecosystem as they used to be in the past can result in biased decision-making, whereas explaining ecosystem dynamics without complete knowledge can produce unrealistic scenarios (Suding and Hobbs, 2009) and promote inefficient or inadequate decision-making, hindering management plans for the reserve (Bruno et al., 2003). Better and more complete knowledge on a system will lead to a deeper understanding and the possibility to interpret empirical data in a mechanistic way, ultimately leading to more robust predictions (Schuwirth et al., 2019). The potential of invasive species to deeply transform native community structure underscores the importance of carefully planning management and restoration strategies based on alternative stable states theory and a deep understanding of the focal ecosystem and its history (Faist and Beals,

2017).

Within this framework, incorporating tools available from dynamic ecological systems for ecosystem conservation and management becomes highly relevant. Keeping resilience as a central concept in management plans does not require great precision in predicting the future, but it needs a description of the qualitative capacity of the system to absorb and respond to future events, no matter how unexpected they might be (Holling, 1973). Due to the increasing speed of environmental changes at present, decision makers cannot afford to perform rigorous tests to determine thresholds, so many models have been used in a heuristic fashion (Suding and Hobbs, 2009). Often, the impact of a regime shift derived from a feedback loop involving an invasive species is identified only when it is extremely difficult to manage or reverse it (Gaertner et al., 2014). In this regard, our ODEs-based modelling predicted trajectories that underscore the urgency of implementing a Eucalypt control programme before it is too late. These models differ from other models previously used to examine alternative states focused on invasive species in that they were based on statistical analysis and similarity indices only (Robinson and Edgemon, 1988; Wearne and Morgan, 2006; Firn et al., 2010; Faist and Beals, 2017). An important exception is the study of Hansen et al. (2013), who made predictions similar to ours for the behaviour of an invasive species in an aquatic system based on time-series modelling that are useful for designing a management program for this species; unlike our modelling, however, their model is parameter-dependant. A balance is needed between the knowledge that may be gained from modelling, on the one hand, and model accuracy on the other, while being realistic for effective decision-making in a context of accelerated environmental change. Every model used for this purpose must be contrasted with the results of their implementation in the management plan, so that it can be adjusted, modified or discarded to build new ones.

It is crucially important that our predictions and recommendations are heeded by SAR managers to control the *E. camaldulensis* population most efficiently, even under the high uncertainty of our predictions. Along with the theoretical developments, ecologists should strive to contribute qualitative ecological evidence on thresholds if we will ever be capable of effectively influencing environmental policies in the future (Andersen et al., 2009). Critical examination of these models and their constant adjustment is fundamental. In our models, the main limitation is the lack of a measure of quantifiable uncertainty of the data (Schuwirth et al., 2019). Despite this limitation, we envision several options to fill this gap.

To calibrate and validate our model, it would be necessary to make it spatially explicit by using remote sensing imagery. We have retrieved eight aerial photographs from 1943 to 1986, and 64 satellite images (Spot 5, 6 and 7) from 1992 to 2019. Increasing the spatio-temporal scale of the input variables would result in improved model robustness and increased prediction accuracy, allowing the incorporation of error measures (Schuwirth et al., 2019). Proper identification of a regime shift requires at least 100 time steps (Andersen et al., 2009); however, usually time series comprise between 20 and 40 steps at the most. Using remote sensing imagery would result in 72 time steps, which we deem sufficient to ascertain whether *B. cordata* dominance became stable already. Incorporating the spatial scale into the models would guide the design of experiments to help calibrate the parameters, interpret the model more adequately, and make better decisions (Suding and Hobbs, 2009; Lin et al., 2012). The expansion mode of Eucalypt is the so called "advance-front" (Segura-Burciaga, 1995); having been sown at the borders of areas that became part of the ecological reserve years later, modelling the expansion dynamics across space of Eucalypt is crucial.

5. Conclusions

By integrating complex and heterogeneous information for a protected plant community in a nature protection area, our modelling approach allowed us to identify potential future scenarios for this

community and its dynamics. Worryingly, one of these scenarios is potentially catastrophic, as it entails absolute dominance of the invasive Eucalypt and the total loss of the two native species. The only possibility to prevent this scenario from becoming true is the application of a Eucalypt management programme that efficiently checks its population growth through tree felling. In addition, the models led us to conclude that any possibility of coexistence between the two native species would require facilitation between them; without this positive interaction, *B. cordata* would eventually outcompete *P. praecox*. These conclusions open a range of possibilities for new research to seek for new management guidelines for this and other reserves and for other human-influenced and managed ecosystems.

Mechanistic mathematical modelling is a powerful tool for a variety of purposes, ranging from the reconstruction of past trajectories of ecological communities to the prediction of the effects of biotic invasions and of future community development stages, both in the presence or absence of disturbances. Also, it may provide valuable support to decision-making through *in silico* experiments to examine alternative ecosystem interventions. Finally, but not less importantly, all this may be achieved by integrating heterogeneous and scattered datasets describing individual ecological processes.

CRediT authorship contribution statement

Jaime Acosta-Arreola: Conceptualization, Data curation, Methodology, Writing – original draft, Writing – review & editing. **Elisa Domínguez-Hüttinger:** Conceptualization, Methodology, Formal analysis, Visualization, Writing – review & editing. **Pablo Aguirre:** Methodology, Visualization, Writing – review & editing. **Nicolás González:** Methodology, Formal analysis. **Jorge A. Meave:** Conceptualization, Supervision, Writing – review & editing.

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.

Data availability

The code is available at https://github.com/ElisaDominguezHuettinger/REPSA_Model

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2023.110449.

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