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RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Autogenic regulation and resilience in tropical dry forest

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Abstract

1. Engineering resilience, a forest's ability to maintain its properties in the event of disturbance, comprises two components: resistance and recovery. In human-dominated landscapes, forest resilience depends mostly on recovery. Forest recovery largely depends on autogenic regulation, which entails a negative feedback loop between rates of change in forest state variables and state variables themselves. Hence community dynamics change in response to deviations from forest equilibrium state. Based on the premise that autogenic regulation is a key aspect of the recovery process, here we tested the hypothesis that combined old-growth forest (OGF) and secondary forest (SF) dynamics should show autogenic regulation in state variables, and thus convergence towards OGF-based reference points, indicating forest resilience.
2. We integrated dynamic data for OGF (11-year monitoring) and SF (16-year monitoring) to analyse three key state variables (basal area, tree density and species richness), their annual rates of change and their underlying demographic processes (recruitment, growth and mortality). We examined autogenic regulation through generalized linear mixed-effects models (GLMMs) to quantify functional relationships between rates of change of state variables (and underlying demographic processes) and their respective state variables.
3. State variables in OGF decreased moderately over time, against our prediction of OGF constancy. In turn, the three state variables analysed showed negative relationships with their respective rates of change, which allows the return of SF to OGF values after disturbance. In all cases, recruitment decreased with increasing values in state variables, while mortality increased.
4. The observed negative relationships between state variables, their rates of change and their underlying demographic processes support our hypothesis of integrated OGF and SF dynamics showing autogenic regulation for state variables. Competition seems to be a major driver of autogenic regulation given its dependence on a resource availability that declines as forest structure develops.
5. *Synthesis*. Based on a straightforward and comprehensive approach to quantify the extent to which tropical forest dynamics is self-regulated, this study highlights the importance of autogenic regulation for tropical dry forest as a basic

component of its resilience. This approach is potentially valuable for a generalized assessment of engineering resilience of forests world-wide.

KEYWORDS
autogenic regulation, community dynamics, constancy, demographic processes, forest dynamics, recovery, stability, state variables

1 | INTRODUCTION

Anthropogenic pressures acting on tropical forests are increasing world-wide (Hansen et al., 2013). Forest exploitation for timber and the expansion of land devoted to food production (Pendrill et al., 2019), currently operating mostly on industrial scales (Austin et al., 2017), represent serious threats to their existence. Hence, evaluating the ability of forests to persist and maintain their properties in the event of disturbance has become critical. This ability, known as resilience (Holling, 1973, 1996; Ingrisch & Bahn, 2018; Willis et al., 2018), is fundamental for the long-term maintenance of forest attributes, including standing biomass and biodiversity.

Engineering resilience, which concerns systems that only have a single basin of attraction (the set of system states that share a single equilibrium; Walker et al., 2004), encompasses two major components: (a) resistance to disturbance, which is the capacity of a system to minimize state modifications in the face of a disturbance, and (b) recovery from disturbance, which is the capacity of a system to return to its pre-disturbance state (Holling, 1973, 1996; Ingrisch & Bahn, 2018; Lloret et al., 2011; Peterson et al., 1998). The interplay between these two components of resilience determines how successful a system will be in retaining its state properties over time (Figure 1A; Ives & Carpenter, 2007; Peterson et al., 1998; Pimm, 1984). However, in the context of human-driven land-use change, forest resistance to disturbance loses importance: humans have developed tools and techniques that allow us to thoroughly remove vegetation no matter how resistant it is. For this reason, the resilience of human-disturbed forests fundamentally depends on its recovery component, making its understanding urgent.

Measuring the recovery component of engineering resilience in ecological systems is challenging because forest state is difficult to quantify directly. Quantification of recovery requires the use of several state variables that define the state of an ecological system at any given moment (Beisner et al., 2003; Ingrisch & Bahn, 2018; Müller et al., 2016; Walker et al., 2004). In forest ecosystems, commonly analysed state variables such as basal area, tree density and species richness (Nikinmaa et al., 2020) are the outcome of basic ecological processes occurring in the plant community (Chazdon, 2003; Norden et al., 2015). Basal area is an easily measurable variable that is closely related to biomass and thus to ecosystem productivity (Chave et al., 2014). Tree density is an essential demographic variable that can be used to estimate tree crowding and, thus, potential intra- and interspecific competition (Westoby, 1984). Species richness reflects the variety of ecological strategies of a certain forest community, as the requirements for resource and environmental conditions are different for individual species, which then influence the ecological performance of the plant community as a whole (Peterson et al., 1998).

Changes in forest state variables, and thus their recovery after disturbance, are driven by underlying demographic processes such as recruitment, growth and mortality (e.g. Lewis, Phillips, et al., 2004; Rozendaal et al., 2017; van der Sande et al., 2017). These processes are antagonistic given their opposite effects on state variables; for instance, tree growth and recruitment increase forest basal area, whereas tree death reduces it (van der Sande et al., 2017). In relatively constant communities such as old-growth forests (OGFs), the effects of antagonistic processes on state variables are balanced (Chambers et al., 2013). By contrast, in non-stable forest communities (Grimm & Wissel, 1997; Müller et al., 2016), such as secondary forests (SFs) recovering from disturbance, such a balance is absent. In SFs, increases in state variables outweigh the losses, which results in a positive net change (e.g. Poorter et al., 2016; Rozendaal et al., 2019). Similarly, under some circumstances, forest state variables may exceed reference (equilibrium) values; for example, demographic inertia results when populations in successional communities grow beyond OGF values due to time-lags in the action of regulating mechanisms (Koons et al., 2007). In these cases, antagonistic processes with negative effects outdo those with positive effects until balance is reached.

Depending on whether state variables are above, below or at their reference value, changes resulting from the imbalance of the underlying antagonistic processes will result in gains, losses or no change (constancy) in state variables (Lewis, Malhi, et al., 2004; Lewis, Phillips, et al., 2004; Rozendaal & Chazdon, 2015; van der Sande et al., 2017). Such autogenic regulation should be apparent when the magnitude and direction of changes in community state variables are functions of the same state variables. Recovery, and thereby resilience, thus largely arises from autogenic regulation of the state variables in the community; autogenic regulation of forest state variables contributes to the recovery component of resilience through the continuous adjustment of forest dynamics in response to deviations from equilibrium. Derived from this reasoning, the premise of this study is that autogenic regulation is a key and distinctive aspect of the recovery process. This premise is fundamental to forest recovery through secondary succession but also for OGF, which also undergoes deviations from reference values.

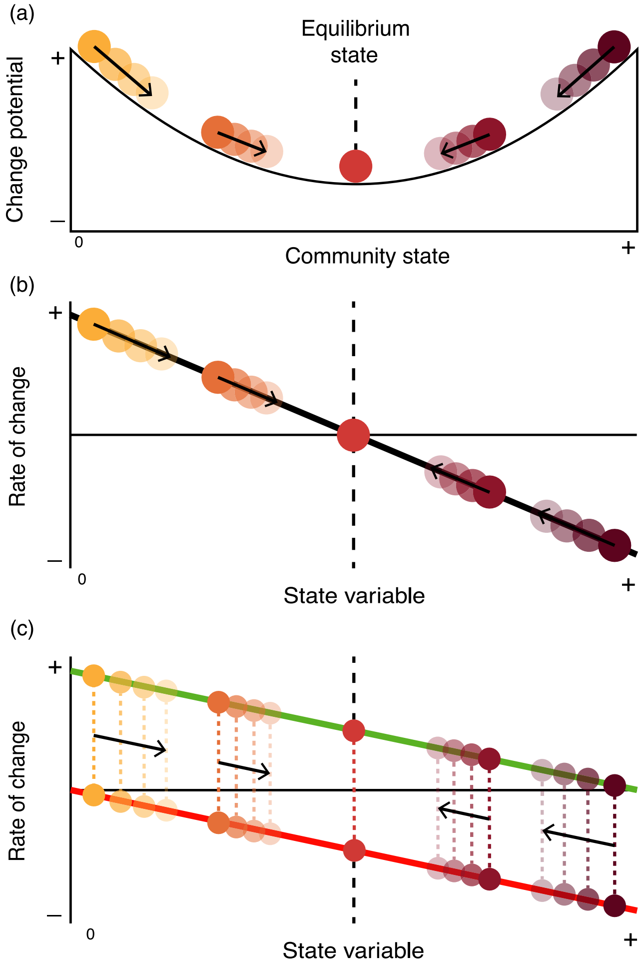

FIGURE 1 Conceptual overview of resilience in ecological systems. In all three panels, each circle/colour represents a different state of the same hypothetical community, while the arrows denote the dynamics of the community. (A) The concept of resilience, here represented with a ball-in-cup diagram, is a theoretical construct that is not amenable to direct evaluation in real ecosystems; neither the overall state of the community nor the potential of change is directly measurable. Thus, proxies for these theoretical variables are required. (B) We propose that resilience may be evaluated by substituting the overall state of the community by one or several state variables (*x*-axis), while the potential of change could be replaced by the rate of change in a state variable (*y*-axis). We hypothesize that resilient systems show an overall negative relationship between state variables and their rates of change. (C) The rate of change of a given state variable results from the balance between antagonistic demographic processes. All changes in forest state variables are referred to as losses or gains, regardless of the underlying antagonistic processes. For example, mortality fluctuates from zero to large negative values, whereas recruitment fluctuates from high positive values to zero as the state variable values increase. Therefore, each community state has two different values, each corresponding to either gains (green line) or losses (red line). Below equilibrium, the net result should be positive, while above equilibrium it should be negative to allow for forest resilience. At equilibrium, positive and negative processes are offset, which results in no change of the state variable. In all panels, the dashed vertical line denotes the equilibrium state of the community

The autogenic regulation of forest dynamics is fundamental for recovery in the context of engineering resilience, and together with the impact of external forces will result in the magnitude of changes in the state of the forest. Autogenic regulation implies a negative feedback loop between rates of change of forest state variables and the values of the state variables themselves, conforming to an overall negative relationship. Below-equilibrium values in a state variable lead to positive rates of change, equilibrium-state values lead to no change and above-equilibrium values lead to negative rates of change in the state variable (Figure 1B). These negative relationships between rates of change and state variables emerge because of the underlying negative relationships between recruitment, growth and mortality with state variables. It must be noted that the negative relationships between antagonistic processes and state variables hold regardless of the sign of these antagonistic processes (Figure 1C).

A pervasive methodological limitation in the study of forest recovery is that the focus is generally restricted to either SF or OGF. This is regrettable: SF and OGF are alternative states of a forest continuum having a single basin of attraction; hence, the two of them are needed to examine the dynamics of the system over a broad range of forest states. Forests as a whole, regardless of successional status, are basically ruled by the same autogenic and allogenic forces. Therefore, the stability landscape of a forest (sensu Beisner et al., 2003) can be described by jointly monitoring the dynamics of SF and OGF within a same basin of attraction (Figure 1A). However, quantifying the state of a forest and its potential for change is not straightforward in real life since these two concepts are theoretical constructs. To this end, state variables (as those discussed previously) can be used as proxies for the state of the forest, and the changes observed in them as proxies for the potential change of the forest.

In this study, we integrated information gathered in both SF and OGF plots to examine community-level autogenic regulation in the basal area, tree density and species richness of a Neotropical dry forest. To this end, we analysed the relationship between forest state variables, their rates of change and their underlying demographic drivers based on multiannual dynamics of SF and OGF plots in a tropical dry forest in southern Mexico. We hypothesized that the integration of OGF and SF dynamic information should show autogenic regulation in forest state variables, and thus convergence towards OGF-based reference points, indicating forests in this study are resilient. Based on this hypothesis, we predicted that the state variables of OGF are constant over time due to the balanced effects of underlying antagonistic processes, while the forest state variables in SF change towards OGF equilibrium values due to an imbalance of their effects. To our knowledge, this is the first study to quantify autogenic regulation for tropical dry forests from a demographic perspective. It examines key community attributes separately to enable comparisons of the strength of autogenic regulation among them. Despite important efforts to assess tropical dry forest resilience (e.g. Poorter et al., 2016; Pulla et al., 2015), this seems to be the first study to fully integrate dynamic information for the SF–OGF ecological continuum from a non-successional perspective; the integrated analysis of OGF and SF illustrates the displacement of a single ecological system within its stability landscape.

2 | MATERIALS AND METHODS

2.1 | Study site and vegetation sampling

The study was conducted in Nizanda (16.66°N, 95.01°W), a small village in southern Mexico located in a region where the natural vegetation cover is mostly seasonally dry tropical forest (Pérez-García et al., 2010; Figure 2). Recent human colonization at this site occurred *c*. 110 years ago and shifting agriculture has been practised since. Hence, SFs representing a wide range of fallow ages are present, although well-preserved stands of OGFs still dominate the landscape (Gallardo-Cruz et al., 2012). Together, OGF and SF span a broad range of values in basal area, tree density and species density (Lebrija-Trejos et al., 2008).

We used a total of 24 plots in both SF and OGF (Figure 2C). Sixteen 400-m^2 SF plots and one OGF plot were set-up as permanent plots in 2003 (Lebrija-Trejos et al., 2008), while seven additional 500-m^2 OGF plots were established in 2008. All plots are located on siliciclastic phyllite-derived soils. OGF plots were selected based on their structural heterogeneity, maximum tree size, OGF-specific species composition and their conservation status (no evidence of logging or other obvious anthropogenic disturbances). The OGF forest in the region has not been exploited in its modern history and its structure, mostly because of the size of the largest trees, suggesting that it could be several centuries old. SF plots range in time since abandonment from 0 to 74 years. All SF plots have regrown after low-intensity, non-mechanized shifting agriculture; land-use history was determined by interviewing landowners and fallow ages were verified by using tree ring counts (Brienen et al., 2009). Plots were fenced to avoid further human or cattle disturbance and monitored annually until 2019.

Stems with a DBH ≥ 5 cm were tagged, identified to species, and measured annually. Stems from 1 to 2.5 cm DBH were monitored in 100- and 125-m^2 subplots in the SF and OGF plots respectively. Similarly, stems from 2.5 to 5 cm DBH were monitored in 200- and 375-m^2 subplots in the SF and OGF plots respectively (Figure S1).

We calculated basal area (m^2/ha), tree density (no. of stems/ha) and species richness (no. of species/plot) for each plot and census. Community-level basal area and tree density were estimated for each DBH category separately through the sums of individual values and expressed on a hectare basis. Species richness was standardized to 400 m^2 by randomly disregarding a 100-m^2 transect from the OGF plots (see legend of Figure S1).

To assess taxonomic representativeness of our plots, we constructed individual-based rarefaction curves for a standardized area (400 m^2) for all SF and OGF plots for the last year of data (2019). Then, we computed the estimated total number of species per plot based on abundance data to provide an estimate of detected species. The observed species detection level for SF and OGF plots was satisfactory and representative of their forest community. For SF plots, an estimated 66 ± 16% of species were detected, while for OGF plots the estimated detection was 69 ± 9% (Figure S2). These rarefaction analyses were conducted with the `R` package `vegan` (Oksanen et al., 2019; R Core Team, 2020).

2.2 | Data analysis

We performed the analysis in three stages (Figure 3). First, we assessed OGF forest constancy by examining whether state variables

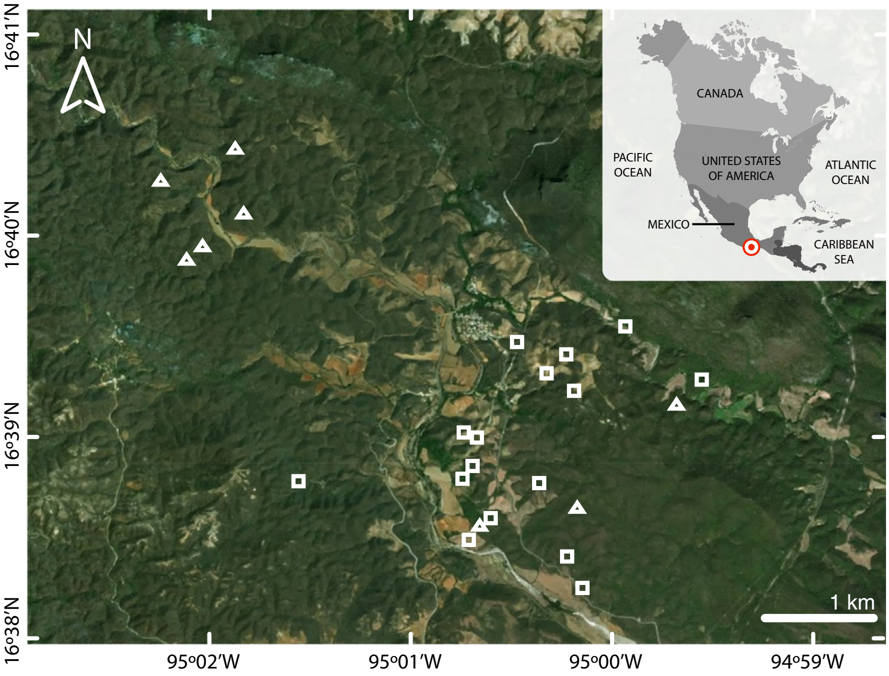

FIGURE 2 Location of study plots in the region of Nizanda. The study was conducted in southern Mexico (inset). The region is a mosaic of well-preserved tropical dry forest, agriculture, pasture and recovering forest with different times of abandonment. White triangles represent OGF permanent plots, and white squares represent SF permanent plots

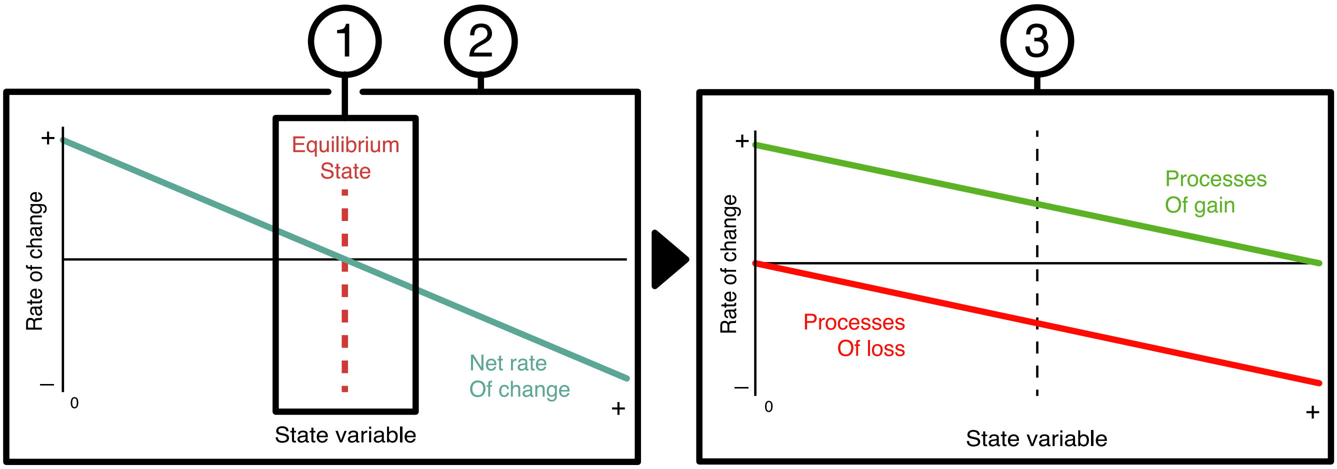

FIGURE 3 Data analysis strategy. (1) Assessment of OGF constancy and OGF reference values, including standard deviation. (2) Relationship between net rates of change and state variables. (3) Dissection of the rates of change into their underlying antagonistic processes and their relationship with state variables. Both panels depict a forest state variable in the horizontal axis and the net rate of change or the effect of an antagonistic process in the vertical axis (positive for recruitment and growth, and negative for mortality). In all cases, the three stages of the data analysis were repeated for each of the three state variables. The colour code matches the colours used to represent OGF reference values (orange), net rates of change (blue), demographic gain processes (green) and demographic loss processes (red)

of OGF plots showed directional changes. Next, we assessed autogenic regulation in forest state variables by examining whether state variables and their rates of change showed negative relations. Finally, we analysed the drivers of autogenic regulation by dissecting the rates of change of state variables into their underlying demographic processes (recruitment, growth and mortality) to determine whether they were negatively related to the state variable.

To assess OGF constancy, we modelled the state variables as a function of time using generalized linear mixed-effects models (GLMMs), with a random intercept for plot to account for between-plot potential differences in soil properties and topography. A slope significantly different from zero would indicate a directional change over time in OGF dynamics.

To evaluate autogenic regulation of state variables in SF and OGF, we modelled the annual rate of change of a state variable as a function of the state variable using GLMMs, with a random intercept for the plots nested within forest type (SF or OGF) and a random intercept for year. The inclusion of a random intercept for each plot nested within forest type enabled us to assess both plot-to-plot differences in the relationship and account for consistently different effects of SF and OGF due to potential legacy effects in SF. We examined whether the slope was lower than zero (i.e. negative relationship), which indicates state variable resilience.

We analysed the drivers of forest autogenic regulation and recovery by identifying those demographic processes leading to changes in state variables (recruitment, growth and mortality). We regressed the demographic processes on the state variable (e.g. basal area loss due to mortality on basal area) using GLMMs, again including a random intercept for plots nested within forest successional stage (SF vs. OGF) and a random intercept for year. We forced the intercept for mortality to zero as no loss is possible when the value of the state variable is zero. We looked for negative relations between demographic processes and state variables. Negative relations imply that demographic processes respond to the state of the forest, and therefore drive the net rates of change that allow autogenic regulation in state variables. Covariance between net rates of change and between the same demographic processes across state variables was not considered in these models.

The random-effects structure in all models was selected a priori based on our hypotheses and experimental design (Harrison et al., 2018). We fitted the models using either the `lmer` (basal area and density) or `glmer` (species richness) function of the `lme4` package (Bates et al., 2015) in `R` (R Core Team, 2020). Basal area and tree density were fitted using a Gaussian distribution, while a Poisson distribution was used for richness-related measures. In all cases, we estimated bootstrapped 95% confidence intervals for model coefficients.

3 | RESULTS

3.1 | Old-growth forest dynamics

Basal area and tree density showed directional, negative changes over time in the OGF plots (Figure 4). Although the change over time for species richness was not significant, it showed a negative trend as its mean coefficient value was slightly negative. The three state variables markedly increased in the period 2011–2013 and sharply declined in the period 2015–2017.

3.2 | Rate of change in state variables

The rates of change showed a negative relationship with the state variables for all three state variables analysed, suggesting resilient

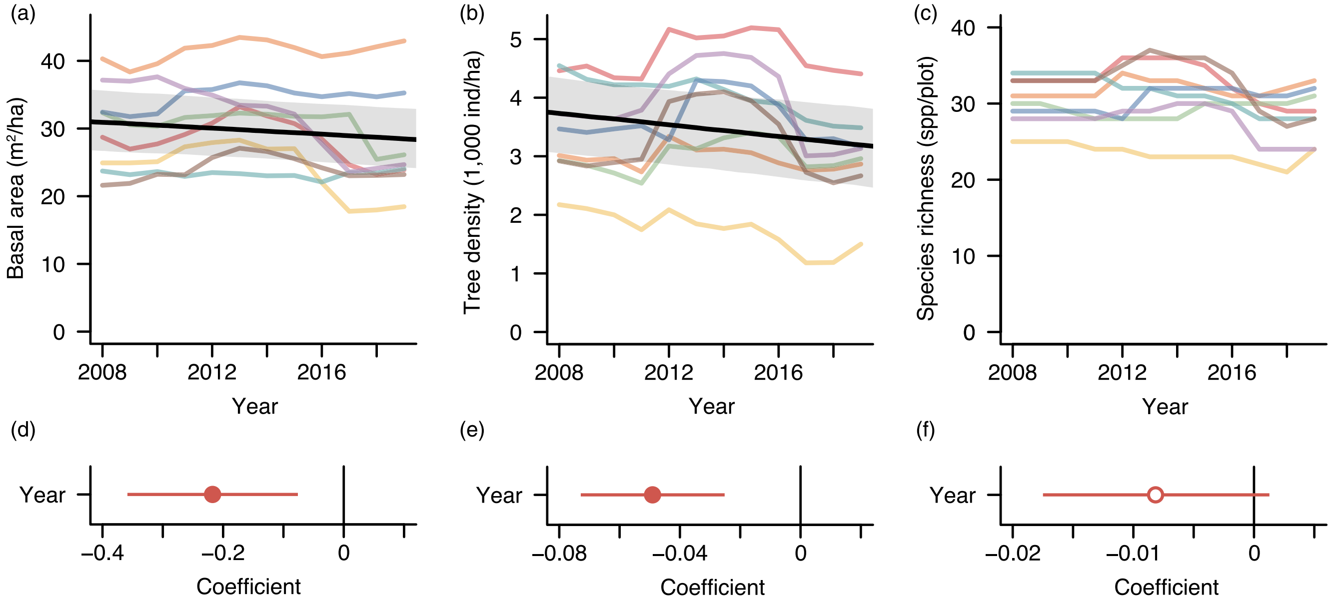

FIGURE 4 Dynamics of OGF state variables. (A–C) Basal area, tree density and species richness dynamics in OGF plots from 2008 to 2018. Coloured lines represent a different OGF plot; solid, black lines depict the linear models with significant slopes; shaded areas around the significant models represent 95% confidence intervals. (D–F) Bootstrapped 95% confidence intervals for the slopes (coefficients) of basal area, tree density and species richness as a function of census year. Slopes were estimated using linear mixed-effects models (LMMs)

behaviour (Figure 5A–C,K–M). The fitted models intersected the *x*-axis (i.e. predicted values reached zero) close to OGF average values for all three state variables, which implies that net rates of change approach zero as the forest approaches OGF values. Species richness was the state variable with the closest match between the OGF average and the point where the model intersected the *x*-axis. In contrast, the function for basal area crossed the *x*-axis at slightly lower values, while the function for tree density did so at slightly higher values than their respective OGF averages, but in all cases within their confidence intervals. These results were consistent with mean rates of change of state variables calculated for segments of the state variable range representing different stages of forest development (Figure S3).

3.3 | Relationship of demographic drivers with forest state

Demographic drivers of resilience showed different responses depending on the process and the state variable analysed (Figure 5D–M; Figure S4). For basal area, recruitment and mortality effects decreased and increased, respectively, with increasing values of the state variable, while growth did not show any response. For tree density and species richness, both recruitment and mortality responded clearly to changes in the state variable, decreasing and increasing with the state variable value respectively. In other words, all the relationships except for growth were negative, since losses due to mortality result in negative changes by definition.

4 | DISCUSSION

This study tested the hypothesis that dynamic information for tropical dry forest stands, in which no distinction is made between OGF and SF, should show autogenic regulation in forest state variables. Self-regulated forests should converge towards OGF-based reference points, implying forest resilience. Unexpectedly, OGF attributes were not overall constant, but decreased over time. However, as expected, we found negative relationships between state variables and their rate of change, suggesting that autogenic regulation drives the dynamics in forest attributes. We also found that demographic processes responded to changes in state variables but, interestingly, this was not the case for tree growth.

4.1 | Old-growth forest dynamics

Against our expectations, state variables in the OGF (basal area, species richness and density) showed mixed dynamic trends over time but all displayed decreasing trends over the sampling period, particularly towards its end. Equilibrium in natural systems occurs when the properties of a system show moderate variation over time (Ives & Carpenter, 2007; Jen, 2005; Naselli-Flores et al., 2003; Pimm, 1984). In our case, OGF dynamics showed a hump-shaped pattern that, overall, led to a significantly decreasing trend for basal area and tree density, and also a decreasing trend for species richness, although this was non-significant. Interestingly, this pattern was observed at most plots for the three state variables analysed. Such coordinated dynamics between plots is unlikely to be a stochastic event and thus suggests the

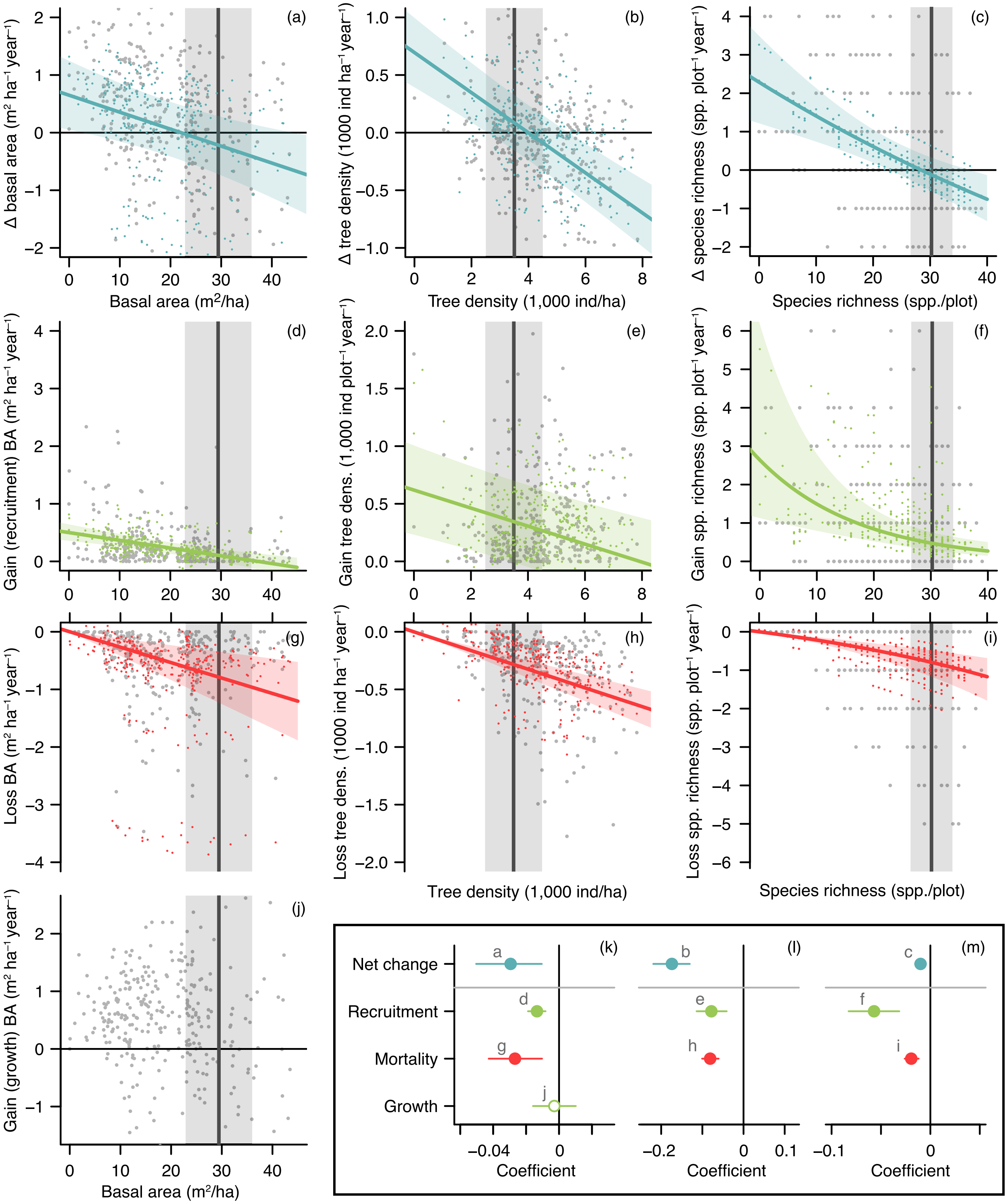

FIGURE 5 Relations between net rates of change, antagonistic demographic processes and state variables in a tropical dry forest. (A–C) Response of the net rates of change to the value of the community state variable. (D–J) Response of the antagonistic demographic processes involved in the changes of the state variables to the value of the state variable. (K–M) Coefficients with 95% confidence intervals for the slope of models shown in panels (A)–(J). Solid lines and their colour-shaded areas represent the fitted models, excluding random effects, with 95% confidence intervals; grey dots represent real plot-year observations; coloured dots indicate the model predictions including random effects; vertical grey lines and their shaded area show the OGF average value ±1 standard deviation for each state variable. Lowercase letters in panels (K)–(M) indicate the correspondence with panels (A)–(J). Overall, the relation between net rates of change and state variables was negative (A–C). Likewise, most demographic processes responded to changes in forest state variables (D–I), except for growth in basal area (J) and recruitment in tree density (E)

existence of a regional-scale factor driving the observed OGF changes. Considering that tropical dry forests are systems strongly limited by water (Murphy & Lugo, 1986), climatic variability is likely to be largely responsible for these changes. The steep increases and decreases observed in the state variables coincided with La Niña and El Niño events respectively. The 2011–2013 increase was coupled with La Niña event of 2010–2012, while the 2015–2017 decrease was coupled with the extreme El Niño event of 2015–2016 (Wigneron et al., 2020; Zhu et al., 2018). On the Pacific coastal region of Mexico, La Niña has been associated with above-average rainy years, while El Niño has been associated with droughts (Caso et al., 2007). Nonetheless, it is interesting that when the analysis focuses on the pre-El Niño years, the rates of change in the mature forest are zero for basal area and species richness, and slightly above zero for stem density (Figure S3).

A directional dynamics in OGF does not necessarily imply that the system's state variables are not constant over time. A short-term directional behaviour could be part of a long-term cyclic pattern with a zero-mean rate of change. Antagonistic demographic processes could act with similar intensities over time, albeit not simultaneously. From our results for OGF, we infer that antagonistic demographic processes are not offsetting immediately, as gains did not offset losses during the study period (Chambers et al., 2013; Lewis, Malhi, et al., 2004).

The directional dynamics observed for the OGF does not necessarily contradict our hypothesis. A possible interpretation for this result is that climate, an allogenic force, is occasionally capable of exerting a stronger influence than autogenic regulation in OGFs. OGFs are systems in relative equilibrium, where mean vegetation properties are largely driven by resource availability (Quesada et al., 2012; Seidl et al., 2012). As shown in the stability landscape depicted in Figure 1A, the potential for change in vegetation is negligible close to OGF values (i.e. the potential for change is lowest at or close to equilibrium). If true, this would imply that autogenic regulation (and, therefore, the potential for recovery) is also negligible at this point, allowing external forces to drive forest dynamics when the community approaches equilibrium. The topography at the bottom of the basin of attraction could determine how resistant the system is to allogenic forces once it achieves equilibrium. A flat and wide bottom could indicate a broad range of values defining the equilibrium of the system, wherein autogenic regulation may play a minor role in driving forest dynamics.

4.2 | Rates of change in state variables

As the system moves farther away from equilibrium, autogenic regulation gains importance. Autogenic regulation should be highest when the state variables are either at zero or very large values, assuming that landscape and soil conditions remain undisturbed. The support for this reasoning is twofold. First, it is consistent with our observation of weakly self-regulated OGF attributes. Second, integrating SF and OGF dynamic information revealed the negative relationship between state variables and their net rates of change (Figure S4A–C). SF plots encompassed the lowest values for basal area and species richness, and the lowest and the highest values for tree density (i.e. they are farther away from equilibrium than OGF; Figure S4). Therefore, one may reasonably expect some SF (particularly very young stands) to undergo stronger autogenic regulation than OGF because the former lie farther away from the equilibrium state compared to the latter. Nevertheless, OGF can undergo strong autogenic regulation if considerably pushed away from equilibrium, as happened for some of our plots after the El Niño event that started in 2015. Similarly, autogenic regulation in SF plots whose attributes are already similar to OGF is expected to be weaker.

The hypothesis of negative relationships between state variables and their rates of change in the studied dry forest was supported by our results (Figure 5A–C). Negative relationships imply that as the value of the state variable increases, the rates of change decrease, thereby resulting in a negative feedback loop. Under conditions of little vegetation development (low state variable values), as in early secondary succession, the rates of change will be positive until they reach their dynamic equilibrium state. Conversely, when the community exceeds the equilibrium state, forest state variables will decrease until they return to equilibrium. This result is consistent with previous findings on autogenic processes as relevant drivers of forest dynamics (Finegan et al., 2015; Lohbeck et al., 2015; Norden et al., 2015;van Breugel et al., 2006) and provides a mechanistic explanation for autogenic forest recovery.

Autogenic regulation is not equally strong for all state variables. Species richness showed the strongest autogenic regulation, as indicated by the relatively narrow confidence interval for the state variable–rate of change relationship (Figure 5C; Figure S3c), and the fact that it was the most constant state variable in OGF plots over time (Figure 4C). Basal area and stem density showed weaker autogenic regulation; these two variables exhibited a slightly directional OGF dynamics (Figure 4A,B), the broadest confidence intervals for OGF reference values (Figure 5B,C), and in the case of stem density, rates of change that were slightly above zero for plots close to OGF reference values (Figure S3b). This finding has important theoretical and practical implications. For the resilience theoretical framework, it points to the need of realizing the multidimensional nature of stability landscapes and hence the different shapes of basins of attraction depending on the state variable/dimension being analysed (Nikinmaa et al., 2020; Walker et al., 2004); from a practical perspective, it shows why the perceived speed of the recovery process may vary depending on the variables used in the assessment (Poorter et al., 2016; Rozendaal et al., 2019).

4.3 | Antagonistic demographic processes

Similar to our results for the net rates of change, most demographic processes showed clear relations with their state variables (Figure 5D–J). This result largely agrees with our proposed mechanism of forest resilience through antagonistic demographic processes. Forest demographics responded to the state of the system, either with increased and/or decreased recruitment, growth or mortality, depending on the value of the state variables.

We suspect that the observed autogenic regulation, which ultimately leads to forest recovery, is driven mostly by competition. Forest structure development has a direct impact on the spatial arrangement of plants and their biotic interactions, yielding in turn changes in forest resource availability and environmental conditions (Lebrija-Trejos et al., 2011; Matsuo et al., 2021; van der Sande et al., 2017). As vegetation develops, competition for space, light, water and nutrients increases (Uriarte et al., 2004). For any given tree, entering the community or increasing in size will be more difficult when the existing resources are shared with more and/or larger individuals (Rozendaal et al., 2020). In forests with higher tree density, species richness and biomass, increased resource consumption is likely to result in (stronger) resource limitation. Resource limitation has direct impacts on recruitment by reducing the reproductive investment of mature trees (Allen et al., 2017), and the probability of seedling establishment (Tripathi et al., 2016). Similarly, resource limitation affects the growth of established trees by reducing photosynthetic capacity and carbon fixation due to reduced water, light and/or nutrient availability (Quesada et al., 2012; van der Sande et al., 2017). Resource limitation increases tree mortality due to the reduction in photosynthetic uptake, which in turn could lead to a lower investment in defensive compounds against biotic agents (McDowell et al., 2008).

Unexpectedly, the analyses demonstrated that tree growth was not related to basal area. The lack of response in this variable is intriguing since some studies have suggested such a relationship (e.g. Rozendaal & Chazdon, 2015; van der Sande et al., 2017, but see Toledo et al., 2011). Growth in basal area might be mostly driven by external factors in our study site, such as climate. Actually, rainfall and its seasonal distribution are likely the main factors influencing this process in tropical dry forests (Allen et al., 2017). This is consistent with studies in other tropical forests, where not only growth but also mortality is largely driven by inter-annual changes in precipitation, particularly by severe droughts (Aleixo et al., 2019; Saenz-Pedroza et al., 2020; Toledo et al., 2011). Moreover, growth is affected by other environmental factors such as temperature or solar radiation, which change continuously (high intra- and inter-annual variability) but are unrelated to autogenic regulation (Lewis, Malhi, et al., 2004).

4.4 | Considerations for the assessment of autogenic recovery

The variability observed in the relationships between the three state variables and their rates of change/underlying demographic processes may arise from the existence of slightly different basins of attraction for each plot (Vandermeer et al., 2004). Even though our plots were carefully selected to be as similar as possible, as this is a requirement for establishing chronosequences (Johnson & Miyanishi, 2008; Mora et al., 2015), subtle inter-plot differences in soil attributes, topography, land-use history or landscape context can shift the location of the bottom of the basin of attraction (representing the equilibrium state) as well as its shape (representing the relationship between forest state and potential of change; Figure 1A). The inclusion of random effects in our mixed-effects models helped account for this fact, as in this way we were able to deal with differences in equilibrium states. Nonetheless, a key requirement of the approach in this study is that all plots should share a similar basin of attraction, as otherwise the interpretation of the overall trends shown by the models could be misleading. Highly heterogeneous environmental conditions could result in differences in the potential of vegetation development among stands (e.g. Durán et al., 2006). Similarly, high landscape degradation and the associated seed-dispersal limitation could result in divergent species assemblages among stands, and thus also to different recovery pathways (Arroyo-Rodríguez et al., 2017). Therefore, it is essential to consider biotic and abiotic differences between sampling units when studying the recovery component of resilience, as they have an impact on the shape of the forest's basin of attraction.

The relatively uniform environmental conditions and the minimal impact of agriculture in our study region are ideal to test our hypothesis because this makes our forest unlikely to have multiple equilibrium states. The region has a low level of landscape fragmentation (Calzada et al., 2018; Gallardo et al., 2018) and a high degree of naturalness (sensu Machado, 2004) compared to other tropical dry forests disrupted by agricultural practices. In SF plots, low-intensity (maximum of two harvesting cycles and no heavy machinery; Lebrija-Trejos et al., 2008), traditional slash-and-burn agriculture was practiced prior to abandonment. In addition, soil properties are relatively similar across SF and OGF plots. The landscape context with a high connectivity of SF and OGF patches makes dispersal limitation unlikely at distances under 2.5 km (Gallardo Cruz et al., 2010). These landscape conditions result from both a complex topography and the regional social context, characterized by a traditional indigenous community that has not yet fully embraced modern agricultural practices (Calzada et al., 2018).

Similar conditions may define many other areas in the tropics. However, landscapes with a very low degree of naturalness, a poor conservation state (e.g. regions with flat topography, higher population density, higher income, lower cultural attachment and/or more intense land-use) or with the presence of potentially hyper-dominant species may result in not one but several equilibrium forest states. Arrested forests, often reported in successional studies, represent systems having at least two alternative stables states: an OGF state and an arrested successional state. For instance, Mesquita et al. (2015) and Neto et al. (2019) reported strikingly different successional pathways in the central Amazon after abandonment of fields with clear-cut or pasture use, for both of which OGF was the original vegetation. Pastures were subjected to an intensive fire regime and soil compaction, changing soil properties and modifying seed and resprout banks at these sites. Land-use legacy in abandoned pastures led to hyper-dominance by plants of the *Vismia* genus, slowing down or arresting the recovery towards OGF reference values. Although arrested succession represents a system's new alternative stable state in which autogenic regulation may also operate, the relationships between state variables and demographic processes could be modified, having parameters leading to the arrested successional stable state rather than to the OGF state. As our approach is based on the engineering resilience framework, and therefore deals with systems with a single stable state in their stability landscape, it would not be possible to replicate our results in systems encompassing multiple stable equilibrium states.

A further consideration in assessing forest recovery is the selection of state variables to be analysed. In this study, we used basal area, tree density and species richness as state variables defining key forest attributes (Chazdon, 2003; Norden et al., 2015). Strictly, the conclusions from this study are valid regarding these state variables only, and the ecological processes they represent. Nonetheless, the negative feedback loops described by our recovery hypothesis are a necessary theoretical requirement for engineering resilience to be achieved, as otherwise recovery from disturbance would be dependent on contingency rather than being the result of autogenic regulation of forest dynamics. Therefore, we expect other forest attributes to resemble the patterns observed for the state variables analysed in this study.

5 | CONCLUSIONS

The validation of our hypothesis in other biomes and landscape contexts (Arroyo-Rodríguez et al., 2017) is required before attempting to make broader generalizations. Nonetheless, our approach provides a simple and comprehensive way to quantify the extent to which forest dynamics are driven by autogenic factors. Certainly, a deeper and integrated study of autogenic and allogenic factors (in particular, climate variability) is needed to gain further insights into forest resilience mechanisms, and ultimately to predict the short- and mid-term dynamics of OGFs and SFs around the globe.

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CONFLICT OF INTEREST

None of the authors have any conflict of interest to disclose.

AUTHORS' CONTRIBUTIONS

R.M. and J.A.M. developed the idea, led the writing of the manuscript and performed fieldwork; R.M. performed data analysis; D.M.A.R. and E.J.G. contributed to data analysis; F.B. and J.M.D. contributed to writing the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.s1rn8pk85 (Muñoz et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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