

'Tales of *Symphonia*': extinction dynamics in response to past climate change in Madagascar rainforests

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Madagascar's rainforests are among the most biodiverse in the world. Understanding the population dynamics of important species within these forests in response to past climatic variability provides valuable insight into current and future species composition. Here, we use a population-level approach to analyse palaeoecological records over the last 5300 years to understand how populations of *Symphonia* cf. *verrucosa* became locally extinct in some rainforest fragments along the southeast coast of Madagascar in response to rapid climate change, yet persisted in others. Our results indicate that regional (climate) variability contributed to synchronous decline of *S. cf. verrucosa* populations in these forests. Superimposed on regional fluctuations were local processes that could have contributed or mitigated extinction. Specifically, in the forest with low soil nutrients, population model predictions indicated that there was coexistence between *S. cf. verrucosa* and *Erica* spp., but in the nutrient-rich forest, interspecific effects between *Symphonia* and *Erica* spp. may have pushed *Symphonia* to extinction at the peak of climatic change. We also demonstrate that *Symphonia* is a good indicator of a threshold event, exhibiting erratic fluctuations prior to and long after the critical climatic point has passed.

Keywords: palaeoecology; competition; global change; population model; soil; threshold

1. INTRODUCTION

The impacts of climate change, coupled with land-use changes, will place increasing pressure on ecosystems and the services they provide, making it urgent that conservationists create the necessary conditions for species to migrate and for ecosystems to adapt (Hannah *et al.* 2002). There has been great emphasis on how species will migrate in response to global change, but less work has been undertaken to examine *in situ* ecological communities. Processes that need to

be considered for *in situ* communities include disassembly (local extinction) and reassembly in new ways (e.g. displacement of reptiles and amphibians along a montane gradient in Madagascar—Raxworthy *et al.* 2008).

In this study, we focus on the extinction of *Symphonia* cf. *verrucosa* (Clusiaceae), a Madagascar endemic tree of evergreen forest, in response to past climatic change in the littoral forest—an ecosystem identified as a top priority for conservation (Goodman & Benstead 2003). *Symphonia* is an important genus in Madagascar as many of its species produce nectar and fruits that are consumed by bats, birds and lemurs (Goodman & Benstead 2003). Evidence from palaeoecological studies from two fragments has indicated that whereas a dominant population of *S. cf. verrucosa* (the only species within this genus in the southern littoral forest (Missouri Botanical Garden 2009a)) became locally extinct 1000 years ago from one fragment (Mandena M15, 230 ha), another population in a different fragment (Saint Luce S9, 377 ha) persisted, despite population fluctuations in both sites over the same time-frame (Virah-Sawmy *et al.* 2009, *in press*; figure 1). Concordant with the palaeoecological data, contemporary botanical surveys have indicated that *Symphonia* is absent in Mandena (and Petriky) forests, but *S. cf. verrucosa* exists in Saint Luce forests on water-logged soils (Missouri Botanical Garden 2009b). Thus, both the fossil and modern records point towards evidence that *S. cf. verrucosa* has not dispersed and/or colonized Mandena from Saint Luce or other regions since its extinction 1000 years ago.

The climatic events that affected *Symphonia* in south-east Madagascar are periodic marine inundations from high sea levels between 2300 and 800 cal. yr BP. Further, the last inundation at 950 cal. yr BP accompanied a pronounced drought in Madagascar (Virah-Sawmy *et al.* 2009, *in press*). These climatic events would have exerted similar forces on the two fragments, as they are located within 4 km from the coast and are less than 50 km distance apart. Further, there is no evidence for human impacts at the two sites over this time frame. Vegetation reconstruction has indicated that *S. cf. verrucosa* persisted in the more coastal and nutrient-poor fragment where nitrogen-fixing *Myrica spathulata* (the only species within this genus in the southeast) was abundant, but became extinct in the nutrient-rich forest, which had moderate levels of *M. spathulata* and *Erica* spp. in the fossil assemblage (figure 1).

We therefore, in this study, use population models, to test whether extinction or persistence of *Symphonia* was modulated by competition with *Erica* spp. or facilitated by *Myrica*, given that species of *Erica* form the dominant vegetation bordering the forest fragments and that *Myrica* facilitates plant growth by adding nitrogen to the soil. We fitted four population models and compared them between the two sites (table 1). The first model is a competition model (*Symphonia*–*Erica* spp.), the second one is a facilitation model (*Symphonia*–*Myrica*) and the third one incorporates both competition (*Symphonia*–*Erica* spp.) and facilitation (*Symphonia*–*Myrica*). The final one is a null model in which neither competition nor facilitation exerts any influences. Although it is apparent from the fossil records that climatic changes have influenced *Symphonia* populations, here we focus on

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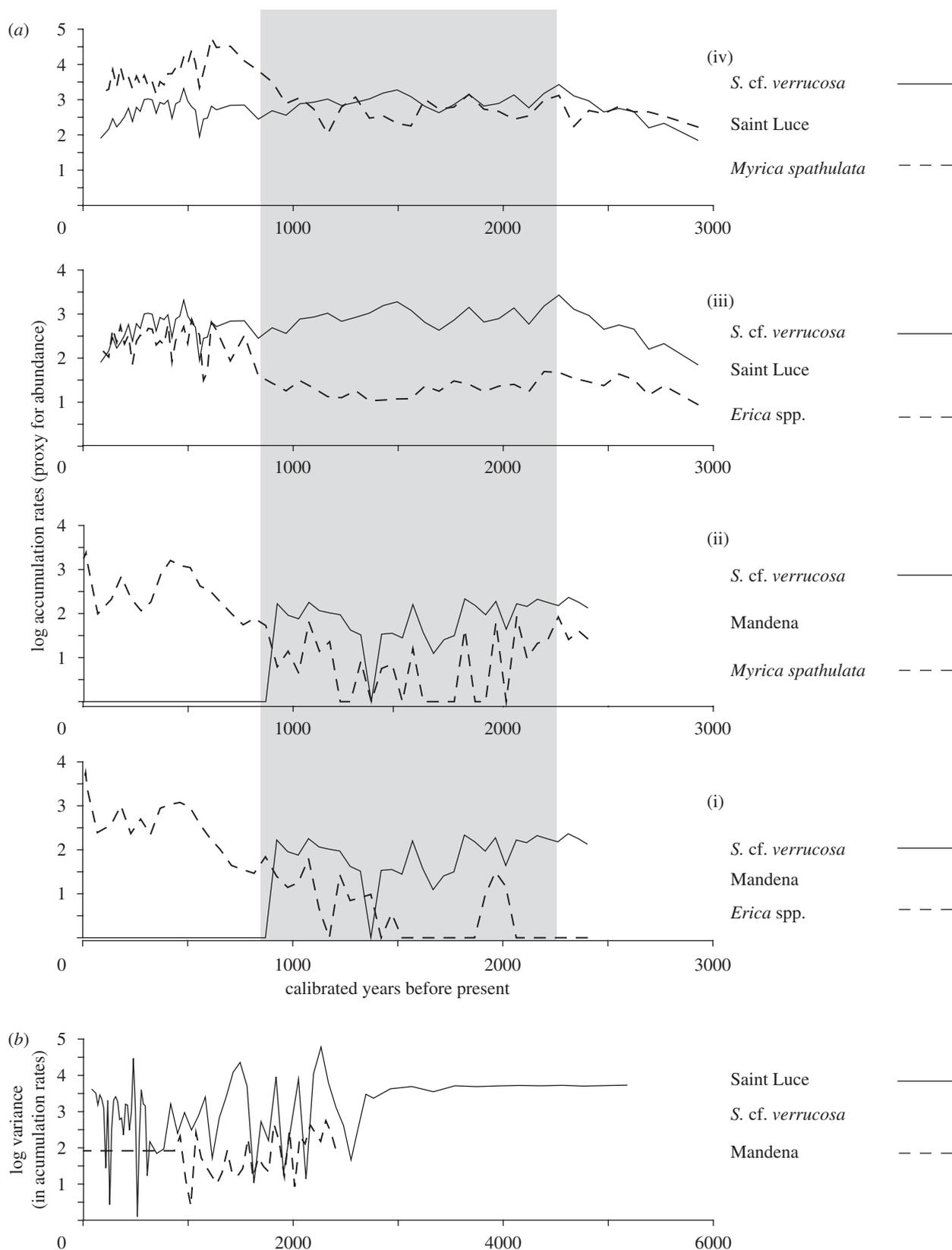


Figure 1. (a) *Symphonia* dynamics in relation to *Erica* spp. and *Myrica* in two forest fragments: at fragment (Mandena M15) where it became extinct at 950 cal. yr BP (i,ii) and another fragment (Saint Luce S9) where it persisted (iii,iv). Note that grey bands are periods of marine inundation between 2300 to 800 cal. yr BP accompanied by climatic desiccation around 950 cal. yr BP. (b) Erratic fluctuation in *Symphonia* before the threshold event and long after the peak of climate change passed.

the local biological dynamics that may have shaped extinction or persistence processes.

Vulnerability of *S. cf. verrucosa* to extinction may also indicate that this species is an indicator of

ecosystem regime shifts. We therefore investigated whether the variance (in fossil accumulation rates) of *Symphonia* (a more sensitive proxy than incremental changes (Carpenter & Brock 2006)) created signals

Table 1. Mechanistic model parameter estimates, log-likelihood (L) and AIC values for four different models. Models are fitted using a negative binomial likelihood and the AIC value for the most parsimonious model is highlighted in bold.

model	Mandena ($n = 52$)	Saint Luce ($n = 72$)
1. competition (<i>Erica</i> spp.– <i>Symphonia</i>) ^a $dE/dt = r_E E/K_E (K_E - E - \alpha_S S)$ $dS/dt = r_S S/K_S (K_S - N_S - \alpha_E E)$	$\alpha_E = 3.481$ $\alpha_S = 0.476$ $K_E = 300.970$ $K_S = 84.656$ $L = 291.365$ AIC = 598.730	$\alpha_E = 0.972$ $\alpha_S = 1.031$ $K_E = 663.230$ $K_S = 681.621$ $L = 642.167$ AIC = 1300.334
2. facilitation (<i>Myrica</i> – <i>Symphonia</i>) with <i>Erica</i> spp. an independent ^a $dM/dt = r_M M (1 - M/K_M)$ $dE/dt = r_E E (1 - E/K_E)$ $dS/dt = r_S S (1 + \lambda_M M) (1 - S/K_S)$	$\lambda_M = 0.700$ $K_E = 1499.460$ $K_S = 78.706$ $K_M = 473.071$ $L = 506.736$ AIC = 1033.473	$\lambda_M = 2.696$ $K_E = 79.064$ $K_S = 301.848$ $K_M = 500.792$ $L = 1200.482$ AIC = 2420.964
3. null Model whereby there is no influence from competition or facilitation ^a $dM/dt = r_M M (1 - M/K_M)$ $dE/dt = r_E E (1 - E/K_E)$ $dS/dt = r_S S (1 - S/K_S)$	$K_E = 643.128$ $K_S = 99.740$ $K_M = 248.489$ $L = 516.583$ AIC = 1051.165	$K_E = 143.074$ $K_S = 774.035$ $K_M = 4619.490$ $L = 1067.9$ AIC = 2153.8
4. competition (<i>Erica</i> spp.– <i>Symphonia</i>) with facilitation (<i>Myrica</i> – <i>Symphonia</i>) ^a $dM/dt = r_M M (1 - M/K_M)$ $dE/dt = r_E E/K_E (K_E - E - \alpha_S S)$ $dS/dt = r_S S/K_S (1 + \lambda_M M) (K_S - S - \alpha_E E)$	$\alpha_E = 0.515$ $\alpha_S = 0.049$ $\lambda_M = 1.021$ $K_E = 318.788$ $K_S = 77.544$ $K_M = 440.677$ $L = 530.059$ AIC = 1084.118	$\alpha_E = 0.930$ $\alpha_S = 0.009$ $\lambda_M = 0.955$ $K_E = 92.953$ $K_S = 395.935$ $K_M = 668.356$ $L = 1225.496$ AIC = 2432.993

^a r is the population rate of increase, α the competition coefficient, λ_M the facilitation coefficient of *Myrica* on *Symphonia* and K the carrying capacity. E , S and M are the accumulation rates for *Erica* spp., *Symphonia* and *Myrica* (fossil proxy for abundance), respectively.

that may have indicated anomalous changes in the ecosystem leading to extinction (a threshold event).

2. MATERIAL AND METHODS

(a) Population data

We calculated accumulation rates for *Symphonia*, *Myrica* and *Erica* spp. from published palaeoecological records from two littoral forest fragments (map in appendix 1 in the electronic supplementary material). Accumulation rate combines the rate at which the taxon falls on a sediment surface and the rate at which the sediment accumulates. Accumulation rates rather than percentage values were used, as the former is independent of changes in other plant types as well as changes in sediment accumulation rates (Bennett & Willis 2001).

(b) Statistical time-series analyses

We plotted accumulation rates and variance in the accumulation rates against time for 72 and 52 samples from Saint Luce and Mandena, respectively. Correlation analyses were performed on the interpolated accumulation rates using SPSS 16.0 in order to determine whether populations were fluctuating synchronously between the two fragments. To do so, we interpolated accumulation rates to a given corresponding time for each sequence, given that the age–depth models indicated that they are of comparable temporal resolutions (of every 50 years) and that there is no evidence of sediment mixing (Virah-Sawmy *et al.* in press). The software PSIMPOLL 4.25 was used to interpolate the data at every 50-year age interval.

(c) Model fitting

(i) Competition and facilitation

The principal aim of this study is to understand whether extinction is modulated by competition and facilitation. To test these hypotheses, we fitted different models that assessed the explanatory power of competition, facilitation and competition with facilitation with a null model using a negative binomial likelihood function (table 1).

By assuming that the noise includes both demographic and environmental stochasticity, the maximum likelihood estimates of the parameters can be obtained (numerically) by solving combined

likelihood functions ($L_j(\mathbf{P})$) for a vector of model parameters (\mathbf{P}) (models 1–4, table 1) for each species (j) (Johnson *et al.* 1993):

$$L_j(\mathbf{P}) = \prod_{t=1}^n \left(\frac{\mu_j(t)}{\mu_j(t) + \kappa} \right)^{y_j(t)} \left(1 + \frac{\mu_j(t)}{\kappa} \right)^{-k} \frac{\Gamma(y_j(t) + \kappa)}{y_j(t)! \Gamma(\kappa)},$$

where n is the length of the time series, $y_j(t)$ the observed abundance of the j th species at time t , $\mu_j(t)$ the expected abundance of the j th species at time t predicted from the density-dependent models (models 1–4, table 1), κ the clumping parameter from the negative binomial distribution and Γ denotes the gamma function. Maximum-likelihood parameter estimates were determined using a Nelder–Mead simplex algorithm (e.g. Bonsall & Hastings 2004). This optimization is relatively robust at finding the minima and maxima of functions and works by using only one likelihood evaluation. We then used an information-theoretic approach (Bonsall & Hastings 2004) and relative goodness-of-fit measure based on the Akaike information criteria (AIC) to evaluate the explanatory power of different models.

3. RESULTS

(a) Time series

(i) Synchrony

Correlation analysis of the time series indicated that populations of *Erica* spp., *Myrica* and *Symphonia* are strongly and positively correlated between the two fragments ($r = 0.627$, 0.672 , 0.445 , respectively; $p < 0.01$; $n = 48$ using Spearman correlation). We therefore confirmed that the dynamics of the populations are in synchrony and from this we infer that they are driven by correlated changes in regional (climate) variability.

(ii) Variance

Anomalous fluctuations in the variance of *Symphonia* populations (using accumulation rates) are observed

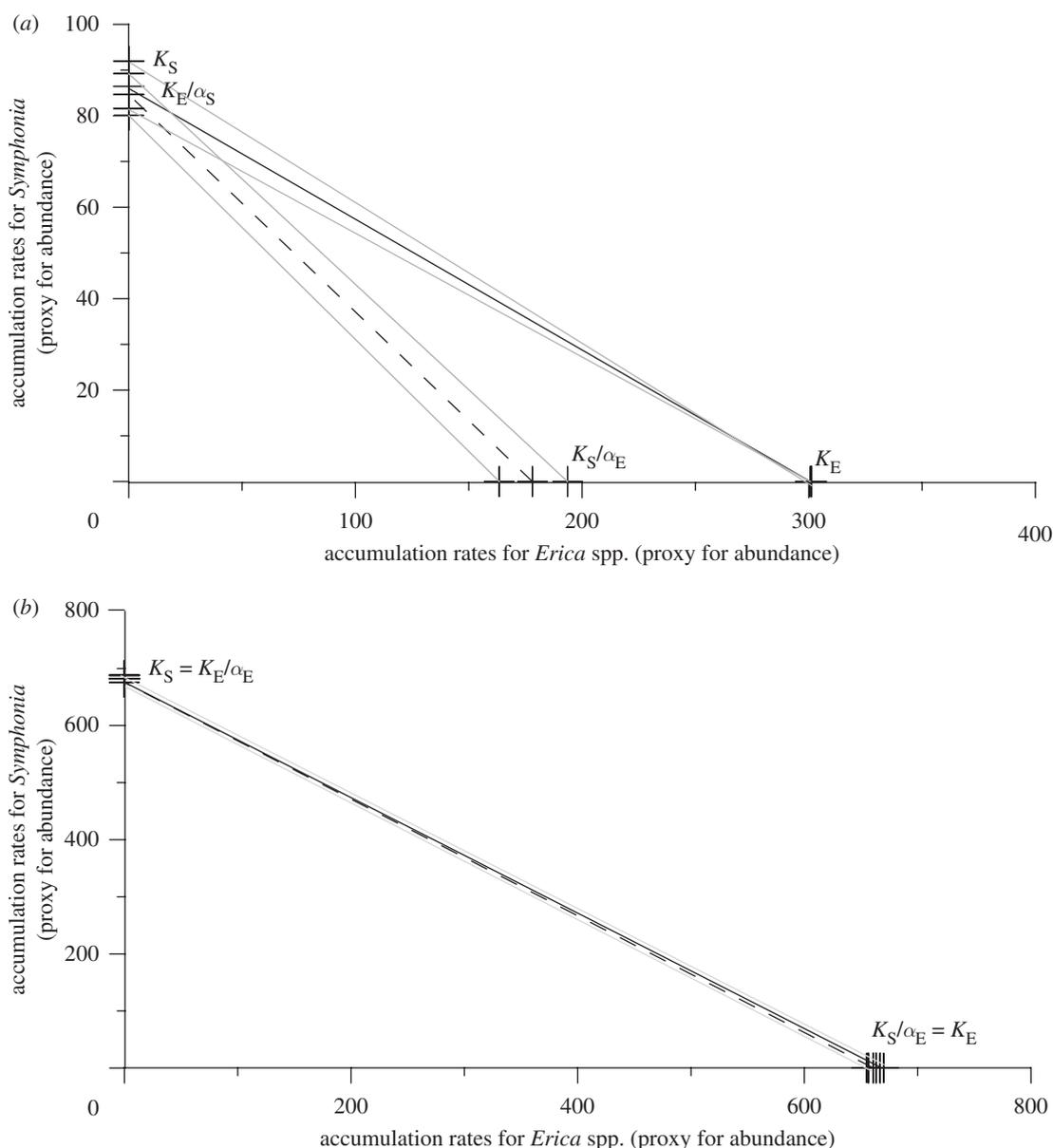


Figure 2. Two different outcomes of the competition model between *Erica* spp. and *Symphonia* in the two fragments. Solid and dashed lines are the competition isoclines for *Erica* spp. and *Symphonia*, respectively, and the grey lines are the 95 per cent confidence regions. K_E and K_S are the carrying capacities for *Erica* spp. and *Symphonia*, respectively. α_E and α_S are the competition coefficients. (a: Mandena; b: Saint Luce).

in both sites from 2300 cal. yr BP prior to the threshold 950 cal. yr BP. Specifically, despite persisting in Saint Luce, *Symphonia* continues to oscillate erratically long after the climatic drivers have passed their critical points around 950 cal. yr BP.

(iii) Model fitting

The comparison of the four models (table 1) indicates that local processes played an important role into the dynamics of population extinction. At both sites, the best model for *Symphonia* dynamics is the competition model with *Erica* spp. (table 1). The AIC values for the other models were much higher and were comparable with the null model (table 1).

The competition model indicated that at the site where *Symphonia* persisted, there was coexistence between *Symphonia* and *Erica* spp. ($\alpha_E = 0.972$, $\alpha_S = 1.031$, table 1 and figure 2). In contrast at Mandena

where *Symphonia* became extinct, the parameter estimates indicated competitive exclusion between *Symphonia* and *Erica* spp. *Symphonia* exerted stronger competitive effects on *Erica* spp. ($\alpha_E = 3.481$, $\alpha_S = 0.476$, table 1) at high *Symphonia* abundances, but it is an unstable equilibrium at lower *Symphonia* abundances (figure 2). At lower *Symphonia* abundances, *Erica* spp. were dominant and reached carrying capacity, possibly driving *Symphonia* to extinction ($K_E > K_S/\alpha_E$, figure 2).

4. DISCUSSION

In this study, we have shown that both regional and local processes could be associated with the dynamics of population extinction. For example, regional climatic variability may have contributed to synchronous fluctuations in the populations of *Symphonia*,

Erica spp. and *Myrica* between the fragments. Superimposed on climatic variability are local processes, in particular, coexistence or exclusion with *Erica* spp. that may lead to or mitigate extinction.

Population model fitting indicated that the best explanatory model for *Symphonia* dynamics is coexistence or exclusion with *Erica* spp. Specifically, population modelling showed that *Erica* spp. and *Symphonia* can coexist in Saint Luce, possibly explaining the persistence of the latter there, but the two species can exclude each other in Mandena. It is hypothesized that mechanisms by which coexistence is favoured in Saint Luce ($K_E = K_S/\alpha_E$ and $K_S = K_E/\alpha_S$; figure 2) may include resource partitioning that then leads to sustained segregation on the moist but nutrient-poor soils, which are particularly deficient in phosphates (Virah-Sawmy *et al.* in press) and nitrogen (M. Virah-Sawmy 2008, unpublished data). By contrast, the more nutrient-rich soils of Mandena would have provided more resources for *Symphonia* and other species. Under high *Symphonia* abundances, *Symphonia* exerted competitive effects on *Erica* spp. ($\alpha_E = 3.481$ and $\alpha_S = 0.476$; table 1). When climatic changes impacted *Symphonia* populations, *Erica* spp. appear to have been released from competition (figure 1a(i)(ii)). It is hypothesized here that as *Erica* spp. expanded and reached maximum carrying capacity, it may have driven the climate-impacted *Symphonia* population locally extinct ($K_E > K_S/\alpha_E$) in Mandena. Nonetheless, it is also possible that other biotic and abiotic factors are also shaping the current observed dynamics.

Facilitation of *Myrica* on *Symphonia* was also expected to play an important role. However, there was no statistical support for the facilitation models. As expected however, the facilitation coefficient of *Myrica* on *Symphonia* was nearly four times stronger at Saint Luce than Mandena, illustrating possibly a more important role that nitrogen-fixing *Myrica* may play on the low nutrient soils of Saint Luce.

Resilience theory suggests that some variables within ecosystems do change before a threshold (such as an extinction event) in ways that may serve as leading indicators of change (Carpenter & Brock 2006). We observed steeper oscillations in the variance of *Symphonia* in response to climatic changes in both sites prior to threshold responses in the ecosystems (figure 1b). Further, these signals continued long after the climatic driver has passed the critical point at 950 cal. yr BP at the site where *Symphonia* persisted.

Such indicators can thus provide advance warnings for the formation of novel ecosystems in response to global change.

In conclusion, this study demonstrates that local factors such as competition with other species and soil conditions may determine whether *Symphonia* could survive under climate change. This finding on the realized niche of a species has important implications for how endangered species and their ecosystems should be managed during future climate change.

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