Plant-microbe symbiosis widens the habitability range of the Daisyworld

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Abstract

Plant-microbe symbiosis is pervasive in the Earth's ecosystems and dates back to the early land colonisation by plants. Mutualistic partnership with rhizobia bacteria and mycorrhizal fungi promotes plant nutrition, growth and diversity, impacting important ecosystem functions. However, how the global behaviour and dynamical properties of an ecosystem are modified by plant-microbe symbiosis is still unclear.To tackle this theoretical question, we resorted to the Daisyworld as a toy model of the global ecosystem. We redesigned the original model to allow accounting for seed production, spreading, germination, and seedling development to mature seed-producing plants to describe how symbiotic and non-symbiotic daisy species differ in these key processes. Using the steady-state and bifurcation analysis of this model, we demonstrate that symbiosis with microbes broadens the habitability range of the Daisyworld by enhancing plant growth and/or facilitating plant access to otherwise uninhabitable nutrient-poor regions.

Keywords:
Mathematical model, symbiosis, ecosystem

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1. Introduction

Symbiosis is the long-term relationship between different species (Margulis, 1981; Arora, 2013), which can be mutualistic, commensal, or parasitic. Mutualism takes place when symbiosis benefits both species involved, commensalism when only one species benefits and the other is unaffected, and parasitism when one species benefits at the expense of the other (Johnson et al., 1997).

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The plant symbiosis with bacterial rhizobia and mycorrhizal fungi are generally considered mutualistic as the symbionts enhance plant nutrients while plants provide the carbon required for their growth and reproduction (Smith and Read, 2008). Several review papers describe in detail the influence of symbiosis on plants at various growth stages, its advantages and implications (e.g., Koide, 1991; Brundrett, 2002; Bonfante and Anca, 2009; Bonfante and Genre, 2010; Hayat et al., 2010; Smith and Smith, 2011; Bücking and Kafle, 2015; Field et al., 2015; Jacott et al., 2017; Bonfante, 2018; Begum et al., 2019; Jacquemyn and Merckx, 2019; Teste et al., 2020). Symbiosis with rhizobia bacteria helps more than 17.000 types of leguminous plants to fix nitrogen (Smil, 2002). This symbiotic partnership provides otherwise limiting resources to plants, protecting against stressful conditions (Hayat et al., 2010; Pieterse et al., 2016; Poole et al., 2018; Cordovez et al., 2019; Afkhami et al., 2020) and improving soil structure and organic matter content (Hayat et al., 2010; Hird, 2010). Symbioses with mycorrhizal fungi are more widespread existing in more than 90% of terrestrial plant species (Trappe, 1987), as indicated by physical, physiological, and molecular evidence in an ample range of ecosystems (Simard et al., 2012). Furthermore, evolutionary success indicates that the advantages of this symbiosis overcome the risks associated with the fungal loss of saprotrophic capabilities (Bonfante and Genre, 2010). Mycorrhizal fungi have been implicated in improving plant growth and yield under stressed and unstressed regimes (see Fig. 1 in Begum et al., 2019) due to the gain on tolerance to abiotic stresses such as extreme temperatures, salinity, drought, diseases and metals (Rodriguez et al., 2008; Bonfante and Anca, 2009; Abdel-Salam et al., 2018; Begum et al., 2019; Chandrasekaran et al., 2019), as well as biotic stresses such as pathogens and herbivores (Smith and Read, 2008; Bücking and Kafle, 2015; Kaur and Suseela, 2020). Besides, they may enhance the nutrients uptake, mainly phosphorus and nitrogen (Read, 1991; Leake and Miles, 1996; Aerts, 2002; Bonfante and Anca, 2009; Hodge et al., 2010), but also sulfur, magnesium, copper, and zinc (Bücking and Kafle, 2015; van der Heijden et al., 2015); and soil health. This can result in an increase in the photosynthetic rate, and consequently, in the plant biomass (Smith and Read, 2008; Bonfante and Genre, 2010; Birhane et al., 2012).

The main objective of this work is to investigate how the partnership between plants and microbial symbionts, such as mycorrhizal fungi or rhizobia, may affect the global properties of ecosystem dynamics. As biota and their relationships with other components of the Earth's system are too complex to be described by tractable mathematical equations, we worked with a toy model, the Daisyworld, following the lead of Boyle et al. (2011). The Daisyworld was used to illustrate how planetary temperature regulation could arise from the interaction between living organisms and their environment (Watson and Lovelock, 1983; Lovelock, 1992). As the archetypal model for Gaia's theory (Lenton et al., 2020), it has been widely scrutinised as a way to critically examine the theory (Lenton and Lovelock, 2001). Regardless of whether Gaia's theory is correct, this toy model has helped to think about the biosphere-geosphere interaction (Lovelock, 1992; Von Bloh et al., 1999; Wood et al., 2008) and has become an excellent "tutorial" model for answering "what if ...?" questions due to its simplicity and stability

(Bloh et al., 1997; Lenton and Lovelock, 2001).

The Daisyworld model has been studied and modified in multiple ways in an attempt to reduce the simplifications and to understand the conditions for regulation (Lenton et al., 2020). These modifications include extensions to one dimension (Adams et al., 2003; Biton and Gildor, 2012; Alberti et al., 2015) and two spatial dimensions (Von Bloh et al., 1999; Punithan et al., 2012; Punithan and McKay, 2014; Kageyama and Yagi, 2020), the effect of greenhouse gases (Maddock, 1991; Nordstrom et al., 2005; Viola et al., 2013; Paiva et al., 2014; Alberti et al., 2015; Rueangphankun et al., 2018), multiple species and trophic levels (Keeling, 1991; Lovelock, 1992; Lenton and Lovelock, 2001), the role of the hydrological cycle (precipitation, evapotranspiration, clouds, etc.) (Nordstrom et al., 2005; Salazar and Poveda, 2009), mutation (Robertson and Robinson, 1998), destructive environmental feedbacks (Watson and Lovelock, 1983), discretisation of the albedo trait space (Lovelock, 1992), physical constraints on adaptation (Lenton and Lovelock, 2000), time scales perspective (Weaver and Dyke, 2012), and habitat fragmentation (Von Bloh et al., 1999). Lenton and Lovelock (2001) and Wood et al. (2008) review the main modifications of the Daisyworld model.

Here we ask what happens to planetary temperature regulation and habitability if symbiotic daisies are introduced in the Daisyworld ecosystem. To our knowledge, the only extension of the Daisyworld model that takes into account the effect of symbiosis is that of Boyle et al. (2011), who added a costly but more temperature-tolerant mutualistic symbiosis between one dark and one light daisy variant. The new growth function expresses an increase in tolerance of sub-optimal conditions due to the symbiosis, and the albedo of symbiotic daisies switches between dark and light daisies albedo. Their results indicate an extension of the luminosity range with habitability, the ability to maintain residual oscillatory regulation, and succession dynamics in which the tolerant symbiotic daisies colonize the planet but are later replaced by free-living species that have greater local fitness once conditions improve.

Unlike the approach of Boyle et al. (2011), we develop a model to understand the effect of plant symbiosis with microbial species that facilitate nutrients that would be otherwise inaccessible to the plants. We redesign the original model to describe seed spreading, germination and seedlings growth and how these processes differ quantitatively between symbiotic and non-symbiotic daisies. For that, we assume that the planet is partitioned into two regions, one with rich soils and the other with poor soils with insufficient nutrients. We postulate that only symbiotic daisies can grow in the poor region, while both symbiotic and non-symbiotic daisies can grow in the rich soils. We analysed the possible solutions of the proposed system of equations and carried out some scenarios to evaluate the effect of the parameters.

2. Symbiotic Daisyworld model

We consider a unit area planet constituted by two regions, A and B, as shown in Fig. 1. Region A is constituted by rich soils, having adequate conditions for all types of plants to grow. The proportion of the planet area in region A is defined by $\theta \in [0, 1]$, whereas that in region B is defined by $1 - \theta$. Region B has insufficient nutrient conditions, so only symbiotic plants can grow there because microbial symbionts facilitate the nutrients. The microbial symbionts are not described explicitly; their effects are captured implicitly in the distinct dynamics of symbiotic or non-symbiotic daisies, assuming that they are available and never limiting in both regions.

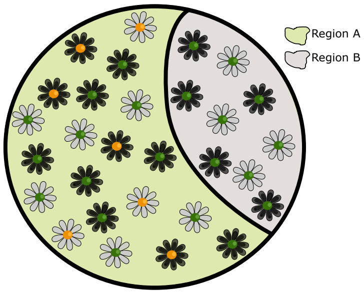

Figure 1: Schematic model of symbiotic Daisyworld, whose surface is covered by symbiotic and non-symbiotic dark and light daisies. Region A, with an area of θ, has soils rich in nutrients, whereas region B, with an area of $(1-\theta)$, has poor soils with insufficient nutrients. Symbiotic daisies (green disc florets) can grow in both regions A and B, whereas non-symbiotic (yellow disc florets) daisies can grow in region A but no in region B.

As in the Daisyworld model proposed by Watson and Lovelock (1983) (referred here as the original model), two types of daisies, dark (b) and light (w), can grow on this planet occupying areas measured by a_b and a_w, respectively. Dark and light daisies can be of two types that can or cannot engage in symbiotic relationships with fungi and/or bacteria. Dark and light symbiotic daisies are denoted b^* and w^*, and their respective areas a_b^* and a_w^*. In all equations throughout the manuscript, the asterisk superscript (*) indicates symbiotic daisies.

Each daisy species produces a quantity of seeds per generation (s) that is proportional to the area covered by the species at time t, as:

$$\begin{aligned} s_i &= \sum_j \kappa_{i,j} a_{i,j} \\ s_i^* &= \sum_j \kappa_{i,j}^* a_{i,j}^* \end{aligned} \tag{1}$$

where κ is the rate of seed production per unit area, i denotes the colour of the daisies (b or w) and j is the region of the planet that daisies occupy (A or B). For simplicity, we assume that non-symbiotic plants do not produce seeds in the poor soil region, i.e., $k_{i,B} = 0$. The equation that describes κ is analogous to the growth rate equation of the original model (see Eq. A.2), so it depends on the local temperature (T_i) and is given by:

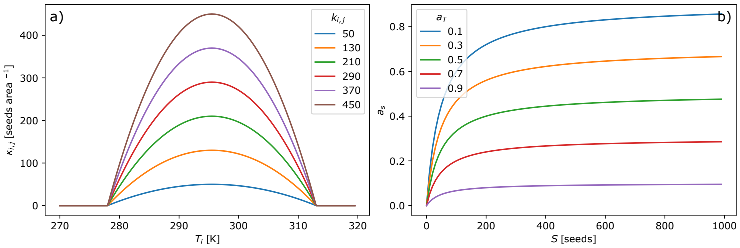

Figure 2: Seed production rate by each daisy type per unit of area as a function of local temperature T_i and maximum number of seeds produced per unit area $k_{i,j}$ (a) and relationships among the area seeded by daisies a_s, the total number of seeds S, and the total area covered by daisies a_T(b).

$$\begin{aligned}\kappa_{i,j} &= k_{i,j}[1 - k_o(T_{op} - T_i)^2] \\ \kappa^*_{i,j} &= k^*_{i,j}[1 - k_o(T_{op} - T_i)^2]\end{aligned} \tag{2}$$

where T_i is the local temperature, T_{op} is the optimal temperature, $k_{i,j}$ is the maximum number of seeds produced per unit area, and k_o is a universal sensitivity constant from the growth rate equation of the original model. k_o restricts the temperature range in which the growth rate is non-zero (in this case, the range in which the seed production rate is non-zero). Fig. 2a shows the rate of seeds produced by each daisy when the temperature (T) varies and for different values of k. The number of seeds produced is defined as non-zero when the temperature is between 278 and 313 K, its maximum value takes place at 295.5 K (which is the optimal temperature, T_{op}), and corresponds to the value of k.

The total number of seeds (S) and the total area covered by daisies (a_T) on the planet are given by:

$$S = \sum s_i + \sum s^*_i \tag{3}$$

$$a_T = \sum_{i,j} a_{i,j} + \sum_{i,j} a^*_{i,j} \tag{4}$$

The likelihood that the seeds land and initiate germination takes the form of an adsorption isotherm, analogous to the Michaelis-Menten kinetics function (see Fig 2b), such that the area of the planet seeded by daisies (a_s) is:

$$a_s = \frac{S}{S_M + S}(1 - a_T) \tag{5}$$

S_M is a constant that defines the number of seeds that will seed an area of the planet that is half the maximum value. Notice that a_s is proportional to the number of seeds when this number is small and saturates at $1 - a_T$ for very large values of S (Fig. 2b). This functional form assumes that seeds compete for available space among themselves to germinate from seedlings and, furthermore, mature daisies prevent the seeds from germinating in the areas they occupy.

The fractions of area seeded in regions A and B are θa_s and $(1-\theta)a_s$, respectively, and the fraction seeded by each type of daisies is calculated as:

$$a_{i,A} = \theta a_s \frac{s_i}{S} \tag{6}$$

$$a^*_{i,A} = \theta a_s \frac{s^*_i}{S}$$

$$a_{i,B} = (1-\theta) a_s \frac{s_i}{S} \tag{7}$$

$$a^*_{i,B} = (1-\theta) a_s \frac{s^*_i}{S}$$

The above development assumes that the seeds produced by each daisy type, independently of the region they originated from, can seed and grow in any region (i.e., as if the seeds would be pooled and randomly spread). The area covered by daisies is thus given by the following set of differential equations:

$$\frac{da_{i,A}}{dt} = \mu_{i,A}\theta a_s \frac{s_i}{S} - r a_{i,A} = \mu_{i,A}\theta \frac{s_i}{S_M + S}(1 - a_T) - g a_{i,A} \tag{8a}$$

$$\frac{da_{i,B}}{dt} = \mu_{i,B}(1-\theta) a_s \frac{s_i}{S} - r a_{i,B} = \mu_{i,B}(1-\theta) \frac{s_i}{S_M + S}(1 - a_T) - g a_{i,B} \tag{8b}$$

$$\frac{da^*_{i,A}}{dt} = \mu^*_{i,B}\theta \frac{s^*_i}{S_M + S}(1 - a_T) - r a^*_{i,A} \tag{8c}$$

$$\frac{da^*_{i,B}}{dt} = \mu^*_{i,B}(1-\theta) \frac{s^*_i}{S_M + S}(1 - a_T) - r a^*_{i,B} \tag{8d}$$

where $\mu_{i,j}$ is the probability that the seed will develop into a fully grown plant that can produce seeds, and r is the plant death rate. Note that since we assume that non-symbiotic daisies cannot grow in the poorer soil (region B), Eqs. 8b are set to zero.

Symbiosis can result in some cost to plants. For example, it has been reported that mycorrhizal fungi may consume up to 20% of the net primary production that would otherwise be allocated to plant biomass (Wright et al., 1998; Fisher et al., 2010; Brzostek et al., 2014)). Some authors proposed that the cost is less than growing their roots to obtain the lacking nutrients, while others hypothesised that the carbon investment represents a disadvantage (Harley, 1989; Hobbie, 2006). Our extension of the Daisyworld does not explicitly consider the cost of symbiosis as that of Boyle et al. (2011), but this can be accommodated in the values of μ and κ.

The energy balance equation is the same as Nevison et al. (1999), who replaced the exact balance between incoming solar radiation and outgoing longwave radiation from the original model by the ODE:

$$\frac{dT_e}{dT} = \frac{S_0 L}{c_p}(1-\alpha) - \frac{\sigma}{c_p}T_e^4 \tag{9}$$

where T_e is mean planetary temperature, S_0 is the solar constant, L is the luminosity of Daisyworld's sun relative to the Earth's sun, σ is the Stefan-Boltzmann constant, c_p is the specific capacity heat, and α is the planetary albedo. The planetary albedo (α) is a function of the occupied area and the albedo of light (w) and dark (b) daisies, and the bare ground (g), and is expressed by:

$$\alpha = \left(1 - \sum_{i,j} a_{i,j} - \sum_{i,j} a^*_{i,j}\right)\alpha_g + \left(\sum_{i,j} a_{i,j} + \sum_{i,j} a^*_{i,j}\right)\alpha_i \tag{10}$$

where the albedos of the bare ground (α_g) and each type of daisies (α_i) are assumed to be constant (see values in Table 1). Furthermore, the albedo of daisies depends only on colour and not on their symbiotic nature.

Lastly, the local temperature (T_i) is related to the planetary temperature through the same equation of the original model, i.e.:

$$T_i^4 = q(\alpha - \alpha_i) + T_e^4 \tag{11}$$

where q is a constant that provides a measure of the degree of redistribution of solar energy amongst the three types of surface (Watson and Lovelock, 1983).

The values of the parameters used in the analyses described in sections 3 are in Table 1 unless otherwise specified.

3. Results

3.1. Stable equilibria and temperature regulation in the symbiotic Daisyworld

When the planet is uninhabited by daisies, the temperature is not regulated and increases directly with the luminosity. The relationship between L and T_e is the Stefan-Boltzmann equation (black line in Fig. 3a,b), as in the original model (see Fig. A.7a). However, if the planet is inhabited by daisies, the relationship between L and T_e is more complex, exhibiting self-regulation and multistability. These properties are similar to those in the original model (Lenton and Lovelock, 2001), however, in the symbiotic Daisyworld, the permutations of dark and light types with symbiotic and non-symbiotic types of daisies, lead to more rich dynamics and potential steady states. As depicted in the bifurcation diagrams in Fig. 3a,b, all stable steady states (full lines) have symbiotic dark and/or light daisies that outcompete non-symbiotic plants. The states with at least one non-symbiotic daisy type are always unstable because the symbiotic variant will always invade and outcompete the non-symbiotic daisy with the same colour.

Table 1: Parameters values of the symbiotic Daisyworld model.

Parameter	Description	Value
c_p	Specific capacity heat [erg cm^{-2} K^{-1}]	$3 \cdot 10^{13}$
k	Rate of seed production [seeds/area]	300
k_o	Constant that restricts the temperature range	0.003265
q	Heat transport coefficient [K^{-4}]	$2.06 \cdot 10^{9}$
r	Death rate	0.3
S_0	Incoming solar radiation [ergs cm^{-2} s^{-1}]	$9.17 \cdot 10^{5}$
S_M	Value of S corresponding to $a_T/2$ [seeds]	50
T_{op}	Optimal temperature [K]	295.5
α_g	Albedo of bare ground	0.5
α_w	Albedo of light daisies	0.75
α_b	Albedo of dark daisies	0.25
θ	Percentage of the planet's area with rich soil	0.20
μ	Probability of a seed become a fully grown plant	1
σ	Stefan-Boltzmann constant [ergs cm^{-2} s^{-1} K^{-4}]	$5.75 \cdot 10^{-5}$

Stable states with symbiotic daisies qualitatively recapitulate the luminosity dependence of the original model. When $L \sim 0.69$, the planet is warm enough for dark symbiotic daisies to sprout (Fig. 3c,d). There is positive feedback on growth because dark symbiotic daisies continue to warm the planet until they begin to compete with light symbiotic daisies for space. As the luminosity increases, temperature also does, creating adequate conditions for light daisies to sprout. Then, for a range of L ($\sim$ 0.73-1.44), both symbiotic daisy types coexist stably. In this range, the temperature is almost constant and close to the optimum temperature T_{op}, and actually, it decreases slightly with the luminosity (dark blue lines in Fig. 3a,b,c,d). Increasing L results in an eventual advantage of light symbiotic daisies, causing them to dominate the planet until $L \sim 1.75$ (Fig. 3c,d). Above this luminosity, the temperature becomes too high for daisies to survive. When solar radiation at the surface of the planet decreases, light symbiotic daisies cannot reestablish until $L \sim 1.26$, defining a hysteresis loop at high luminosities. Likewise, if the luminosity continues to decrease, then the dark symbiotic daisies can persist down to $L \sim 0.57$, defining another hysteresis loop at low luminosities.

The steady states with dark and light daisies that are non-symbiotic also show the qualitative dependence on luminosity, corresponding to the branches in light orange and blue dotted lines in Fig. 3a, respectively. As the dotted lines indicate, these non-symbiotic states are unstable equilibria, and the only way they can be observed is if symbiotic daisies of the same colour are forbidden (e.g., by forcing either $a^*_{b,j} = 0$ or $a{*}_{w,j} = 0$). Then, the coexistence of non-symbiotic dark (light) daisies with symbiotic light (dark) daisies is possible, as indicated by the quasi-horizontal wine and sky blue colour lines. Furthermore, the range of L in which symbiotic daisies can grow is greater than that of non-symbiotic daisies when the parameters that describe the dynamics of seed and

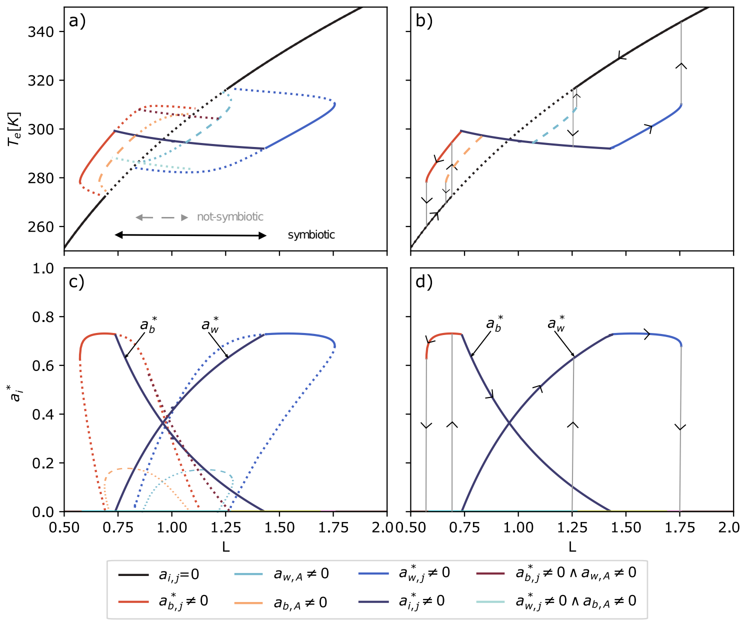

Figure 3: Bifurcation diagrams. Planetary temperature (T_e) (a and b) and fractional coverage of daisies (a_i) (c and d) at steady state as a function of luminosity (L) in the symbiotic Daisyworld. a) and c) depict the values at the steady states that are uninhabited (black) or inhabited (coloured) by daisies in all possible combinations of dark, light, symbiotic and non-symbiotic daisies as indicated in the legend. Solid and dotted lines represent the stable and unstable steady-states, respectively. Dashed lines indicate the stable steady-states when daisies are free-living. b) and d) exhibit the stable equilibrium trajectories as L increases and decreases. The arrows indicate the directional hysteresis loops. The parameters values are those shown in Table 1 with $\theta = 0.2$.

growth (k and μ) are the same, as in the scenario in Fig. 3. The magnitude of this difference depends on the values of the model parameters, as shown in sections 3.2, 3.3, and 3.4.

Whereas temperature is stably regulated close to T_{op} when both dark and light daisies are symbiotic, the coexistence of non-symbiotic light (respectively dark) daisies and symbiotic dark (light) daisies occurs around 307.7 (284.6) K. This difference is easy to interpret considering that symbiotic daisies partake with non-symbiotic daisies of the opposite colour the region A but cover an extra area in the region B that only symbiotic daisies can access. Therefore, when dark daisies are in symbiosis, the planet's temperature rises as they absorb more energy, whereas when light daisies are symbiotic, the temperature decreases as they reflect more energy.

Note that since the equations for the growth dynamics of the symbiotic and the original Daisyworld models are different, the ranges of L values in which the planets are habitable cannot be compared. The steady-state of the temperature response of the original model and that corresponding steady-state obtained by forcing the presence of exclusively non-symbiotic daisies in the extended model are compared in Fig. A.7, showing that the qualitative behaviours are similar despite the slight quantitative differences.

However, in the extended model, the luminosity range at which the planet is inhabitable by daisies is broader when symbiotic plants are introduced than when exclusively non-symbiotic daisies are allowed to grow. Perhaps more important, the symbiotic daisies can regulate planetary temperature closer to the optimal temperature in a wider range of solar luminosity when compared to their non-symbiotic counterparts (as indicated by the horizontal arrows in Fig. A.7a).

3.2. The luminosity range in which the planetary temperature is regulated depends on daisies in symbiosis and the proportion of poor soils

In this section, we will explore how symbiosis affects global temperature regulation and habitability in Daisyworld and how these effects depend on parameters. Lenton and Lovelock (2001) proposed the luminosity range as a measure of regulation, defining a range of L over which the planet is inhabited by daisies. We use a modification of this measure, considering only the range in which the planet is inhabited and partaken by daisies of both colours (ΔL), i.e., the difference of the maximum (L_{max}) and minimum (L_{min}) value of L indicated by double-head arrows in Fig. A.7a. This choice is justified because the coexistence equilibrium is the one that results in the regulation of planetary temperature T_e close to T_{op}.

Fig. 4 shows the coexistence luminosity range for different values of θ when both types of daisies are symbiotic ($a^*_{i,j} \neq 0$) and when daisies of only one colour are symbiotic ($a^*_{w,j}$=0 or $a^*_{b,j}$=0). Here, the values of k and μ are the same for both colours, symbiotic conditions, and regions. When both types of daisies are in symbiosis (black points), the luminosity range is the same regardless of the value of θ because daisies can grow in both regions with the same conditions. If only one type of daisies is symbiotic (coloured points), ΔL is highly dependent on θ. For large proportions of the planet with poor soils (low θ values), ΔL is

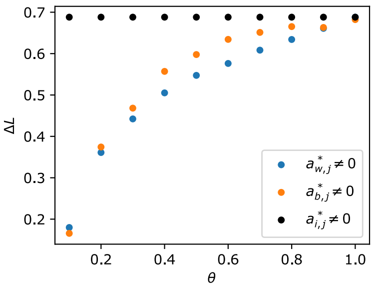

Figure 4: Luminosity range ($\Delta L = L_{max} - L_{min}$) as a function of the proportion of rich soils θ when both daisies types are symbiotic (black points), only dark daisies are symbiotic (orange points), and only light daisies are symbiotic (blue points). The parameters of symbiotic and non-symbiotic daisies in both regions have the same values and are those shown in Table 1.

very small since non-symbiotic plants, of the opposite colour of the symbiotic daisies, can grow but have little space available to do so. In contrast, when region B does vanishes or is small ($\theta \sim 1$), ΔL is the same as in the scenario in which daisies of both colours are symbiotic. This is because, in rich soil conditions, under the parameter settings adopted, there is no difference between symbiotic and non-symbiotic daisies.

The value of ΔL also depends on the colour of the non-symbiotic daisies. ΔL values of only symbiotic dark daisies (orange points) are more similar to the scenario for both types of symbiotic daisies than ΔL values of only symbiotic light daisies (blue points). This is because the effects of changes in L are not symmetrical, being greater for light daisies than for dark daisies (see differences between symbiotic and non-symbiotic daisies of each colour in Fig. A.7a).

As mentioned above, if symbiotic daisies are only of one colour and the value of θ is different from 1, the regulation temperature value is not the same as when both types of daisies are in symbiosis (see Fig. 3). Symbiotic dark daisies cool the planet below T_{op} while symbiotic light daisies heat it above T_{op}.

3.3. Symbiosis with microbes allows daisies to explore poor soils with lower yields than in rich soils

In the present model, the planet has complementary regions with nutrient-rich and nutrient-poor soils and only symbiotic plants can grow in the poor soil region B. In the previous sections, we assumed that the symbiotic daisies grow equally well in both regions. However, this is a very restrictive scenario. The limitation of minerals such as nitrogen and phosphorus may have some effects on the plant yield (Kirschbaum, 2011; Adams et al., 2003; Terrer et al., 2019), being lower than in rich soils. To represent this scenario, we simulate region B of the planet with lower values of μ and k than region A. This means that plants growing in the poor region do not have the same ability to produce seeds ($k^*_{i,A} > k^*_{i,B}$) and that seed germination and growth to mature plants is less efficient in region B than in region A ($\mu^*_{i,A} > \mu^*_{i,B}$).

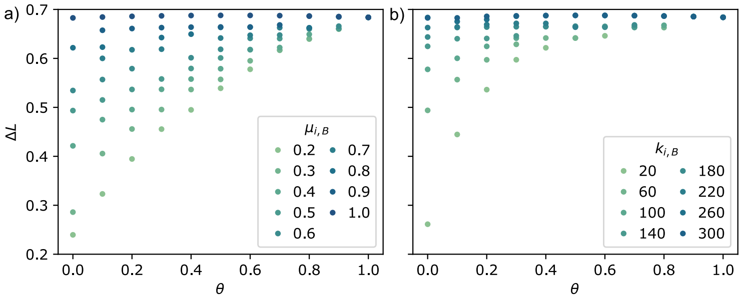

Figure 5: Luminosity range ($\Delta L = L_{max} - L_{min}$) of symbiotic dark and light daisies coexistence as a function of the proportion of rich soils θ and for different values of $\mu^*_{i,B}$ (a) and $k^*_{i,B}$ (b). $\mu^*_{i,A} = 1.0$ and $k^*_{i,A} = 300$.

Fig. 5 shows the variation of ΔL with the proportion of the planet composed of rich soils (θ) for different values of μ and k in region B (poor soils). For low values of μ and θ (see Fig. 5a), the luminosity range is very low since although symbiotic daisies can grow in poor soils, the chance of them becoming adult plants is low. For low values of μ and high values of θ, ΔL is large because most plants grow in the rich region, where they have all the necessary nutrients to reach their maximum capacity to become adults. Otherwise, for high values of μ, the luminosity range is very similar for all θ values since if the plants cannot grow in the rich area, they can do so in the poor region, where the conditions are similar to those of the region A ($\mu^*_{i,A} \sim \mu^*_{i,B}$).

The changes of ΔL with $k^*_{i,B}$ for different values of θ (Fig. 5b) are analogous to those described above for variations in $mu^*_{i,B}$, i.e., there are notable differences when the performance of seed production in both regions is distant. However, the variation of ΔL with θ for different values of μ is almost linear, while the variation for different values of k is a logarithmic-like relationship. This suggests that the model is more sensitive to μ than to k because the former multiplies the entire growth expression in the equations that describe the population dynamics of each type of daisies (Eqs. 8).

3.4. Symbiosis with microbes has a cost for daisies

Symbiosis may have some cost to the host, in this case, the plants (Lapointe and Molard, 1997; Hoeksema and Schwartz, 2003; Smith and Read, 2008; Simard et al., 2012). We do not directly consider the effect of this cost, but it can be represented by the k and μ values of symbiotic plants. Variations in k illustrate a reduction in seed production, while variations in μ illustrate a reduction in the ability of seeds to become adult plants.

Fig. 6 shows the values of ΔL as a function of θ for the coexistence of non-symbiotic daisies and the coexistence of symbiotic daisies with the same or lower performance than the non-symbiotic ones ($\mu^*_{i,j} \leq \mu_{i,A}$ or $k^*_{i,j} \leq k_{i,A}$). The values of μ and k for non-symbiotic daisies are constant and equal to 1.0 and 300, respectively. The luminosity range of non-symbiotic daisies is highly dependent

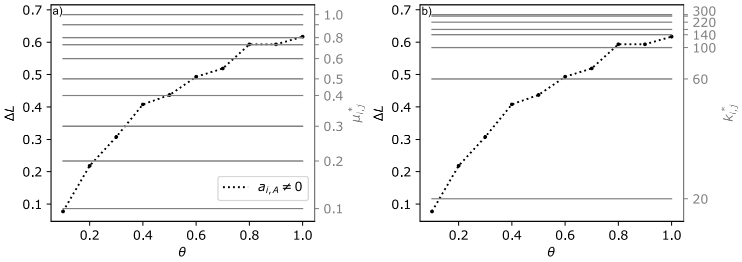

Figure 6: Luminosity range ($\Delta L = L_{max} - L_{min}$) of the coexistence of dark and light daisies as a function of the proportion of rich soils θ. Black dotted lines indicate the coexistence of non-symbiotic daisies with the parameters of Table 1 ($\mu_{i,A}$ and $k_{i,A}$ are constant). Solid grey lines indicate the coexistence of symbiotic daisies with different values of $\mu^*_{i,j}$ (a) and $k^*_{i,j}$ (b). The left vertical axis corresponds to the luminosity range and the right vertical axis to the values of μ (a) and k (b).

on θ because they cannot grow in region B, so this parameter defines the space available to them. Differently, ΔL of symbiotic daisies is independent of θ since although their performance is lower than that of non-symbiotic daisies, it is the same in regions A and B. However, the trade-off between costs and benefits of microbial symbiosis to the daisies relies upon the values of $\mu^*_{i,j}$, $k^*_{i,j}$, and θ. For low θ, the benefits of having more space available for symbiotic daisies outweigh the cost of reducing seed production and the lower yield in maturating to full-grown plants (horizontal grey lines are above the dotted black line), even when these penalties are significant (very low values of $\mu^*_{i,j}$ and $k^*_{i,j}$).

In contrast, when the proportion of rich soil is high, non-symbiotic plants can grow over much of the planet, so the costs associated with symbiosis may not be compensated by the benefits. In this case, the range of habitability of non-symbiotic daisies is greater than that of symbiotic daisies (horizontal grey lines are below the black dotted line). For example, for $\theta = 0.6$, the benefits of symbiosis exceed the costs only if $\mu^*_{i,j}$ is greater than 0.5 or $k^*_{i,j}$ is greater than 60 seeds. The symbiosis costs reflected in μ and k do not have the same effect on the regulation dynamics. Reducing the probability of seeds becoming adult plants (Fig. 6a) has a greater impact on plant coexistence than reducing seed production (Fig. 6b). This is highlighted by the concentration of the horizontal lines representing the values of k in the highest values of ΔL (Fig. 6b).

Another possible scenario is that in which symbiotic daisies grow better than non-symbiotic daisies in region A because symbiosis may improve their ability to obtain minerals in nutrient-rich soils ($k^*_{i,A} > k_{i,A}$ and $\mu^*_{i,A} > \mu_{i,A}$). Nevertheless, the results of this scenario can be inferred from Fig. 5, since also here the conditions in region A are better than in region B, although only for symbiotic daisies. As mentioned above, when symbiotic daisies perform the same as (or better than) their non-symbiotic counterparts, the latter go extinct by competitive exclusion, so ΔL correspond to the coexistence of symbiotic daises, and the conditions of non-symbiotic daisies do not affect the regulation of the planet's temperature.

4. Discussion

The Daisyworld is not a real climate model but, as a "toy model", it has been very useful in understanding the relationship and feedback among its components. Like the original Daisyworld model and its earlier extensions, the proposed model oversimplifies the processes that occur in the bioclimatic system, so its results should only be considered qualitatively. This work focused on the evaluation of the effect of symbiosis between plants and other organisms such as mycorrhizae and bacteria on the habitability and regulation of Daisyworld. We analyzed this type of symbiosis as it is the most common due to the complementary capacities between members of different kingdoms (Leigh, 2010) (see Box 2 in Boyle et al. (2011)). The model considers that a part of the planet is composed of nutrient-poor soils, where only symbiotic daisies can grow as their symbionts facilitate otherwise unavailable nutrients (e.g. by managing to enter smaller spaces and go further than the roots (Marschner and Dell, 1994; Bever et al., 2010; Field et al., 2015; Begum et al., 2019)). This extension assumes the spreading of daisies through seeds and adds three new parameters: i) θ represents the portion of the planet with rich soils, i.e., where symbiont-free daisies can grow, ii) μ is the probability that a seed develops into an adult plant, and iii) k is the maximum number of seeds produced by each plant. The latter two parameters manage to describe the improvements (benefits) and deteriorations (costs) as a result of the symbiosis.

Like other modifications of the Daisyworld model in which equations such as Lotka's and its extensions are used, the dynamics of the symbiotic Daisyworld are very similar to those of the original model (Lovelock, 1992), varying mainly in quantitative terms (see Fig. A.7). Unlike the original model that has four possible fixed point solutions (uninhabited, only dark, only light and dark and light coexistence), the symbiotic model has nine (involving colour permutations and symbiotic nature of daisies). However, stable equilibria involve symbiotic daisies (see Fig. 3) as long as the symbiosis provides greater benefits than costs for the plants. This means that in an ecosystem the non-symbiotic daisies would be competitively excluded, which is consistent with the fact that competitive species are frequently in symbiosis (Hempel et al., 2013; Tedersoo et al., 2020) and that mutualistic symbiosis results loss of non-mutualistic plants (Bever et al., 2010; Humphreys et al., 2010; Boyle et al., 2011; Simard et al., 2012). According to the plant-soil feedback theory, mutualistic symbiosis may reduce plant biodiversity because symbiotic plants monopolize resource acquisition (Bever et al., 1997). Non-symbiotic daisies can only exist when there are no symbiotic daisies of the same colour or when symbiosis has very high costs for plants (low values of $\mu^*_{i,j}$ and $k^*_{i,j}$), which means that symbiosis is not longer mutualistic.

Whether symbiosis improves or has no effect on plant performance ($\mu^*_{i,j} \geq \mu_{i,A}$ and $k^*_{i,j} \geq k_{i,A}$), a planet with symbiotic daisies can regulate its temperature in a wider range of L than a planet with exclusively non-symbiotic daisies (see Fig. 3). Our analysis suggests that symbiotic daisies (provided that microbial symbionts are widespread and not limiting anywhere on the planet) will invade and substitute the obligatory non-symbiotic variants and, in doing so, lead to an ecosystem more resilient to changes in solar irradiation. Similar results were obtained for the symbiosis between daisies (Boyle et al., 2011) and random mutations (Lenton and Lovelock, 2001). The uptake of nutrients allowed by symbionts can influence the coexistence of species and botanical diversity in ecosystems with limited nutrients (Aerts, 2002), extending the ecological range and enhancing the stress tolerance of plants (Begum et al., 2019). Besides, the symbioses between plants and mycorrhizae usually form mycorrhizal networks, defined as the link of roots of at least two plants through the mycorrhizal mycelium, mediating the transfer of nutrients and the transmission of phytochemical signals among plants (Simard et al., 2012; Tedersoo et al., 2020). These networks influence plant establishment, resource competition, species diversity, and succession within plant communities (Tedersoo et al., 2007; Smith and Smith, 2011; Simard et al., 2012); and regulate plant coexistence on a local scale (Tedersoo et al., 2020).

When the only difference between symbiotic and non-symbiotic daisies is the availability of space to grow (k and μ are the same for each daisy type and symbiotic condition), the luminosity range of coexistence does not vary with θ since symbiotic daisies will grow in the same conditions regardless of the region (see Fig. 4). However, if only daisies of one colour can be in symbiosis, ΔL becomes a function of the proportion of the planet with rich soils because free-symbionts daisies cannot reach nutrients in areas where they are limited. Each colour of daisies has a different effect because light daisies are more sensitive to changes in L and live in a wider range than dark ones (see Figs. 3 and A.7). Furthermore, the temperature value at which the planet is regulated depends on the colour of the symbiotic daisies. If symbiotic daisies are dark, T is greater than T_{op} since their growth is more favourable and they have a lower albedo, warming the planet. The opposite happens when symbiotic daisies are light.

The amplitude of the coexistence luminosity range is sensitive to parameter settings. If the soils of region B are very poor in nutrients, although symbiotic plants manage to grow there, they do not reach their maximum performance in seed production and maturation to seed-producing plants (low values of $\mu^*_{i,B}$ and $k^*_{i,B}$). In this case, the dependence of ΔL on θ is inversely proportional to the values of $k_{i,B}$ and $\mu_{i,B}$ since large areas with poor soils result in more plants growing in sub-optimal conditions (see Fig. 5). However, this dependence is different for μ and k, the first being like-linear and the second like-logarithmic. μ multiplies the entire terms representing the daisies' growth in Eq. 8, while k multiplies the parabolic function describing how κ depends on T, affecting S, s_i, a_T, and a_i.

The symbiosis may imply costs for the plants due to the carbon consumption by, e.g. mycorrhizal fungi, that would otherwise be allocated to biomass (Wright et al., 1998; Fisher et al., 2010; Brzostek et al., 2014). In fact, several studies have shown null or negative growth responses in mycorrhizal-colonised plants (Smith et al., 2003, 2004; Hoeksema et al., 2010; Jacott et al., 2017), and even that this can represent a disadvantage for plants (Hobbie, 2006). These effects were represented in the symbiotic Daisyworld model by reducing the values of

μ_{i,j^*} and k_{i,j^*} (see Fig. 6). Here, the luminosity range of coexistence does not depend on θ because the cost is the same for daisies growing in both regions. One way to determine if the benefits surpass the costs is by comparing the luminosity range of coexistence when the planet has and does not have symbiotic daisies. So, since ΔL of non-symbiotic daisies varies with θ, the definition of the type of symbiosis (mutualistic, commensal or parasitic) also depends on θ. For lower values of θ, symbiosis benefits outweigh the costs because, although non-symbiotic daisies have higher performance, they have only a small area to grow. This scenario represents the case where, regardless of the plant's growth response, symbionts deliver nutrients to the host under conditions in which it cannot allocate them on its own (Smith and Smith, 2011). For high values of θ, if the plant's performance is highly reduced ($\mu^*_{i,j}$ and $k^*_{i,j}$ are much lower than $\mu_{i,A}$ and $k_{i,A}$), costs exceed benefits, and the symbiosis becomes parasitic for the plants.

Symbiosis has also been related to increasing the growth and survival rate of seedlings (Harley, 1989; Nara, 2006; Smith and Read, 2008; Smith and Smith, 2011; Cordovez et al., 2019; Tedersoo et al., 2020; Teste et al., 2020), improving plant performance. In this case, the parameters k and μ of symbiotic daisies have higher values than those of non-symbiotic daisies, expanding the range of L in which the planet's temperature is regulated.

Notice that symbiosis in our model does not manipulate the albedo of daisies like that of (Boyle et al., 2011), but only considers an extra area of the planet to grow which represents the increase in the capabilities of plants to acquire nutrients. This is because we assumed symbiosis between the daisies and microbes and not between different types of daisies.

Our description of the partnership between plants and microbial symbionts was made without explicitly describing the dynamics of the latter partner. The model implementation implies that these microorganisms are transmitted vertically or widespread, never limiting in rich or poor soils and have no impact on albedo. For this reason, we talked about daisy uninhabited planet instead of a sterile or lifeless planet. This simplifying assumption seems to be a reasonable first approximation given that the partnership with, e.g., mycorrhizas seems to be as ancient as land colonisation by plants (Humphreys et al., 2010; Field et al., 2015; Jacquemyn and Merckx, 2019; Rich et al., 2021). However, this is clearly an assumption to be relaxed in future more realistic studies of how symbiotic relationships affect and modify the global ecosystem dynamics.

If the original Daisyworld model was instrumental to illustrate how the climates of living planets are expected to be more homeostatic than those of uninhabited planets, the analysis of the present model featuring plant-microbe symbiosis suggests that symbiosis may enhance planetary homeostasis and broaden the habitability range under exposition to variable solar energy.

Appendix A. Original Daisyworld model

Original equations of the Daisyworld model are presented in Watson and Lovelock (1983) and Maddock (1991), and correspond to a system of ordinary differential equations for the densities of light (w) and dark (b) daisies and the planet's temperature. The fractional coverage (a) of each type of daisy is:

$$\frac{da_i}{dt} = a_i \left[\left(1 - \sum_{j=w,b} a_j \right) \beta_i - r \right] \tag{A.1}$$

where $i = \{w, b\}$, and r and β are the death and growth rates, respectively. β is a function of the local temperature (T_i), a universal sensitivity constant (k_o), and the optimum growth temperature (T_{op}), and is given by:

$$\beta_i(T_i) = 1 - k_o(T_i - T_{op})^2, \quad |T_i - T_{op}| < k_o^{1/2} \tag{A.2}$$

Planet's temperature (T_e), albedo (α), and local temperature (T_i) equations are Eqs. 9, 11, and 10, respectively.

Fig. A.7 shows the phase diagrams of the original model and the non-symbiotic condition of the proposed model, using the parameters' values shown in Table 1. Note that although the quantitative values of the two models are different, the dynamics of each type of daisies are similar.

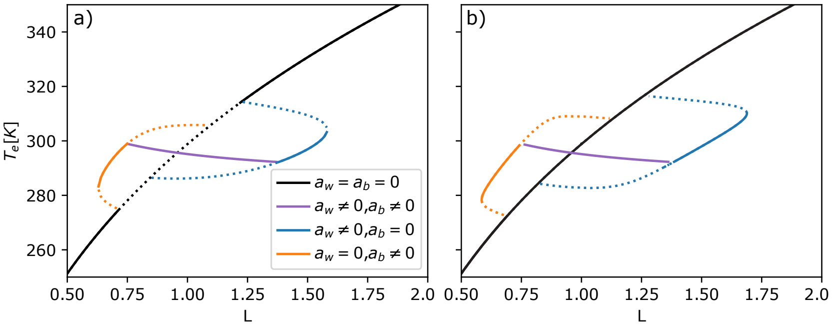

Figure A.7: Bifurcation diagrams of the original Daisyworld model (a) and the non-symbiotic condition of the proposed extended model ($a^*_{i,j} = 0$) (b). Solid (dotted) lines correspond to (un)stable conditions and each color to a combination of live daisy types, as indicated in the legend.

Appendix B. Increased growth rate due to symbiosis in the Daisyworld model

One of the most cited consequences of symbiosis in plants is the increase in their growth, net productivity, or biomass (e.g., Smith and Read, 2008; Bonfante and Genre, 2010; Hayat et al., 2010; Smith and Smith, 2011; Birhane et al., 2012; Simard et al., 2012; Arora, 2013; Jacott et al., 2017; Begum et al., 2019; Cordovez et al., 2019; Teste et al., 2020). Therefore, we decided to evaluate the response of the original model to increases in the growth rate (β). We assume that symbiotic daisies have a growth rate multiplied by a factor ρ that indicates the strength of the symbiosis effect, i.e.:

$$\beta_i^* = \rho\beta_i \tag{B.1}$$

Fig. B.8 shows the phase diagrams of the original model for ρ ranging from 1 to 1.9. $\rho = 1$ represents the non-symbiotic condition or no symbiosis effect on growth, and $\rho = 1.9$ indicates that symbiosis increases plant growth by 90%. The dynamics of uninhabited and only light (dark) conditions are identical to the original model when there are only symbiotic dark (light) daisies, but the dynamics of only dark (light) daisies and both colors coexisting change (Fig. B.8a(b)). Symbiosis causes the dark daisies to sprout at lower values of L, shifting the curve of the left branch to the left and making possible their existence within a greater range of luminosities than that of no symbiosis condition ($\rho = 1$). When symbiotic dark and non-symbiotic light daisies coexist, the planet's temperature increases with ρ (Fig. B.8a). This is because dark daisies have a higher chance of survival and their albedo is very low, reflecting less energy outward. The results for only symbiotic light daisies are analogous to the above, but instead of sprouting at lower values of L, symbiotic light daisies survive until higher values of L than the non-symbiotic ones (Fig. B.8b). As expected, the range of L values in which there is life also increases, but the planet's temperature decreases with ρ as light daisies reflect more energy.

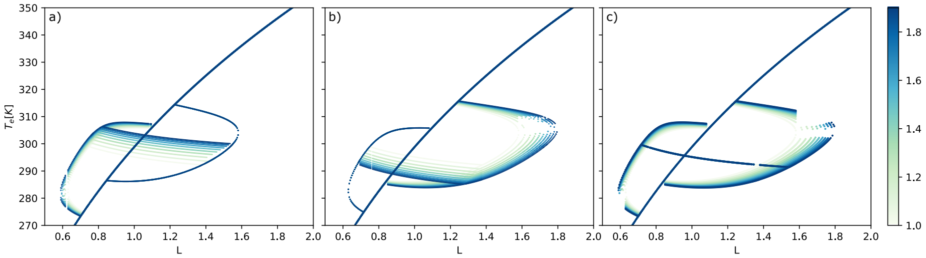

Figure B.8: Bifurcation diagrams of the original Daisyworld model for $\beta = \beta^*$. Only dark daisies in symbiosis (a), only light daisies in symbiosis (b), and dark and light daisies in symbiosis (c). Colors represent the value of ρ. The quasi-horizontal lines indicate the coexistence of both types of daisies, the left branch the existence of only dark daisies, the right branch the existence of only light daisies, and the line with quasi-linear increase the uninhabited condition (see Fig. A.7 for clarity).

When dark and light daisies are in symbiosis (Fig. B.8c), the dynamics of single species conditions are the same as described above. However, the planet's temperatures for each L value are the same for any value of ρ when the two species coexist, but the range of habitability expands for $\rho > 1$. This results in a more robust model when the daisies are symbiotic. Note that the increases in the L ranges for symbiotic dark and symbiotic light daisies are not symmetrical, but the effect of light daisies is greater.

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