



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.

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).

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). 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 (Rodríguez 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 sulphur, 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). 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).

Although the consequences on the species involved in these relationships have been widely studied, little has been done to understand how the dynamics of ecosystems and global variables are affected by these symbioses. Therefore, the main objective of this work is to investigate how the partnership between plants and microbial symbionts,

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such as mycorrhizal fungi or rhizobia, may affect the temperature of ecosystems and their habitability.

The biota and its relationships with other components of the Earth's system are too complex to be described by tractable mathematical equations, which led us to work 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 (Wood and Coe, 2007), 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 to 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 colonise 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. For this, we assume that the planet is partitioned into two regions, one with rich soils and one with poor soils with limited nutrients. We postulate that only symbiotic daisies can grow in the poor region, while both symbiotic and non-symbiotic daisies can grow in rich soils. This allows us to represent the benefits provided by symbionts resulting in plant species colonising soils where they cannot grow on their own because nutrients are not readily available or water is at distances that roots cannot reach on themselves (Pirozynski and Malloch, 1975; Thonar et al., 2011; Treseder, 2013; Field et al., 2015; van der Heijden et al., 2015; Menzel et al., 2016).

The proposed model describes seed spreading, germination and seedlings' growth and how these processes differ quantitatively between symbiotic and non-symbiotic daisies. The new equations have parameters that can be modified to account for the effects of symbiosis costs and the ability of plants to reproduce and grow in each soil region. After describing the modified equations, we analyse the possible solutions to the new system of equations and perform some scenarios to evaluate the model's sensitivity to the parameters.

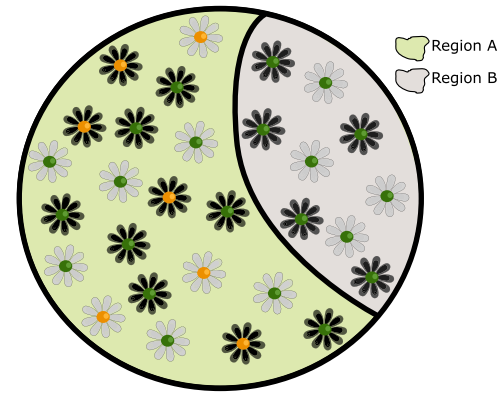


Fig. 1. Schematic model of symbiotic Daisyworld whose surface is covered by symbiotic and non-symbiotic dark and light daisies. Region A, with area θ , has nutrient-rich soils, whereas region B, with area $(1 - \theta)$, has poor soils with insufficient nutrients. Symbiotic daisies (green disc florets)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

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's area in region A is defined by $\theta \in [0, 1]$, whereas that in region B by $1 - \theta$. Region B has insufficient nutrient conditions, so only symbiotic plants can grow there because microbial symbionts facilitate nutrient acquisition. Microbial symbionts are not explicitly described; their effects are implicitly captured in the distinct dynamics of symbiotic or non-symbiotic daisies, assuming that they are available and never limiting in both regions.

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

2.1. Seed production

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

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

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., $\kappa_{i,B} = 0$. 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 and is given by:

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

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 constrains the temperature range in which

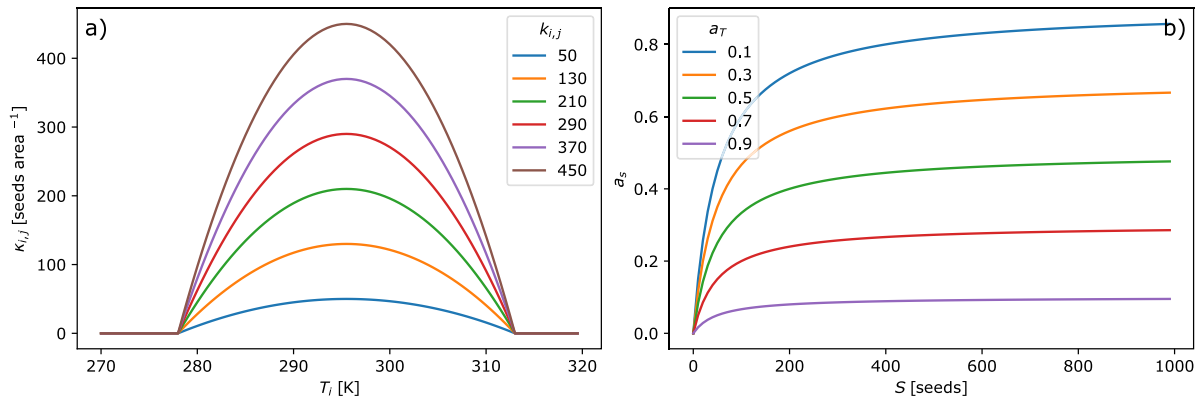


Fig. 2. Seed production rate by each daisy type per unit of area as a function of local temperature T_i and the maximum number of seeds produced per unit area $k_{i,j}$ (a) and relationships among the area seeded by daisies a_s , the total number of seeds S , and the total area covered by daisies a_T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

the growth rate is nonzero (in this case, the range in which the seed production rate is nonzero). Fig. 2a shows the rate of seeds produced by each daisy when the local temperature varies and for different values of k . The number of seeds produced is nonzero when the temperature is between 278 and 313 K, and 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) on the planet is $S = \sum s_i + \sum s_i^*$.

2.2. Fractional coverage of daisies

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:

$$a_s = \frac{S}{S_M + S}(1 - a_T) \quad (3)$$

a_T is the total area covered by daisies on the planet, defined as $a_T = \sum_{i,j} a_{i,j} + \sum_{i,j} a_{i,j}^*$, and 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 S when this number is small, and it saturates at $1 - a_T$ for very large values (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 the 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:

$$a_{i,A} = \theta a_s \frac{s_i}{S} \quad (4)$$

$$a_{i,A}^* = \theta a_s \frac{s_i^*}{S}$$

$$a_{i,B} = (1 - \theta)a_s \frac{s_i}{S} \quad (5)$$

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

The above development assumes that the seeds produced by each type of daisy, regardless 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:

$$\frac{da_{i,A}}{dt} = \mu_{i,A} \theta a_s \frac{s_i}{S} - r a_{i,A} = \mu_{i,A} \theta \frac{s_i}{S_M + S} (1 - a_T) - r a_{i,A} \quad (6a)$$

$$\frac{da_{i,B}}{dt} = \mu_{i,B} (1 - \theta) a_s \frac{s_i}{S} - r a_{i,B} = \mu_{i,B} (1 - \theta) \frac{s_i}{S_M + S} (1 - a_T) - r a_{i,B} \quad (6b)$$

$$\frac{da_{i,A}^*}{dt} = \mu_{i,A}^* \theta \frac{s_i^*}{S_M + S} (1 - a_T) - r a_{i,A}^* \quad (6c)$$

$$\frac{da_{i,B}^*}{dt} = \mu_{i,B}^* (1 - \theta) \frac{s_i^*}{S_M + S} (1 - a_T) - r a_{i,B}^* \quad (6d)$$

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. (6b) are set to zero.

Symbiosis may result in some costs to plants. For example, it has been reported that mycorrhizal fungi can consume up to 20% of the net primary production that, otherwise, would 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). Although our Daisyworld extension does not explicitly consider the cost of symbiosis as Boyle et al. (2011) does, it can be accommodated in the values of μ and κ .

2.3. Energy balance

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 with the ODE:

$$\frac{dT_e}{dt} = \frac{S_0 L}{c_p} (1 - \alpha) - \frac{\sigma}{c_p} T_e^4 \quad (7)$$

where T_e is the 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:

$$\alpha = \left(1 - \sum_{i,j} a_{i,j} - \sum_{i,j} a_{i,j}^*\right) \alpha_g + \left(\sum_{i,j} a_{i,j} + \sum_{i,j} a_{i,j}^*\right) \alpha_i \quad (8)$$

The albedos of bare ground (α_g) and each type of daisies (α_i) are assumed to be constant (see values in Table 1), and 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.,:

$$T_i^4 = q(\alpha - \alpha_i) + T_e^4 \quad (9)$$

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 Section 3 are in Table 1 unless otherwise specified.

Table 1
Parameters values of the symbiotic Daisyworld model.

Parameter	Description and units	Value
c_p	Specific capacity heat [erg cm ⁻² K ⁻¹]	$3 \cdot 10^{13}$
k	Rate of seed production [seeds area ⁻¹]	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	Fraction 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]	$5.75 \cdot 10^{-5}$

2.4. Measure of temperature regulation

In order to explore how symbiosis affects global temperature regulation and habitability in Daisyworld and how these depend on model parameters, we use a modification of the luminosity range, a measure of regulation proposed by Lenton and Lovelock (2001). The luminosity range is the range of values of L over which the planet is inhabited by daisies. However, we consider only the range in which the planet is inhabited and partaken by daisies of both colours, i.e., the difference between the maximum (L_{max}) and minimum (L_{min}) values of L (ΔL), indicated by double-head arrows in Fig. 3a. 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} .

3. Results

3.1. Stable equilibria and temperature regulation in the symbiotic Daisyworld

When the planet is uninhabited, the temperature is not regulated and increases directly with 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 of the original model (Lenton and Lovelock, 2001), but in the symbiotic Daisyworld, the permutations of dark and light daisy types with symbiotic and non-symbiotic conditions lead to richer dynamics and more 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 of the same colour. 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 luminosity increases, temperature also does, creating adequate conditions for light daisies to sprout. Then, for the range of L between ~ 0.73 and 1.44, both types of symbiotic daisies coexist stably. In this range, the temperature is almost constant and close to the optimum temperature T_{op} , and in fact, it decreases slightly with luminosity (dark blue lines in Fig. 3a,b). 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, the dark symbiotic daisies can persist down to $L \sim 0.57$, defining another hysteresis loop at low luminosities. It is important to note that the changes in solar luminosity L described above illustrate how regulation of planetary temperature can be potentially achieved according to the model. Although changes in solar luminosity are well documented on geological timescales, increases or decreases in the bifurcation parameter L , as just described, are illustrative examples of potential luminosity dynamics.

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 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 the 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 in which the planet is inhabitable for 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. 3a).

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

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 very small since non-symbiotic plants, of the opposite colour of 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

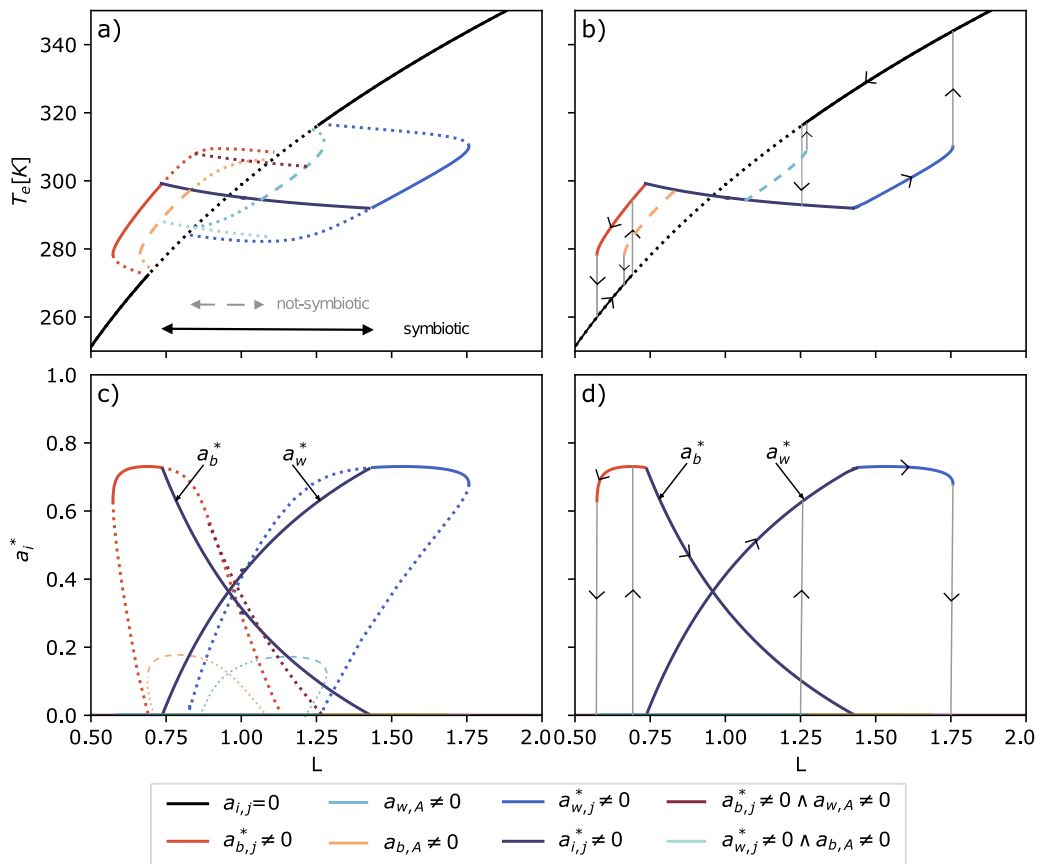


Fig. 3. Bifurcation diagrams. Planetary temperature (T_e) (a and b) and fractional coverage of daisies (a_i) (c and d) at steady state as a function of luminosity (L) in the symbiotic Daisyworld. (a) and (c) depict the values at the steady states that are uninhabited (black) or inhabited (coloured) by 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 parameter values are those shown in Table 1.

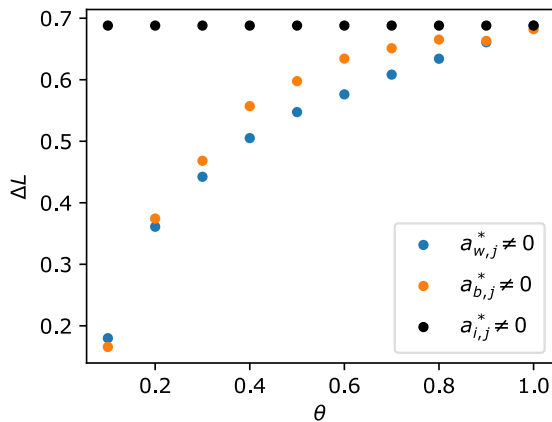


Fig. 4. Luminosity range ($\Delta L = L_{max} - L_{min}$) as a function of the proportion of rich soils θ when both daisies types are symbiotic (black points), only dark daisies are symbiotic (orange points), and only light daisies are symbiotic (blue points). The parameters of symbiotic and non-symbiotic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

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), since the effects

of changes in L are not symmetrical. The effects of light daisies are greater than those of dark daisies (see differences between symbiotic and non-symbiotic daisies of each colour in Fig. 3a).

On the other hand, 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. 3a). Symbiotic light daisies cool the planet below T_{op} while symbiotic dark 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 extension 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 assume that 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 ($\mu_{i,A}^* > \mu_{i,B}^*$).

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 small because although symbiotic daisies can grow in poor

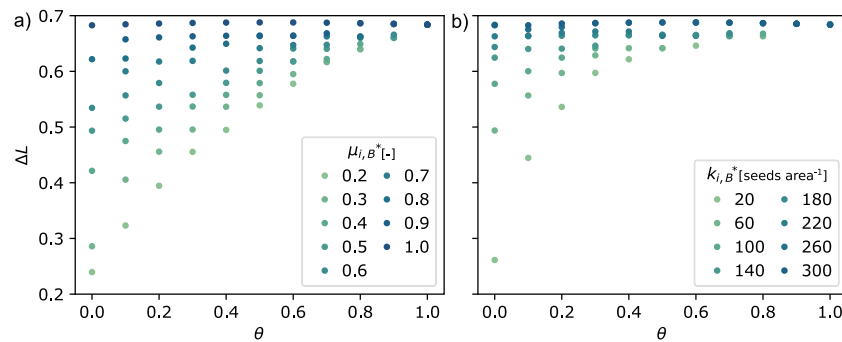


Fig. 5. Luminosity range ($\Delta L = L_{max} - L_{min}$) of symbiotic dark and light daisies coexistence as a function of the proportion of rich soils θ and for different values of $\mu_{i,B}^*$ (a) and $k_{i,B}^*$ (b). $\mu_{i,A}^* = 1.0$ and $k_{i,A}^* = 300$.

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 conditions are similar to those of 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. (6)).

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). As mentioned before, we do not directly consider the effect of this cost, but it can be represented by the values k^* and μ^* values. 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 when their performance may be affected by the symbiotic association ($\mu_{i,j}^* \leq \mu_{i,A}^*$ or $k_{i,j}^* \leq k_{i,A}^*$). The values of μ and k for non-symbiotic daisies are given in Table 1 ($\mu_{i,A}^* = 1$ and $k_{i,A}^* = 300$), $\mu_{i,j}^*$ varies between 0.1 and 1, and $k_{i,j}^*$ between 20 and 300. The values of $\mu_{i,j}^*$ and $k_{i,j}^*$ lower than those of non-symbiotic daisies indicate that the symbiosis results in a cost for plant's fitness.

The luminosity range of non-symbiotic daisies is highly dependent 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 values, the benefits of having more space available for symbiotic daisies outweigh the cost of reducing seed production and the lower yield in maturing 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 outweighed 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 at high values of k^* (Fig. 6b).

Another possible scenario is that in which symbiotic daisies grow better than non-symbiotic daisies in region A because the symbiosis may improve their ability to obtain minerals in nutrient-rich soils ($k_{i,A}^* > k_{i,B}^*$ and $\mu_{i,A}^* > \mu_{i,B}^*$). 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 corresponds to the coexistence of symbiotic daisies, and the conditions of non-symbiotic daisies do not affect the regulation of the planet's temperature.

4. Discussion

Daisyworld is a “toy model” of the climate that has been 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 analysed 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 aftereffect of the symbiosis.

As in other modifications of the Daisyworld model using equations such as Lotka's and its extensions, 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). The original model has four possible fixed point solutions (uninhabited, only dark, only light, and dark and light coexistence), while the symbiotic model has nine (involving colour permutations and symbiotic nature

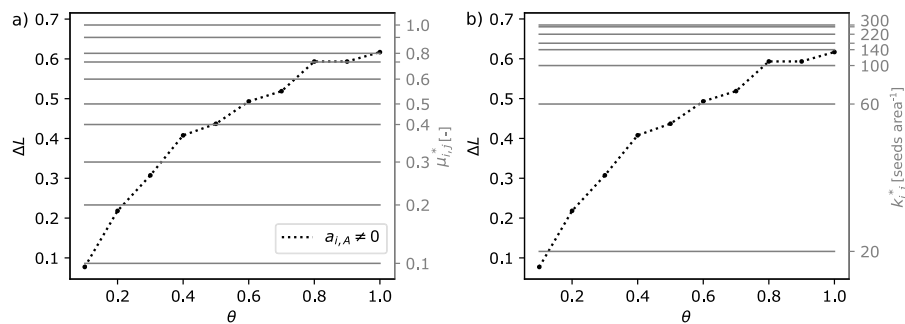


Fig. 6. Luminosity range ($\Delta L = L_{max} - L_{min}$) of the coexistence of dark and light daisies as a function of the proportion of rich soils θ and values of μ and k . Black dotted lines indicate the coexistence of non-symbiotic daisies with the parameters of Table 1 ($\mu_{i,A} = 1$ and $k_{i,A} = 300$). Solid grey lines indicate the luminosity range of coexistence of symbiotic daisies when symbiosis modifies the fitness of the symbiotic plants by reducing the probability of a seed becoming an adult plant $\mu_{i,j}^*$ (a) or the rate of seed production $k_{i,j}^*$ (b). $\mu_{i,j}^*$ varies between 0.1 (symbiosis results in a high reduction in the probability of a seed becoming an adult) and 1 (symbiosis does not affect the probability of a seed becoming an adult), and $k_{i,j}^*$ between 20 (symbiosis reduces seed production) and 300 (symbiosis does not affect seed production). The left vertical axes correspond to the luminosity range and the right vertical axes to the values of μ^* (a) and k^* (b).

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 monopolise 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 no 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 limited 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, 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 at 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 symbiont-free 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. When the soils of region B are very nutrient-poor, 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. (6), 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 $\mu_{i,j}^*$ 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 , the benefits of symbiosis outweigh the costs because, although non-symbiotic daisies have higher performance, they only have a small area to grow. This scenario represents the case where, regardless of the plant's growth response, the symbionts deliver nutrients to the host under conditions where 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. Additionally, and considering that among the most cited consequences of symbiosis involving plants are

increases in their growth, net productivity, and 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), we evaluate the response of the original model to increases in growth rate (β_i in Eqs. (A.1) and (A.2)) (see Appendix B). Fig. B.8 indicates that an increased growth rate results in a more robust model, extending the range of luminosity in which both types of daisies coexist. Notice that the 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.

Although the partition of the model into two regions allows representing the improvement in the acquisition of nutrients or water of symbiotic plants, it does not directly consider the availability of nutrients and water, nor the competition for light or pollinators between different plant species. Furthermore, this model assumes that plants only affect climate through temperature (as the original Daisyworld model and most of its extensions) and does not consider water balance responses. However, since the water and energy balances are deeply coupled, future extensions could consider the effect of symbiosis on the different components of the water balance. 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 daisies' 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. Lastly, this extension, as the original Daisyworld model, is zero-dimensional, so it excludes the spatial structure of the planet. Although local temperatures refer to the temperature of each daisy based on its colour, its individual effect is unknown. Neither the number of daisies of each colour nor its spatial distribution is modelled, but only the proportion of the planet covered by it. Some approaches to representing the spatial distribution of daisies in one and two dimensions have been presented (e.g., Von Bloh et al., 1999; Adams et al., 2003; Alberti et al., 2015; Kageyama and Yagi, 2020) and could be used as a reference for future analyses that contemplate the spatial dynamics of the symbiosis.

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

5. Conclusions

The effect of plant-microbe symbiosis on the global properties of an ecosystem has been little studied. For that purpose, we described here an extension of the Daisyworld model that includes symbioses between daisies and microbes such as mycorrhizal fungi and rhizobia. With this extension, we assessed the planet's habitability and temperature regulation. We divided the planet into two regions, one with nutrient-rich soils and the other with nutrient-poor soils, allowing only symbiotic plants to grow in the latter. The extended model considers the spread of daisies through seeds and incorporates two parameters that indirectly take into account the costs and benefits of the symbiosis.

The symbiotic Daisyworld has nine possible fixed point solutions, however, if symbiosis generates greater benefits than costs to plants, stable equilibria involve only symbiotic daisies. This suggests that symbiont-free daisies would be excluded from the planet by competition. Furthermore, the inclusion of symbiotic daisies results in an inhabitable planet over a wide range of luminosity, being able to regulate the planet's temperature under exposition to variable solar energy.

We simulated several scenarios to analyse the extended model sensitivity to the three parameters introduced, namely, the fraction of the planet with nutrient-rich soils (θ), the rate of seed production (k), and the probability of a seed becoming a fully grown plant (μ). The symbiotic Daisyworld model is sensitive to θ when only one colour of daisies is in symbiosis and when k or μ values are distinct for symbiotic and non-symbiotic daisies. The temperature regulation range shows significant differences when varying μ and k in both regions, especially in μ , due to the form of the differential equations that describes the daisy coverage fractions (Eqs. (6)).

Daisyworld and this extension are oversimplified models, so their results should only be considered qualitatively. However, due to its simplicity and stability, this approach is useful for illustrating and understanding biosphere-geosphere interaction phenomena and their effects on ecosystems.

CRedit authorship contribution statement

Estefanía Muñoz: Conceptualization, Methodology, Software, Writing – original draft, Writing – review & editing, Visualization. **Jorge Carneiro:** Conceptualization, Methodology, Writing – review & editing, Visualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Since it is a theoretical study, the values used are illustrative. Codes will be provided upon request.

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Appendix A. Original Daisyworld model

The 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 coverage fraction of light (w) and dark (b) daisies and the planet's temperature. The fractional coverage (a) of each type of daisy is:

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

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

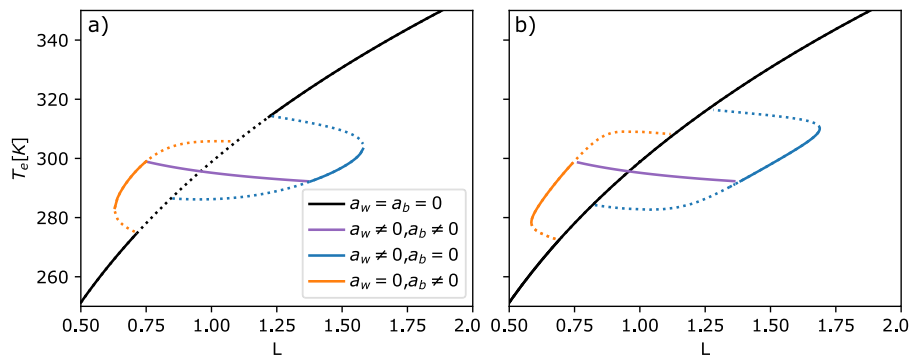


Fig. A.7. Bifurcation diagrams of the original Daisyworld model (a), and the non-symbiotic condition of the proposed extended model ($a_{ij}^* = 0$) (b). Solid (dotted) lines correspond to (un)stable conditions, and each colour to a combination of live daisy types, as indicated in the legend.

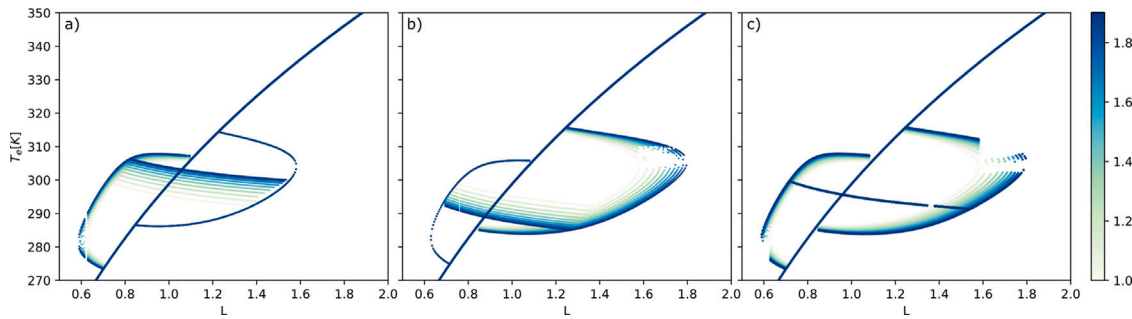


Fig. B.8. Bifurcation diagrams of the original Daisyworld model for $\beta = \beta^*$. Only symbiotic dark daisies (a), only symbiotic light daisies (b), and both dark and light daisies in symbiosis (c). Colours indicate the value of ρ . The quasi-horizontal lines indicate the coexistence of both types 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).

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. (7), (9), and (8), respectively.

Fig. A.7 shows the phase diagrams of the original model and the non-symbiotic condition of the proposed extension of the 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.

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

To evaluate the response of the original model to increases in the growth rate (β_i , Eq. (A.2)), 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 colours 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 larger range of luminosities than that of no-symbiotic 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 the 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 are daisies also increases, but the planet’s temperature decreases with ρ as light daisies reflect more energy. 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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