

The Sun Always Rises: Behavioral Attunement to Abiotic Reins

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Abstract

Behavior has an understated role in the genesis of complex ecologies. Discussion of ecological regulation describes the phenomenon in terms of coupled feedbacks which have been connected by Harvey (2004) to rein control as introduced by Clynes (1969). These descriptions have motivated the question of how communities that instantiate such feedbacks can evolve in the first place, especially with respect to global regulatory effects such as those supposed in Lovelock and Margulis' Gaia theory (1974). While Gaian regulation is not incompatible with evolution, it appears there are intermediate steps that are necessary for its establishment, and likely the establishment of coupled ecological regulation at any scale. Here we present a series of dynamical models that show how simple dormancy behavior can help account for that differential survival across a variety of seasonal conditions. Furthermore, the combination of that behavior and a traditional rein control mechanism lead to a significant increase in survivable conditions, providing a hypothesis for how ecological regulation may be scaffolded. Further discussion suggests that effective behavior of pioneer species is a requirement for the establishment of robust ecosystems.

Introduction

Biotic and abiotic feedback relationships have long been phenomena of interest in ecology, biology, and cybernetics. These feedbacks mechanize the creation, destruction, and maintenance of species' niches and provide insight into how biotic activity can create the environmental circumstances that facilitate further biotic activity. At a global level, these phenomena have garnered significant attention under James Lovelock and Lynn Margulis' Gaia hypothesis, suggesting our entire planet is a self-regulating complex system, and Lovelock's subsequent formalization of the theory in the Daisyworld model (Watson & Lovelock, 1983). Daisyworld has gone on to inspire many more sophisticated models (e.g., Williams et al. 2007; Christenson et al. 2010) and extensions ranging from the application of thermodynamics to more complex ecologies (e.g., Lenton et al. 2018; Nicholson et al. 2018), all with the goal of mimicking ecological

regulation in real ecosystems at various scales.

One such extension by Harvey (2004) connects the homeostatic phenomena examined in Daisyworld to rein control as introduced by Clynes (1967). Rein control extends from Clynes previous work on unidirectional rate sensitivity (Clynes, 1961), which demonstrated the many cases in which physiological mechanisms can only change some variable in one direction. Clynes suggests that biological systems typically have at least two means of regulating a certain variable that operate in opposing directions. In emphasizing rein control, Harvey's analysis of a simplified Daisyworld invokes a familiar conclusion; for homeostatic regulation of an environment, we need feedbacks that point in both directions of change in the environmental variable.

However, a criticism historically levied against Gaia theory suggests the selection of opposing reins is not compatible with evolution (Doolittle, 1981; Dawkins, 2016). In short, depending on the independent evolution of two species with opposing effects on the environment is unsatisfying as it relies too much on some other source of fine tuning. These critiques in part have led many to conclude that Gaia theory is not a useful explanation of environmental regulation (Tyrell, 2013). That said, nuanced analyses of natural selection have shown that regulation of this kind is possible in natural systems if it arises not by selection through reproduction but by differential persistence (Doolittle & Inkpen, 2018). As such, environmental regulation via rein control may occur in nature, but it appears to be a survival-promoting pattern rather than a guaranteed evolutionary outcome. So, to uncover the origin of rein control in an ecological community, we must examine how differential persistence may facilitate its origin.

One source of inspiration for a solution is the facilitation model of ecological succession, in which the activity of a pioneer species makes the environment suitable for other species to enter (Whittaker, 1975; Connell & Slayton, 1975). While this is not the only model of succession, it is one that applies particularly well to substrates that have yet to be influenced by organisms or sustain biotic activity, and has found relevance in study of niche construction, environmen-

tal engineering, and related phenomena. It has been found that one particular feature that allows pioneer species to be successful is the ability to go into long periods of dormancy (Marks, 1974). Behavioral ecology is a robust field (for one survey see Piersma & Van Gils, 2018) that has time and again demonstrated the impact of organismal perception and decision-making on organism-environment outcomes. Here, behavior may be the key to facilitating ecological regulation via rein control in the uncolonized environments that once constituted much of the planet's surface.

Importantly, the planet we live on does not provide static abiotic conditions. Daisyworld and its progeny were built on the premise that the abiotic condition of interest (luminosity) is constant locally and only changes over millenia, allowing the biota to evolve to a stable equilibrium. However, the seasonal nature of most organisms' life histories suggests they must be able to accommodate a range of abiotic conditions rather than a fixed value. Furthermore, Harvey's (2004) analysis also reveals that much of the Daisyworld model's success has nothing to do with the biota, but rather implied spatial separation between the species and in turn the creation of microclimates. This seems to be a special case of ecological regulation, and does little to explain how such regulation may work on the local spatial scales that are often suggested in community ecology and origins of life work, and are likely if we rely on an evolutionary mechanism of differential selection.

Here, we will demonstrate through a series of dynamical models that (1) simple behavior on the part of a single species can buffer large amounts of seasonal variability that cannot be accounted for by rein control between two species, (2) the addition of behavioral feedbacks to that two-species rein control mechanism allows for super-additive increases in survivable ranges in seasonal environments, and (3) any useful concept of rein control or biotic/abiotic regulation more broadly must take the organism/environment (biotic/abiotic) dynamics into account as the unit of study rather than forces exerted by just one or the other. In sum, rein control of the organism-environment system mediated by simple behavior may provide the circumstances for the emergence of ecological regulation, perhaps even on the global scale originally proposed by Gaia theory.

Before moving forward, we would like to delineate between homeostasis at a species level and at a community level. Most frequently, homestasis pertains to a certain organism or population of organisms. However, the paradigm in question here is one of communities, and as such we will be discussing *community homeostasis* as the persistence of multiple species while *species homeostasis* refers to the persistence each species independently. In a community of one species, these terms would be synonymous. Lastly, there are many scales at which one can examine these phenomena. Daisyworld and related studies have traditionally appealed to the global level. However, we choose to analyze a local

ecosystem to focus on the impact of behavior on community function and the succession process without making any hard claims about its application on a global level. Global application is an area for future research.

Behavior Increases Single Species Survival

To begin, we will appeal to the argument that species are not necessarily introduced to new environments as well-balanced pairs but rather are introduced incrementally with characteristics that facilitate independent survival. As such, these species must be able to survive without the benefit of an ecologically coupled partner. Congruent with Clynes' unidirectional rate sensitivity, these species can only "pull" the environment in one direction (e.g., increase the amount of atmospheric oxygen). Despite this limitation, it is possible that the simple ability to moderate that pull can facilitate more robust survival. Two cases will be presented, one in which the species pulls indiscriminantly to try to maximize growth and one in which the species may temper its growth in less preferable environmental conditions. These "single rein" models are specified as follows:

$$\frac{dS}{dt} = f(R)S\left(1 - \frac{S}{c}\right)(1 - a(R - v)^2) - dS \quad (1)$$

$$\frac{dR}{dt} = xSf(R) + i\left(1 - s_{\text{int}} \sin\left(\frac{t}{s_{\text{len}}}\right)\right) - oR \quad (2)$$

Imagine an aqueous environment with a single species of organism S that is physiologically coupled to a certain abiotic condition R (e.g., pH level). The metabolic activity of organism S 's population increases pH level R . There is no explicit food resource, rather we assume that species S lives in enough abundance to follow logistic growth to carrying capacity c . A certain proportion d of the species dies at each time unit, a rate that is independent of R . The current state of R affects the growth rate of species S depending on the distance of that state from the species' ideal condition v , linearly scaled by a . Change in the abiotic state R is scaffolded on a chemostat with a constant influx amount i and outflux proportion o . R undergoes seasonal change with sinusoidal variation of the influx amount (s_{int}) at a given seasonal length (s_{len}). This time-varying input makes the systems non-autonomous, and importantly leads to periodic forcing of what would otherwise be fixed equilibria like those in the original Daisyworld model. Lastly, the metabolic activity of S , increases the value of R linearly scaled by x . $f(R)$ describes the behavioral coupling between S and R :

$$f(R) = \frac{k^\beta}{k^\beta + R^\beta} \quad (3)$$

In cases with no behavioral coupling, we set $f(R) = 1$ giving it no influence over the system's behavior. In cases with behavioral coupling, its value depends on the parameterization of $f(R)$, where β determines the severity of the behavioral shift and k aligns with the abiotic ideal. As such,

Parameter	Label	Value
Abiotic Impact	a	0.001
Death Rate	d	0.1
Abiotic Influx	i	10
Abiotic Outflux	o	0.2
Ideal Abiotic Value	v	45
Carrying Capacity	c	200
Biotic Impact	x	0.5
Season Intensity	s_{int}	0 - 3
Season Length	s_{len}	10 - 50
Behavioral Hill Exponent	β	4
Behavioral Hill Threshold	k	45
Cutoff Threshold	γ	0.1

Table 1: Parameter values used for all simulations.

when R is higher than the abiotic ideal, $f(R)$ will be a low value. When it is lower than the abiotic ideal, $f(R)$ will move closer to 1. Notably, death rate d is not impacted by this behavioral coupling, only the growth rate. Any population that falls below the cutoff threshold γ is considered extinct. We want to determine how each variation of the single species model fares in a variety of seasonal conditions, as any case that allows for survival in a wider range of seasonal circumstances implies that the species is more resilient to environmental change. In turn, it is more likely to survive in a larger area of the planet and thus has a greater chance of participating in a rein control schema. As such, we conducted parameter scans varying the season's length (s_{len}) and intensity (s_{int}) and evaluated the efficacy of the single species model with and without behavioral coupling¹. The parameters used in all simulations are shown in Table 1.

Behavioral coupling allows for survival in a significantly broader range of seasonal conditions despite no difference in the underlying death rate or peak growth rate, as shown in Figure 1 which compares the behaviorally coupled and uncoupled case. It also allows for greater average populations in those survivable conditions. The behavioral coupling reduces the species' growth rate when the abiotic condition becomes too much greater than the species' ideal. This lessens the contribution of the species' metabolic activity to the increase of the abiotic condition, and in turn when the seasons shift, the abiotic condition does not have as far to fall back to the species' preference. The species is then free to grow at its maximal rate until the seasons shift once again. The losses from the longer return period in the non-behaviorally coupled case are greater than those sustained by the behaviorally-coupled species' reduction in growth during the down season.

Notably, in the absence of seasons the model without behavioral coupling has a marginally greater survivable range

¹Code for the simulations and analyses in this paper can be found at <https://github.com/eforbes24/BARC>

of inputs (i) than the model with behavioral coupling (see individual species populations in Figure 3). Slowed growth that is beneficial in the seasonal case is detrimental in the non-seasonal case, as dormancy merely delays death without environmental fluctuation. That being said, the difference is marginal, especially relative to the seasonal benefit.

Here we see a version of rein control, but this time between the species and its environment. The species is able to pull the abiotic condition toward its ideal state during one season and in turn can allow the environment to do the pulling in the opposite season where the species has no ability to adaptively shift the environmental state. So, simple behavior appears to be a mechanism by which a species may increase its chances of survival and of participating in later ecological regulation.

Combined Rein Control and Behavior

Now we continue to two-species cases to examine how the survival-enhancing behavioral coupling and the established between-species rein control interact. All examined cases are truly mutualistic, in that each species "pulls" the environment in the opposite direction (e.g., one species increases oxygen while the other decreases it). Once again, two cases are presented, one in which both species pull indiscriminantly to maximize growth and one in which both species may temper their growth in less preferable environmental conditions. These two rein models are specified as follows:

$$\frac{dS}{dt} = f(R)S\left(1 - \frac{S+Q}{c}\right)(1 - a(R-v)^2) - dS \quad (4)$$

$$\frac{dQ}{dt} = g(R)Q\left(1 - \left(\frac{S+Q}{c}\right)(1 - a(R-v)^2)\right) - dQ \quad (5)$$

$$\frac{dR}{dt} = x(Sf(R) - Qg(R)) + i\left(1 - s_{\text{int}} \sin\left(\frac{t}{s_{\text{int}}}\right)\right) - oR \quad (6)$$

We imagine the same circumstances as the single species model with the addition of a second species Q that is also physiologically coupled to the abiotic condition R . The two species share the same abiotic preference v and are subject to the same carrying capacity c as they share a spatial constraint from the environment. However, activity of species Q has the opposite effect on the abiotic state R as the activity of species S (but is likewise scaled by x). Furthermore, species Q 's behavioral coupling is opposite that of species S :

$$g(R) = \frac{R^\beta}{k^\beta + R^\beta} \quad (7)$$

These opposing directions of behavior are symmetric and congruent with the original pulls of the rein control mechanism. When $f(R)$ and $g(R)$ are set to 1, there is no behavioral coupling in the system. Without behavior, this model is similar to the simplified version of Daisyworld presented by Harvey (2004; Figure 4) with maximum conductance between the daisy patches (and therefore a shared local environment). With behavioral coupling, each species shares the

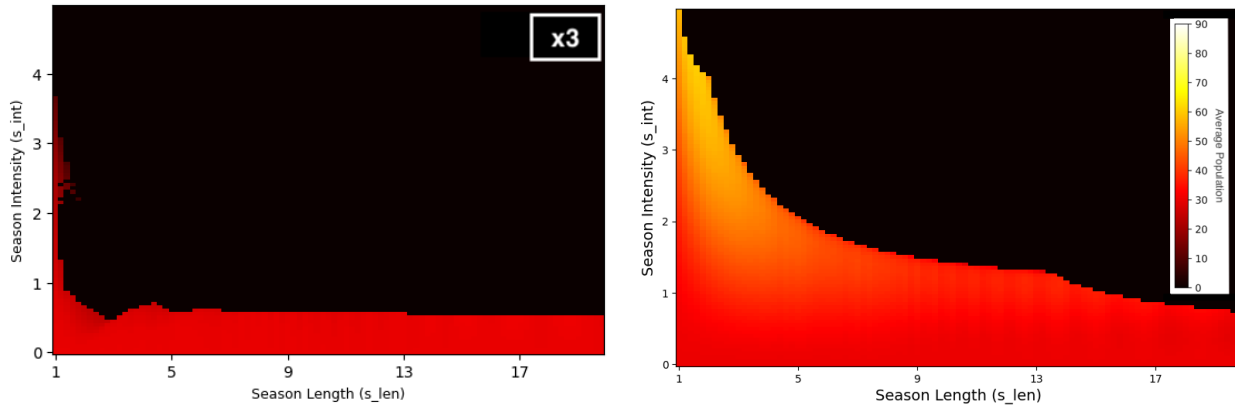


Figure 1: Behavioral coupling significantly increases survival of a single species in seasonal environments. Here, parameter scans of the single species model without (left) and with (right) behavioral coupling are shown. Each scan examines season length s_{len} from 1 to 20 at intervals of 0.2 and season intensity (s_{int}) from 0 to 5 at intervals of 0.05. The color of each point represents the average value of the species population S over the course of the run (1000 timesteps, with a 100 timestep transient for the system to reach quasi-stability). Note that the color mapping on the left is three times as bright, so an average population of 1 appears to be an average population of 3. The constant pull to maximize growth in the non-coupled case contributes to greater seasonal shifts in the abiotic state R and in turn lower average populations resulting from less time spent near the species' ideal value. Conversely, while the coupled case lowers its growth rate at times with no change in death rate, this reduction of activity keeps the abiotic state closer to the species' ideal value, allowing for greater average populations and more robust survival.

same parameterization of β and k that determines their activity based on the abiotic state.

Once again, we want to determine how these variations of the double species model fare in a variety of seasonal conditions. As such, we conducted the same parameter scans of seasonal length (s_{len}) and intensity (s_{int}) used to assess the single species models. The parameters for these scans are identical to those used previously.

In the two species case, behavioral coupling not only allows for survival across a significantly broader range of seasonal conditions, it increases in tolerance to seasonal intensity as seasons lengthen, as shown in Figure 2. The model without behavioral coupling ($f(R)$ and $g(R) = 1$) shows high average populations, but otherwise a similar pattern of results as the single species model with behavioral coupling. In fact, the behaviorally coupled single species model facilitated survival in a broader range of parameter space than the two species model without behavioral coupling. In the cases this model fails, seasons are either too intense and the rein control mechanism does not have ample time to compensate for the sudden shift, or the seasons are too long in which case the abiotic condition spends too long in what would be an unsustainable regime (where the species would not survive if i was held constant) leading to population collapse.

When behavioral coupling is added to the two-species model, it yields a significantly different pattern of results. Not only does it outclass the other models in survivable parameter space, survivable season intensity increases as season length increases. This has an asymptotic limit (see Figure 2, bottom), but regardless the model performs significantly better and salvages the long-term community home-

ostasis of the original Daisyworld model that was lost when both species were made to share a local environment as noted by Harvey (2004) (for a visualization, see Figure 3).

Species S increases activity when the abiotic state R is low and its activity increases the abiotic state R . Conversely, species Q decreases activity when the abiotic state R is high and its activity decreases the abiotic state R . When the abiotic variable drifts below v , species S decreases its activity while species Q increases its activity. This would rapidly push the abiotic state back to the other side of the ideal, at which point the behaviors would switch roles, pulling the abiotic state back the other way. This continues until the abiotic state approximates the ideal value, and the species' activity becomes equal. As seasons change, the behavioral regimes adjust accordingly, allowing that environmental change to be buffered by changes in the species' behavior and populations.

Characterizing the Survivable Parameter Space for Behavioral Coupling

How does the formalization of behavior explain why longer seasons allow this model to survive more intense fluctuations? Increases in seasonal intensity amplify the underlying shape of the seasonally forced oscillation of the populations and the abiotic state (Figure 4A). As such, increases in intensity will eventually lead the oscillation to intersect with a population boundary $S = \gamma$ or $Q = \gamma$, in this case $\gamma = 0.1$, at which point the system becomes identical to the single species cases we previously considered. However, when season length is increased, the oscillation changes in shape rather than size (Figure 4B), the benefit of which varies in

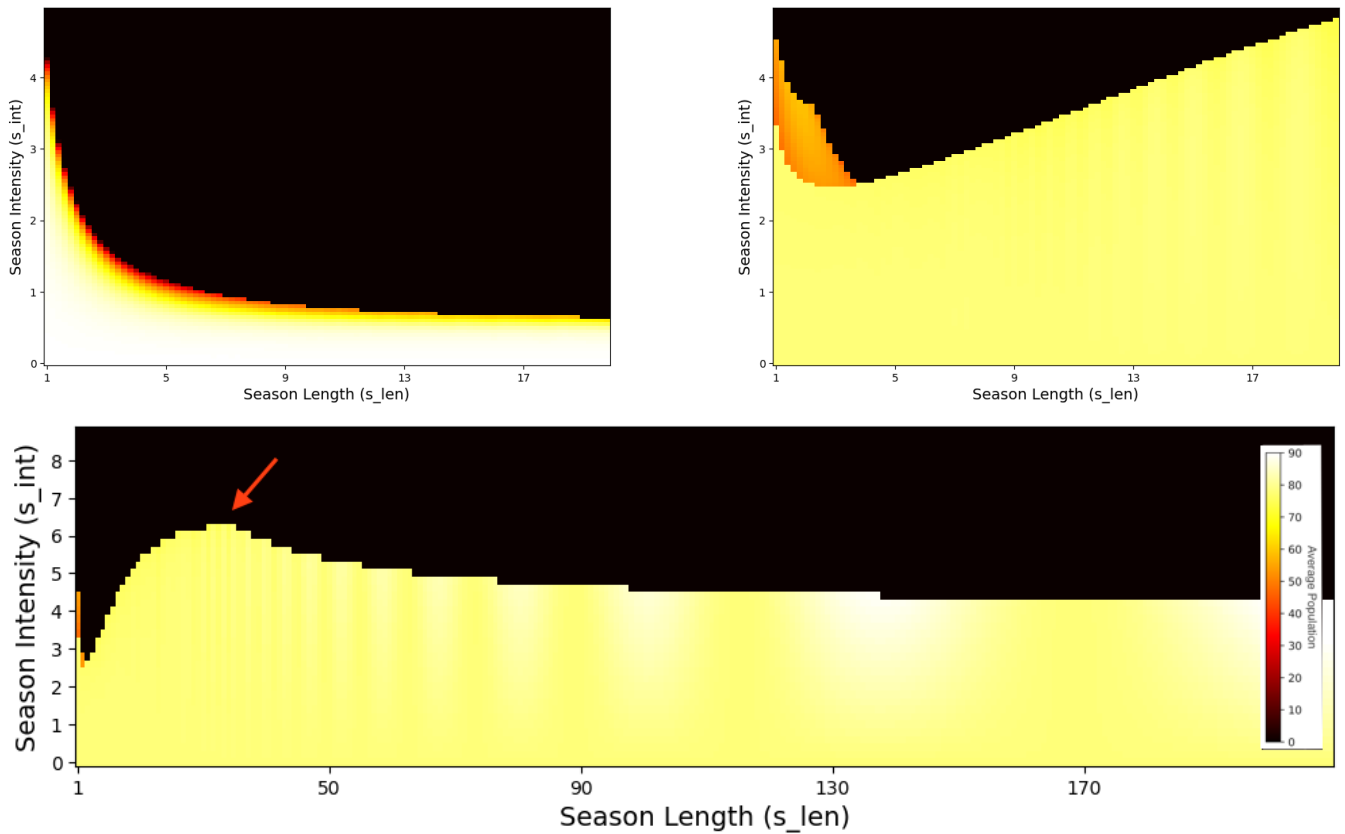


Figure 2: While rein control leads to high average populations, behavioral coupling leads to a massive increase in survivable season parameters. Here, the same parameter scans of the rein control model without (top left) and with (top right) behavioral coupling are shown, as were described in Figure 1. Notably, the heat map in this case still applies specifically to the population of species *S*. Species *Q* is not shown. However, the survival of species *S* is almost always contingent on the survival of species *Q*, and therefore we can infer mutual success. The one exception to this is the small orange area at the top of the behaviorally coupled two-species case (top right). Here, only species *S* survives, and the system falls back to the results we see in Figure 1. All brighter areas show survival of both species *S* and *Q*. The third scan (bottom) expands the behaviorally coupled case in the top right and examines it along expanded parameter ranges of season length (s_{len}) from 1 to 500 at intervals of 2 and season intensity (s_{int}) from 0 to 9 at intervals of 0.2. The non-coupled case performs in a similar range to the single-species coupled case, albeit with greater population outcomes. The coupled case however shows not only a wider parameter range of survival, it shows that there is a sweet spot in season length where the community can sustain significantly greater seasonal intensities (the peak of which is denoted by the red arrow).

each model.

Without behavioral coupling, increased season length warps the two-species system's oscillations toward extinction (Figure 4C). As previously described, the abiotic state spends more time beyond the range where the rein control mechanism can effectively pull it back and the population dips lower and lower. It comes as no surprise then that there is limited change in season length that allows for a successful community unless the season intensity is very low.

When behavioral coupling is introduced, the oscillations appear to be flattened toward the abiotic ideal v (Figure 4D). This flattening suggests that like the previous model some of the seasonal variability in the abiotic condition is being translated into population fluctuation, but in this case those fluctuations hold the abiotic state R closer to the ideal value

and in turn allows populations to rebound much quicker when seasons change.

The apparent increase in survivable intensities with increased season length is conditional on how the oscillation in the behaviorally coupled case changes shape, a feature that is sensitive to several parameters in the model (see again Figure 2). The asymptote of the curve shows that below a certain intensity it is arbitrary how long a season is, as both species are able to reach a stable population at all abiotic ranges that the chemostat might present. That is, if both species can reach an equilibrium above the cutoff (γ) at fixed chemostat states of $i(1 - s_{int}) - o * R$ and $i(1 + s_{int}) - o * R$, the length of the season becomes redundant. Again, see the long-term behavior in Figure 3.

Figure 5 describes the origin of the humped peak in pa-

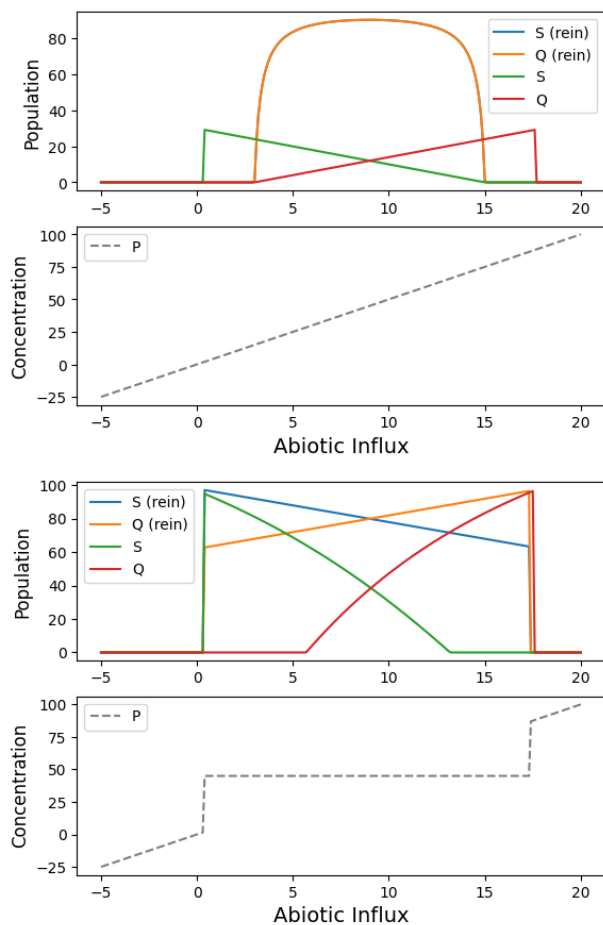


Figure 3: Behavioral coupling recreates the long term community homeostasis generated in the original Daisyworld model that was lost by putting both species in the same local environment. Here we show long-term behavior of the behaviorally coupled (bottom) and uncoupled (top) version of the rein control model along a gradient of influx (i) values according to the Daisyworld paradigm. Equilibrium values for each species individually and each species in the combined case are displayed. The gray line depicts the abiotic equilibrium in the environment at that value of influx, which notably converges on the ideal value (v) in the behaviorally-coupled case. Without behavior, the species can only survive in circumstances where both species would survive independently. With behavior, that range extends to all circumstances in which either species could survive independently.

parameter space (see red arrow in Figure 2). Increased season length allows the population change to better follow the abiotic input, in turn holding the state of R closer to the species' ideal v . However, longer seasons can drop populations below the viable threshold imposed by the cutoff value (γ). More simply, at first longer seasons allow for tighter regulation of the abiotic state, but too long leads the species to be dormant for so long they die out entirely.

Parameters especially relevant to the shape of the hump include the species proportional impact on the abiotic state

(x), the proportional impact of the abiotic state on the species' growth rate (a), the inherent death rate of the species (d), and the distance between the chemostat's non-seasonal equilibrium (it's average value, denoted by i/o) and the species' ideal value (v). Manipulations for these parameters can be found in the model code.

Mutual proportional effects of species and abiotic state x and a have an inverse relationship. Raising x increases the range of seasonal intensities in which the model is successful, including an increase in the previously described asymptote. This follows as x implies the impact of the populations on the abiotic state, effectively magnifying the amount of regulation they are capable of. Conversely, raising a leads to lower survivable intensities for the opposite reason; greater a leaves less margin for error between the species ideal state and the current state before growth rate falls below 0.

Lower death rate d not only increases survivable intensities and the asymptote as one may expect following the analysis of x , but stretches the entire shape out, leading to a peak in survivable intensities at a greater season length than the original parameter set. At lower death rates, it takes longer for increasing season length to stretch the population beyond (γ) as also shown in Figure 5. As such, the season length at which this peak occurs is scaled linearly with d .

Lastly, the distance between v and the chemostat equilibrium has little effect on the asymptotic seasonal intensity, but has significant impact on the early shape of the curve. The hump in fact only exists if the two values are close enough together; otherwise the curve appears to approach that asymptote logarithmically, necessitating some amount of seasonal length for any chance of survival at all. As that difference increases, that asymptote lowers until eventually no survival is possible in any case.

In sum, the two-species model suggests that the addition of simple dormancy behavior not only benefits the single species case, it can lead to a super-additive increase in survivable seasonal environments when present in a rein control schema. In terms of the differential survival of interest, this all the more suggests that behavior and the synchrony of behavior within an ecological community may have provided some of the early flexibility that allowed for later community-level regulation. More concisely, in both these models behavior is more effective than physiology at allowing a species to survive in a wider range of seasonal environments. While this is by no means a universal rule, it shows we should highlight behavior as well as physiology in discussions of environmental regulation and its evolution.

Discussion

These models suggest that the rein control phenomena in ecology is not constrained to the biota of the ecosystem. Rather, effective environmental regulation is conducted by both the biotic and abiotic components of the ecosystem, a conclusion that is also consistent with Harvey's (2004)

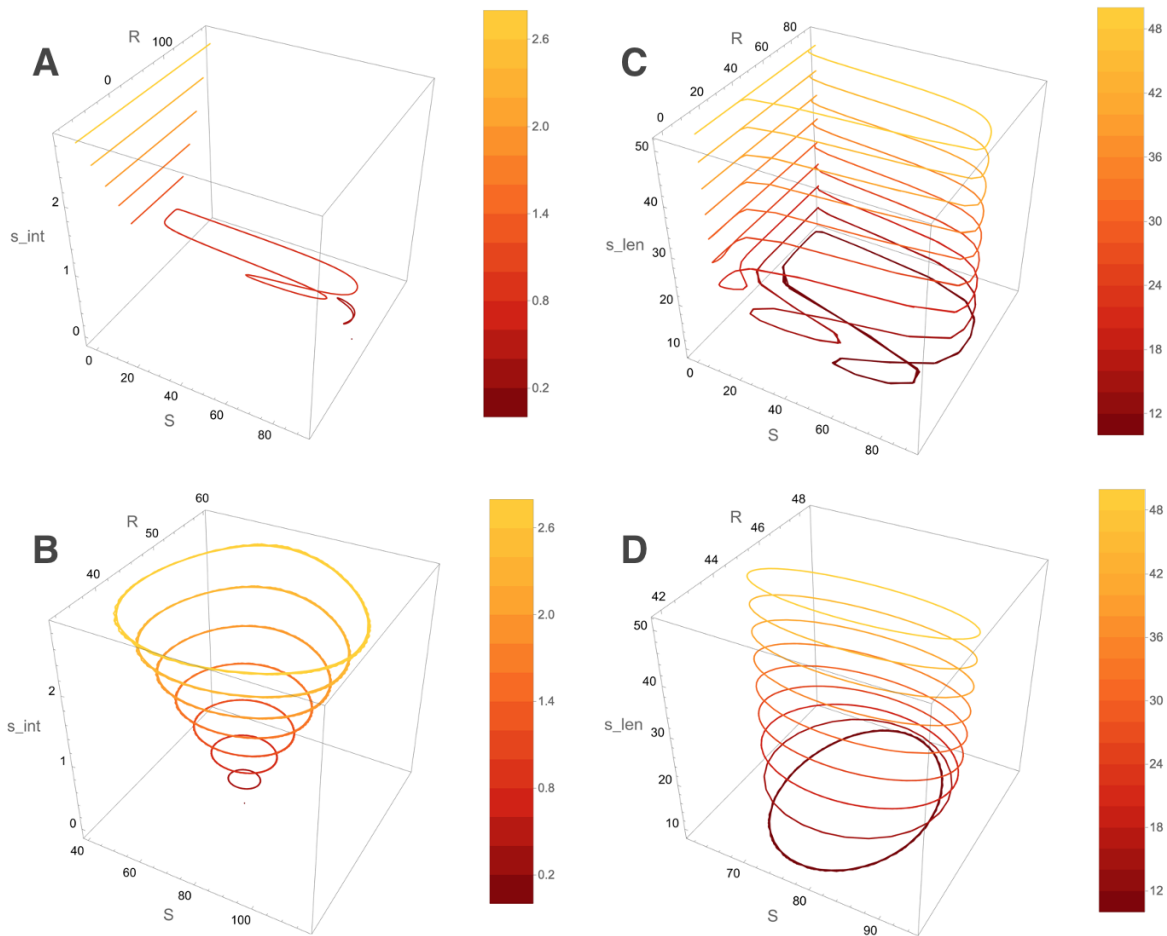


Figure 4: Behavioral coupling better stabilizes change in the abiotic state as season length and intensity increase. Here, the cyclical behavior of the rein control model without (top) and with (bottom) behavioral coupling is shown. The left column shows species S population and abiotic state trajectories of the system at various seasonal intensities (season length = 10) for the non-behaviorally-coupled (top) and behaviorally-coupled (bottom) model. Increased intensity amplifies the underlying shape of the trajectory. The right column shows the same trajectories at various season lengths (season intensity = 0.8) for the non-behaviorally-coupled (top) and behaviorally-coupled (bottom) model. Increased length changes the underlying shape of the trajectory. Any trajectories that send the population too close to 0 are not survivable cases as they fall below the cutoff threshold (γ) imposed in the parameter scans.

emphasis on the microclimates of Daisyworld. We have demonstrated that a single species with rudimentary behavioral capabilities (dormancy) allows the environment to participate more in the ecosystem's regulation, and in turn can survive in more seasonal environments than a two species rein control system with no behavioral coupling. Furthermore, the addition of behavioral coupling to a two species rein control system leads to super-additive improvement and robustness across wide ranges of seasonal circumstances.

This account also provides a means of abiotic regulation that does not demand the simultaneous genesis of complex ecological circumstances criticized in evolutionary arguments against Gaia. Rather, succession may occur in a piecemeal fashion, as biota may survive independently and even selfishly. However, if rein control does emerge bio-

logically, the community is all the better for it, and as such it still remains as an important principle to consider given that it may be well-represented in biology due to survivor bias. So, the account provided here frames rein control by the biotic community being an occasional consequence, but not a fated outcome of ecological succession. Rein control by a biotic community is a sub-type of a broader suite of rein control relationships that help scaffold the genesis and succession of ecosystems. Another type we have described here is that between organisms and their environments, mediated by the behavior of organisms. We hope to have shown that behavior is fundamental to the scaffolding of ecological succession, especially in harsh environments.

We have used Gaia here contextually and heuristically and have appealed to its evolutionary and cybernetic interpreta-

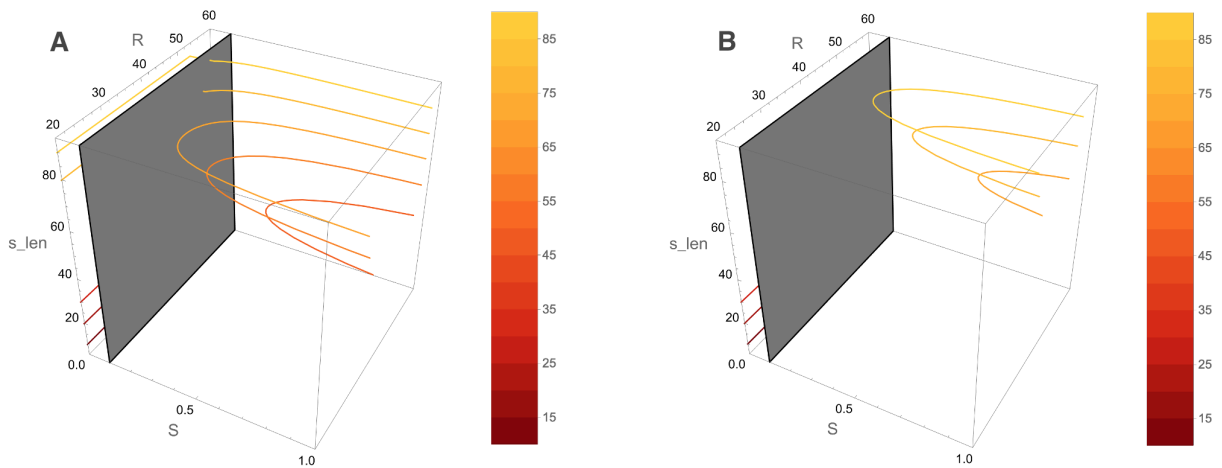


Figure 5: Decreases in inherent death rate d in the behaviorally coupled model leads to a peak of survivable seasonal intensity at a greater seasonal length. Left shows the edges of the cyclical behavior of the model at various season lengths (s_{len}) and a d of 0.1. Right shows the same for a d of 0.075. The gray plane indicates the imposed cutoff value (γ) below which populations are deemed to have collapsed and the trajectories continue to 0. Lowering inherent death rate also increases the range in seasonal lengths where extra survival, that above the asymptotic value, is possible.

tion, which are just some of the debate’s many branches. It is important to note that some have argued Gaia loses its original meaning when sublimated with neo-Darwinism and cybernetic arguments. Interpretation of Gaia as an autopoietic system, more in line with the original inspiration of the hypothesis from Schrödinger’s “What is Life?” (1951), may be more appropriate, albeit less tractable, in computer modeling (Rubin and Crucifix, 2019). We still believe assessing the role of behavior in any interpretation is an important step in the development of Gaian-esque theories, or theory of ecological regulation more broadly.

Lastly, we are left with a commentary on the continuity of life and mind. Biological minds never emerge with complete control over their circumstances. In fact, much of effective behavior lies in waiting for the environment to do something for you. This is emphasized in these models in that the only behavioral flexibility is, in fact, not to behave at all. This trust and attunement to change in the environment underlies the interest of predictive capabilities of agents across the mind sciences. Survival is often contingent on when, where, and how hard organisms “pull” on the reins they do have, and learning when, where, and how hard the environment will “pull” back. As such, we anticipate that the sensory and actor capabilities of organisms are scaffolded on these relationships and are tuned to pull their reins accordingly.

Effective behavior becomes all the more important when we recognize that most abiotic environments undergo dramatic spatial and temporal fluctuations within the lifetimes of the organisms that inhabit them due to seasons, resource depletion, and critical transitions. The needs of the organism are just as variable, as hunger, developmental periods, reproductive processes, injury, and comfort are all responsible for

variations in what abiotic state is needed or preferred.

It is important to note that these models lack grounding in real biological data. They are conceptual models, albeit derived from models that are evidenced by real biological and ecological systems. Reference to realistic parameters may better describe the utility of the model and the application of the conclusions. It is also worth noting that we have explicitly used a case of rein control deemed non-homeostatic by Harvey (2004). This may appear to be a straw man, however we hope to have justified its use through the theoretical setup, namely the coexistence of both species in the same local environment and therefore the same abiotic condition. That being said, extending this work to account for the micro-climate-like effects that stabilize Daisyworld and observing how they interact with the behavioral coupling described here could show how rein control phenomena can be realized across scales of interest. Compartment-based spatial models may enrich our conclusions. Other potentially fruitful extensions would be to examine how much complexity is added when there is more than one abiotic state to be regulated and to apply the model to a real biological data set based on some of the many periodically dormant species.

Organisms and minds as we know them emerge not as isolated wholes, but as parts larger environmental systems that allow for the persistence of life on both local and global scales. Effective behavior of organisms provides a great deal of flexibility for the regulation of ecosystems. So, we find it important to keep the mind in ecology, and ecology in mind.

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