

The maintenance of habitability across multiple scales: A meta ecosystem view of Gaia.

Submitted by Robert Owen, to the University of Exeter as a thesis for the degree
Masters by Research in Geography, October 2020.

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Robert Owen



8th October 2020

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Abstract

The Gaia hypothesis postulates that life and the abiotic environment of planet Earth form a self-regulating system, capable of maintaining planetary habitability. Previous studies have highlighted mechanisms by which environmental regulation can emerge. The majority of prior work has modelled life-environment interactions at the level of organisms interacting with their local environment. The model presented in this thesis uses a meta ecosystems approach to look at not just how organisms interact with their environment but how ecosystems interact with each other and a shared global environment. It is hypothesised that interaction through a shared environment decreases the probability of ecosystem collapse within a world consisting of numerous ecosystems. To test this hypothesis a version of the flask model is used where numerous ecosystem flasks exist within a global flask and interact with a shared environment. It is found that when ecosystems are able to interact with, and through, a shared global environment the probability of ecosystem collapse is reduced. It is postulated that this is caused through a novel form of meta-ecosystem dynamics where, through interaction with a shared environment, ecosystems are able to affect one another's population and therefore likelihood of extinction. This appears to be another way, apart from regulation of abiotic factors and nutrient recycling, in which life environment feedbacks can affect the habitability of a global system.

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Author's Declaration

This was a joint project in partnership with Arwen Nicholson.

Arwen contributed to the project through writing the structural code for the model from which the data was produced. This entailed the production of a document of code based on a discussion where I explained my hypothesis, concept for a model and experimental method.

My role in this project was as follows:

- I conceptualised the model and experimental method used
- I ran all simulations and tests
- I analysed the data produced by the simulations
- I wrote the following thesis based on my findings.

Acknowledgements

Firstly I would like to thank my supervisors Tim Lenton and Hywel Williams for their unwavering support through this process. I will always be grateful for Tim taking the time to listen to my ideas after a random email from Colombia, taking the risk of bringing me into the department and then offering solid and honest advice throughout my degree. I thank Hywel for our chats outside and for connecting me with Arwen.

Arwen Nicholson has been instrumental in me producing this thesis, as a friend, a teacher and a colleague. As a colleague Arwen produced the structural code that allowed me to test the hypothesis in this study, she helped guide me in my analysis and she was a sounding board when it all fell apart. As a teacher explained to me how the flask model worked and supported me as I crashed through learning to programme. As a friend, she was there for me throughout. Checking in when it was just me working on my own in the department on weekends, joining me on walks through Devon's nature and exploring ideas of Gaia and who we are within her. I will always admire her direct approach to life, she does more on a weekend for Gaia than many will do in their career.

I would also like to thank Rudy Arthur for introducing me to new ways to view Gaia and for taking the time to talk with me about his theories of Gaian evolution. I will also always appreciate him teaching me Jujitsu after work, although I think I gave him a fair amount of amusement in the process.

Thanks also goes to Tom Powell who has continually offered an open hand. Tom is not only a colleague in Gaian research but shares the same passion as me in the creation of food systems that integrate into our living world. Our work in Kenya has allowed me to blend my two worlds of academia and agriculture and for that I will forever be

grateful. My final academic thankyou goes to Chris Bolton for his support and guidance with statistical analysis and for being so patient in doing so.

I would also like to thank those individuals I have worked with on the land over the past 3 years. To spend time with people who are firmly rooted in our natural systems whilst producing this thesis has allowed me a level of perspective that I will be eternally grateful for. Their support when my confidence in my academic journey was failing, their interest in the work I am doing and their gentle pushes into the right corner of the woods or my brain will always be appreciated. Thanks goes especially to Bart Bagnall, for all of the above and for being a friend and a teacher.

Finally, I would like to thank my family. Without their care across multiple scales i would not be here writing this today.

Introduction

The Gaia hypothesis was first postulated by James Lovelock and Lynn Margulis (Lovelock and Margulis, 1974; Margulis and Lovelock, 1974), it hypothesises that, within the Earth system, life, the hydrosphere, lithosphere and atmosphere form a self-regulating planetary-scale system with habitability maintaining properties. The hypothesis was invoked to help explain the persistence of life within the Earth system, despite increasing solar luminosity and in the face of the many perturbations it has experienced.

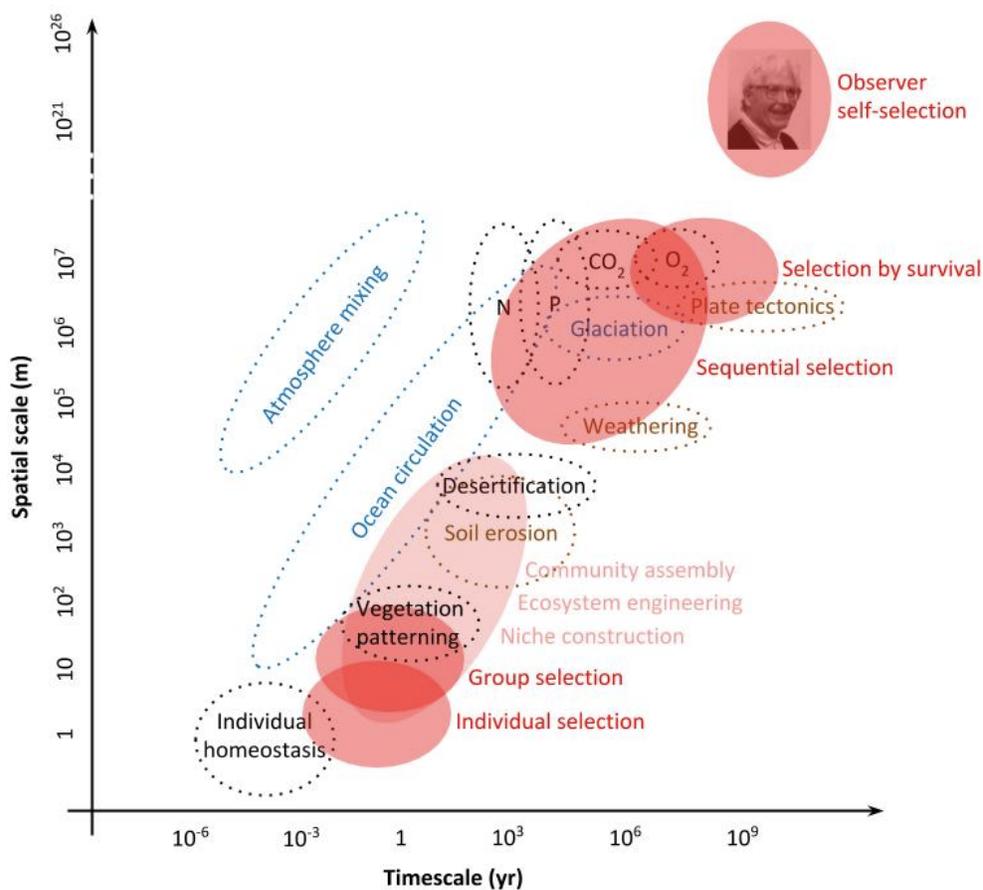
The hypothesis has been widely debated for several reasons. Firstly, it is very difficult to design experiments and empirically test such a hypothesis as we only currently know of one planet with life upon it. Along with the difficulty of a single data point, the Gaia hypothesis was introduced into a very inhospitable scientific context. At a time of focus on competition based selection at the level of the gene, the Gaia hypothesis was perceived as an unworkable form of global scale altruism. It underwent fierce criticism at a philosophical level and the proponents of Gaia utilised computer models to explore these criticisms.

The first criticism of Gaia to be tackled was that it implied teleology. It was argued that the hypothesis suggested an awareness of life, that life was conscious of the way it was interacting with the environment and knowingly regulating it (Doolittle, 1981). From these criticisms, the first Gaian model was born, Daisyworld (Watson and Lovelock, 1983). Daisyworld showed how global regulation of temperature can emerge from localised selection of traits at the level of individual organisms, without awareness or consciousness. The Guild model (Downing and Zvirinsky, 1999) also displayed the evolution of global regulation of chemical ratios through local selection for individuals that improve their environment.

Both Daisyworld and the Guild model were able to show that Gaian regulation does not imply teleology. They demonstrated a form of niche construction (Odling-Smee, 1988) as a possible mechanism to explain Gaian regulation. However, they both held the limiting assumption that traits selected for at the level of the individual will always improve the global environment. Another criticism of these models was the absence of “cheats” (Dawkins, 1982; Smith and Szathmáry, 1995), species that do not contribute towards environmental regulations but benefit from it. Through not paying the “cost” of regulation, these species could outcompete those that regulate the environment and eventually destroy the regulatory mechanisms.

A number of models then appeared in order to assess these criticisms and further develop our understanding of Gaia. The Daisyworld model was adapted numerous times, with the concept of cheats being tested (Lovelock, 1992) and it was shown that regulation still emerges. Later adaptations of Daisyworld (McDonald-Gibson et al., 2008) and ‘Daisystat’ (Dyke, 2010) removed localised environments to each organism and still observed environmental regulation. In the absence of localised environments niche construction was no longer the mechanism of regulation but ‘rein-control’ (Clynes, 1969; Dyke and Weaver, 2013) was observed. These models showed a form of rein control involving “push” and “pull”. This is where one party acts to increase an abiotic parameter while preferring this parameter to be low, and another party acts to lower the abiotic parameter, while preferring this parameter to be high. With these two parties pulling the system in opposite directions, it is possible to maintain environmental regulation. These models led to an advancement in our understanding of Gaian regulation, they not only negated many of the criticisms of previous models but also introduced us to rein control, another mechanism by which Gaian regulation can be realised. As research in this area has continued it seems as though there are a number of processes and mechanisms at play across temporal and spatial scales that lead to

self regulation in natural systems (Lenton et al., 2018). These processes are displayed in Figure 1.



Source: Lenton (2018: 2)

Figure 1: Space and Time Scales of Earth System Processes and Selection Mechanisms.

Simultaneously the Flask model was being developed and explored (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010). This model removes localised environments that surround and are specific to each individual organism and instead groups of individuals share a common local environment. The flask model also negated any potential problems caused by cheats. It did this through building on the work of Volk, Lenton and Wilkinson who argued that environmental regulation did not need to be selected for at the level of the individual but could emerge from the by-products of life processes, making it selectively neutral (Volk, 1998; Lenton, 1998; Wilkinson, 1999). Within the model both nutrient recycling and regulation of abiotic parameters could be observed. The model used in this study is an extension of the body of work using the flask model to explore Gaian regulation. For this reason I will not describe the working of the flask model in depth, as this can be found later in the methods section below.

To summarise, through the models described above, regulation was shown to emerge even in the presence of “cheats” and when the limiting assumption that traits selected for at the level of the individual will always improve the global environment was removed. The introduction of the flask model now allowed for a randomly evolving microbial model to be used to explore Gaia in a way that mitigated many criticisms and limitations of previous models. Still, the process by which a self regulating biosphere evolves was unclear.

Among other models, versions of the flask model have been used to look at the evolutionary theory for global regulation emerging. A spatial version was created where multiple flasks with distinct local environments were connected by inflows and outflows (Williams and Lenton, 2008). This model showed environmental regulation across the network of flasks that implied a form of multi-level selection at work. Communities that improve their environment are able to grow to large numbers and, through migration,

colonise those flasks containing environmentally degrading communities, which exist at smaller numbers.

Recently, Nicholson et al. (2018) adapted the flask model to empirically test “selection by survival” a theory of ecosystem selection that aims to explain why we see stability emerge and evolve in natural systems (Doolittle, 2014). It proposes that the persistence of a system alone increases the likelihood it will acquire further persistence-enhancing traits, so the longer that it exists the greater its probability of future persistence.

Nicholson et al. found that “selection by survival” can indeed increase the probability of persistence of a natural system.

As well as looking at the evolutionary processes behind global regulation the flask model has recently been adapted to look further into the mechanisms by which life-environment feedback can maintain habitable conditions (Nicholson et al., 2017). This adaptation of the flask model presents a model of self-regulation by ‘microbes’ in a single flask, with no local environment and a shared microbial preference for a single abiotic parameter. Through this approach the mechanisms behind Gaian regulation could be further explored and our understanding developed in a number of ways. Firstly, the study developed our understanding of “feedback on growth” as a mechanism for regulation (Lenton, 1998), Nicholson coined this form of regulation as ‘single rein control’. This is where the change in temperature caused by microbes is maintained close to constant though the total population expanding and contracting to mitigate the impacts of new mutants on the average environmental effects of the community of microbes. This differs from previous descriptions of rein control (McDonald-Gibson et al., 2008) as, due to a universal abiotic parameter preference, two parties that pull and push the environment in different directions are not able to regulate the temperature. Instead, the size of the population acts as a regulator, growing and shrinking in order to mitigate internal or external perturbations.

The second key contribution to our understanding of Gaian mechanisms from this paper is the further exploration and explanation of how the three potential regulatory regimes in which regulating systems can be found work.

Nutrient limited regimes occur when abiotic environmental conditions are not limiting the microbes' ability to consume. All available nutrients are consumed and, at this point, the microbial population will stabilise at a level at which the inflow of nutrients into the system can sustain that population size. It is at this point when a population reaches a carrying capacity determined through resource availability that we describe that system to be in a nutrient limited regime.

Systems in high or upper temperature limited regimes are those whose aggregate effect on the environment is to warm it. These populations limit themselves through warming their environment to a temperature at which they are unable to consume nutrients. As their metabolism slows or stops, the environment begins to equalise to that of its inflow and conditions return to a point at which they can consume again and the cycle above continues. It can be seen as these systems are continually rebounding off the upper temperature limit at which microbes can metabolise.

Systems in low or lower temperature limited regimes are those whose aggregate effect on the environment is to cool it. They can be seen as the mirror of the upper temperature limited regimes, but instead bouncing off the lower temperature limit for microbial metabolism.

The ideas within this thesis are an extension of those from the previous flask models discussed above. It aims to take the updated single flask model (Nicholson et al., 2017) and the idea of multi flask interactions (Williams and Lenton, 2008) and further explore how multiple flasks in multiple regulatory regimes interact with one another to affect global habitability.

Most previous flask models have approached the emergence of environmental regulation at the level of communities of organisms interacting with a shared environment. The multi flask model (Williams and Lenton, 2008) did look into flask level interactions but through direct interaction with neighbours, the model presented in this study is the first flask model to contain a global environment with which flasks interact. This allows us to start to take another view of how the action of individual organisms can in turn affect conditions at a global scale. Through modelling life environment feedbacks in this way and allowing interactions at multiple scales we can draw new insights. We can explore the interactions that occur within ecosystems, between them and any global scale properties that emerge.

Multi flask models allow us to observe system-to-system interactions and the properties that emerge from these interactions. In other words, they allow us to model Gaia as a meta-ecosystem (Loreau, Mouquet and Holt, 2003). Meta ecosystem theory is a development of metapopulation (Levins, 1969) and metacommunity theory (Gilpin & Hanski, 1991), where a meta ecosystem is seen as a set of ecosystems connected by flows of energy and biotic and abiotic materials that as a whole form one large ecosystem. The difference between meta-ecosystem and meta-community approaches lies in the inclusion of the non-living elements of a system in the meta ecosystem approach compared to just biotic elements in the metacommunity approach. This stems from the fact that communities are defined as populations of species living in a certain area and the interaction between them. The definition of an ecosystem, however, includes not just the living organisms in an area but the non-living factors too.

Through modelling Gaia as a meta ecosystem it is possible to explore the emergent properties that arise from the interactions between ecosystems exhibiting localised environmental effects. Some real world applications of meta-ecosystem theory exist in

which forms of Gaia-like negative feedback within and between systems have been viewed experimentally (Largaespada, Guichard & Archambault 2012). Here it was seen that ammonium and nitrate levels in the water column can be mediated by feedback within and between mussel beds at different depths . However, the body of work surrounding metaecosystem theory has yet to seriously meet that of Gaian regulation and as we continue to explore how global regulation emerges it will be even more important to assimilate these two bodies of work.

The model presented in this study aims to resemble a meta ecosystem view of Gaia in which spatially separate ecosystems interact with, and through, a well-mixed global environment. This could be thought of as separate ecosystems sat within a well-mixed atmosphere or an aquatic system with clearly separate ecosystems, such as reefs and sediments. We hypothesise that interaction through a shared environment decreases the probability of ecosystem collapse within a world consisting of numerous ecosystems. We also hypothesise that a collection of ecosystem flasks will emerge that will act to maintain global conditions and reduce the chance of ecosystems extinctions.

Model

Spatial layout

This model differs from previous multi flask models, which contain rings of connected flasks, in that it consists of one large “Global” flask and “ecosystem” flasks that exist within the global flask. These ecosystem flasks are not directly connected to one another, but sit within, and interact with, the well-mixed Global environment. In this way, the model can be described as a nested flask model.

Abiotic Environment

Within the Global flask, the ecosystem flasks are suspended in a well-mixed fluid matrix. The composition of this fluid matrix determines the “global” environment. Within this there are a selection of chemicals, some are “nutrients” (may be consumed as food and converted to biomass) and others are non-consumable and form the abiotic environment, which will refer to as abiotic factors (these can be thought of as Temperature, pH etc).

Within the small flasks there is again a well-mixed fluid matrix containing nutrients and abiotic factors that forms the “local” environment. However, there also exists microbial populations suspended in this local environment.

Microbial Populations

Microbes are modeled as simple organisms that consume and excrete nutrients and affect the levels of abiotic factors in their environment as a by-product of metabolism. The model microbes have binary genomes that specify their patterns of uptake and excretion of nutrients and their effects on their abiotic environment. In this way, microbes who share the same genome can be seen as of the same species. The genomes are represented as an 8-bit binary string. A rule is set in this model where no microbe is able to consume the same nutrient that it excretes.

Microbes grow by converting consumed nutrients to biomass. Microbe growth is limited by nutrient availability and by the difference between the abiotic environment and the microbial preferred abiotic conditions. Microbes will seek to eat the maximum nutrients possible at each timestep (C_m). Whether this will occur is dependent on the amount of nutrients available at that time. C_m is calculated by assessing the difference between the abiotic environment and the microbial preferred conditions. To isolate the effects of environmental alteration and prevent differential fitness between organisms a universal environmental preference for all microbes is set (A_{pref}).

Microbes reproduce by splitting in half when their biomass reaches a fixed threshold (B_r). Half of the microbes biomass will go to the new microbe and the parent microbe will return to half of its biomass before reproduction occurred. Mutation occurs with fixed probability (P_m) at each locus during each reproductive event. This mutation occurs by a changing of either a 0 to a 1 or 1 to a 0 at the locus at which the mutation occurred. This mutation may affect their consumption-excretion patterns or it may change the effect they have on their abiotic environment.

Microbes have the ability to affect both their nutrient and abiotic environment through the process of biomass creation. They affect their nutrient environment through their patterns of consumption and excretion and affect their abiotic environment as by-products of biomass creation. Each microbe species has a specific effect on abiotic factors per unit of biomass they create. These effects are randomly decided and are placed within the range of $[-1, 1]$.

Alongside these life-environment feedbacks dictating changes to biomass, there is a fixed maintenance cost for each microbe for staying alive. This is created through a set reduction in microbe biomass at every timestep (M_c), which is totally removed from the system. This aims to mimic the energy costs of maintaining life and also inefficiencies in life processes. The effect of this is that a carrying capacity is created within the system. If a microbe is unable to eat, due to lack of available nutrients or inhabitable abiotic conditions, and its biomass drops below a fixed starvation threshold (B_d) it will die and its biomass will be removed from the system. There is also a fixed probability of death for each microbe at each timestep (P_d), this represents death by natural causes that are not starvation such as predation.

Dynamics of the model

After an initialisation period ($T_{initial}$) where flask environments equalise each ecosystem flask is seeded with 100 randomly generated microbes (S_{μ}).

Thereafter at every timestep, at a global scale, there is an inflow that brings with it influxes of nutrients and abiotic factors of a prescribed composition and volume. This is coupled with an outflow that removes the same volume of fluid medium that has been added through the inflow and its composition is a representative sample of global flask before inflow occurred. This maintains a fixed volume for the global flask. It is important to clarify that this differs from the nearly materially closed earth system, to which we are applying the results of this model, where abiotic factors such as temperature are affected by flows of energy into the system rather than matter. However, for the purpose of modelling the impact of the collective action of microbes on the abiotic environment, it is assumed that this difference in model dynamics is acceptable.

A similar process is occurring in the ecosystem flasks, with an inflow from the global environment into the local environment and an outflow from the local environment to the global environment. The end product is a number of localised ecosystem environments that are both being affected by and affecting the global environment.

All of the inflows and outflows described above can be seen as a form of “diffusive mixing” similar to those described in past flask experiments (Williams and Lenton, 2008). This can be imagined as cups of fluid medium being removed, added and exchanged between flasks. This may not be representative of true diffusion and of thermal energy fluxes, but as argued in the previous flask models, this is a sufficient

method of modelling the transfer of physical properties between separate entities. The dynamics of the model are visualised below in figure 2.

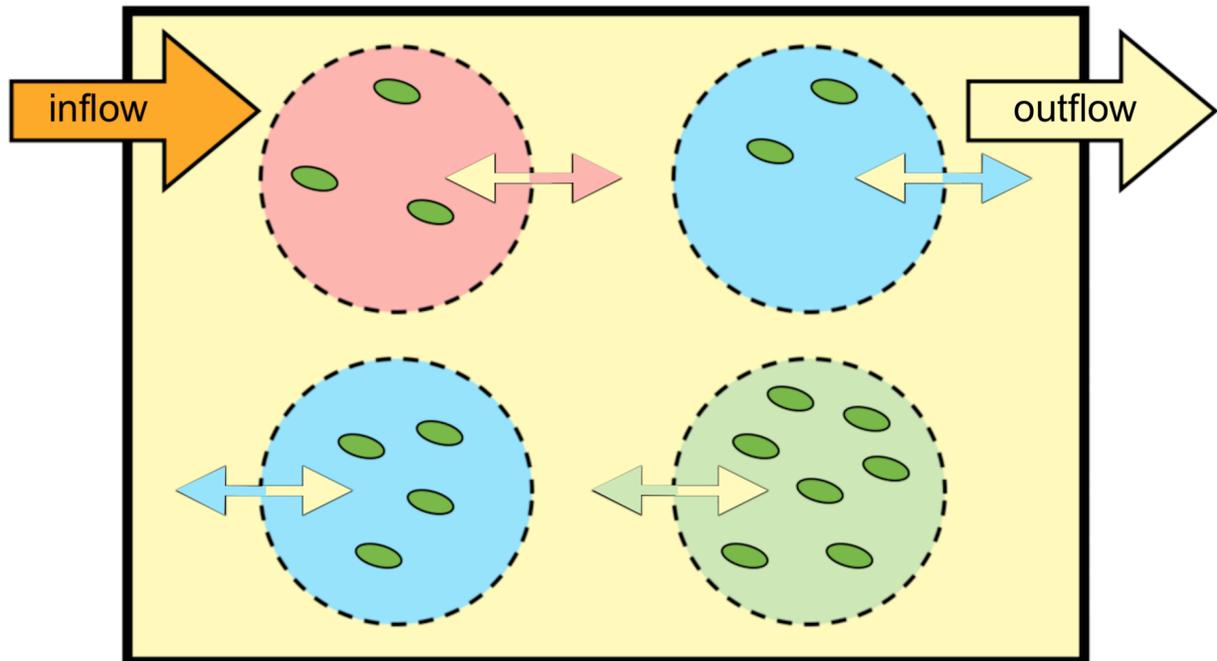


Figure 2 : Fluxes of nutrients and abiotic factors within the nested flask model. The three different coloured ecosystems representing lower temperature, upper temperature and nutrient limited regulatory regimes.

Within each ecosystem flask at each time step a number of iterations occur of the following steps. The number of iterations is based on the number of microbes existing within the flask.

1. Individual randomly selected for a death event
2. Individual randomly selected for a maintenance event
3. Individual randomly selected for a metabolism event
4. Individual randomly selected for a biomass creation event

5. Individual randomly selected for a waste event
6. Individual randomly selected for a reproduction event

Parameters

Table 1: Model Parameters

Parameter	Value	Description
$T_{initial}$	500	Initialisation Period (timesteps)
S_i	100	Initial Seed Population
G	8	Genome Length
B_r	120	Reproduction Threshold
B_d	50	Starvation Threshold
B_i	80	Initial Biomass
C_m	10	Maximum Consumption
C_{eff}	0.6	Efficiency of microbe conversion
M_c	1	Maintenance cost per timestep
P_m	0.01	Probability of mutation per gene
P_d	0.002	Probability of random death per timestep
A_{pref}	150	Ideal temperature for microbes

τ	0.02	Temperature sensitivity of microbes
n_e	8	Number of ecosystem flasks
n_n	4	Number of nutrients
I_n	1200	Units of each nutrient flowing into Global flask at each timestep
I_a	200	Temperature of inflow into Global flask throughout experiment
α	20%	Abiotic Influx. Percentage of the Global flask fluid exchanged for fresh inflow each timestep
E_e	20%	Percentage of ecosystem flask fluid swapped for Global flask fluid each timestep
S_g	1	Defines the size of the Global flask in relation to the ecosystem flask size. Global flask size = $S_g \times n_e$
β	$\frac{E_e}{S_g}$	Percentage of Global flask fluid that is swapped for ecosystem flask fluid each timestep.

Method

The "ecosystem to global heat flux" function was used to explore the hypothesis that "Interaction through a shared environment decreases the probability of ecosystem collapse within a world consisting of numerous ecosystems". This function was used to manipulate the ability of ecosystems to affect the temperature of the global shared environment, whether it was switched "on" or "off" leads to two different scenarios.

Scenario 1 - This is the null case. When the ecosystem to global heat flux function is turned "off" organisms are able to affect their local environment's temperature but are unable to affect the global environment.

At each timestep the global temperature is updated (T_g^{update}) and this is dependent on the global temperature in the previous timestep (T_g), the temperature of the inflow into the main flask (I_a) and the percentage of the global flask fluid exchanged for fresh inflow each timestep (α).

The way in which these interact is described below in equation 1:

$$T_g^{update} = T_g (1 - \alpha) + (\alpha I_a) \quad (1)$$

Here we see that the main factor affecting the global temperature is the temperature of the inflow into the main flask (I_a). This creates a world where ecosystems are unable to affect one another's temperature through interaction with a shared environment.

Scenario 2 - When ecosystem to global heat flux is turned "on" organisms are able to not just affect their local temperature but they can affect the Global temperature too. In this case the factors affecting global temperature are more complex and can be

described using two equations applied in order. These can be seen below as equation 2 and 3.

Equation 2 is identical to equation 1. Equation 3 takes into account the number of ecosystem flasks (n_e), the percentage of global flask fluid that is swapped for ecosystem flask fluid each timestep (β) and the temperature of i^{th} ecosystem flask (T_i).

$$T_g^{update} = T_g (1 - \alpha) + (\alpha I_a) \quad (2)$$

$$T_g^{update} = \frac{1}{n_e} \sum_{i=1}^{n_e} T_g (1 - \beta) + T_i \beta \quad (3)$$

The result of this more complex interaction creates a world where ecosystem flasks are able to affect one another's temperature through interaction with a shared environment.

To summarise, when the “ecosystem to global heat flux” is turned “off” the temperature of the liquid matrix in the global flask is solely dependent on the temperature of the global inflow. This means that any heating or cooling effects that occur in an ecosystem flask due to microbes will not have an effect on the global temperature. It may be seen as there is no temperature leakage from the ecosystem flasks to the global flask.

When the “ecosystem to global heat flux” is turned “on” the temperature of the liquid matrix in the global flask is not only affected by the global inflow but also by the outflow of each ecosystem flask. This means that any heating or cooling effects caused by microbes in an ecosystem flask may “leak” out into the global flask and in turn indirectly affect the temperature of other ecosystem flasks .

Two ensembles of 100 simulations were carried out, one ensemble for each scenario. Each simulation lasts 10^5 timesteps and is identical apart from the initial random seeding.

Results

For each ensemble the extinction rate for ecosystem flasks were assessed, as well as the average global temperature and ecosystem temperature. After this, any differences in extinction rates were further explored.

Average global temperatures, ecosystem extinction rates and ecosystem temperatures

Figure 3 shows two plots displaying average global temperatures, ecosystem extinction rates and average ecosystem flask temperatures against time for ensembles with ecosystem to global heat flux function “on” and “off”. When taking average temperatures both at a global and ecosystem level only living systems (those containing living microbes) were analysed, this prevented results being skewed by extinct systems.

When ecosystem flasks are able to interact with the shared global environment the global temperature is brought down towards A_{pref} (Fig. 3b). This cooling effect happens rapidly in the initial timesteps and then the temperature is held steady at approximately 175 units for the duration of the simulation.

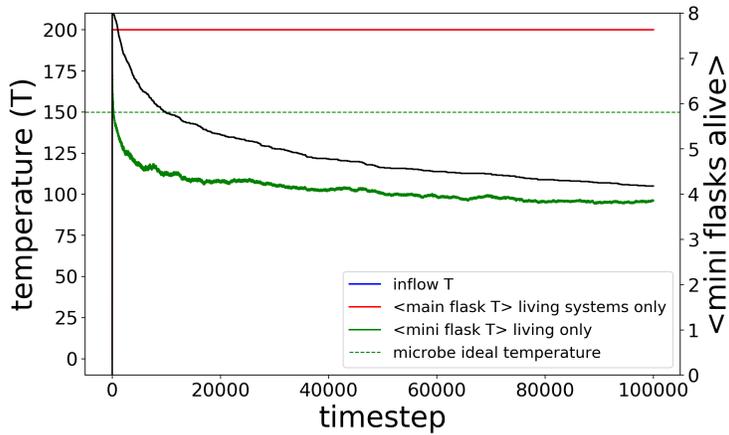
Figure 3 shows that the likelihood of ecosystem extinction is altered when ecosystems can interact with the shared environment. In the ecosystem to global heat flux “off”

ensemble an exponential decay can be seen in the number of ecosystem flasks alive over time. In the first 10,000 timesteps there is a rapid rate of extinction of ecosystem flasks, with approximately a quarter of the ecosystem flasks going extinct in this period. This rate then slows until the end of the experiment where there are on average approximately 4 flasks remaining of the 8 that existed at the beginning of the experiment. The extinction rate behaves much differently in the ecosystem to global heat flux “on” ensemble. Here you see a linear decrease in ecosystem numbers over time on average ending with 7 of the 8 ecosystems remaining at the end of the experiment. To summarise, When ecosystem flasks can interact with their environment the probability of ecosystem survival increases. The other difference is the way in which rate of extinction changes, with the ecosystem to global heat flux “on” condition showing a more linear decrease over time whilst the ecosystem to global heat flux “off” condition shows a pattern that resembles exponential decay.

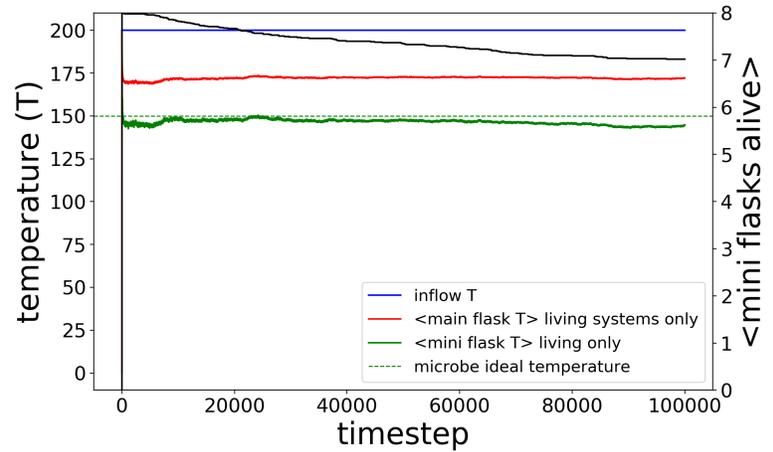
The average temperature of ecosystem flasks is also displayed in Figure 3. In the plot for the ecosystem to global heat flux “off” condition it can be seen that the average ecosystem flask temperature quickly drops below A_{pref} . It initially decreases rapidly over the first 10,000 timesteps, before the rate of cooling slows, eventually reaching a steady temperature of approximately 100 units at around 40,000 timesteps that is maintained until the end of the experiment. This is approximately 50 units below A_{pref} .

In the ecosystem to global heat flux “on” plot the average ecosystem temperature drops rapidly towards A_{pref} , reaching close to A_{pref} almost instantly. It then stabilises just below A_{pref} for the duration of the experiment. Comparing the two we see the average ecosystem temperature is much more stable and closer to A_{pref} when the ecosystem to global heat flux function is switched “on” and the ecosystem flasks can interact with the shared environment. From looking at the ecosystem to global heat flux “off” plot it

seems as though there is a positive correlation between ecosystem survival rate and average ecosystem temperature. This will be further explored in the next sections.



(A)



(B)

Figure 3: Average global temperatures, ecosystem extinction rates and average ecosystem flask temperatures against time. Plot (A) showing results for ecosystem to global heat flux “off”, Plot (B) showing results for ecosystem to global heat flux “on”.

Comparison of average environmental effects per microbe against population with and without ecosystems interacting with their global environment

Figure 4 shows average ecosystem flask population plotted against the average environmental effects per microbe of each ecosystem flask for all not extinct flasks. The average environmental effects per microbe of a flask is derived through summing all the abiotic environmental effects for all microbes in a flask and then dividing by the population size. Within the figure there are two plots, one for the ecosystem to global heat flux “off” scenario and the other for ecosystem to global heat flux “on”.

In the ecosystem to global heat flux “on” plot the lower and upper temperature limited regimes can be seen (left and right curve) along with the narrow nutrient limited regime between the two. The lower temperature limited regime is the left hand curve and shows that the total population decreases as the average environmental effect of microbes becomes more negative. The right hand curve describes the upper temperature limited regime and shows how total population decreases as the average environmental effect becomes more positive. However, the curves show asymmetry and this is due to the temperature of inflow into Global flask (I_a) being greater than the ideal temperature for microbial growth (A_{pref}). This leads to those flasks in the upper temperature limited regime being capped in population size as fewer individuals are needed to become upper temperature limited compared to lower temperature limited.

There is a general reduction in flasks plotted in the ecosystem to global heat flux “off” plot compared to the ecosystem to global heat flux “on” plot. This is further evidence of the difference in extinction rates seen in figure 3. Looking closer into this, in the ecosystem to global heat flux “off” plots one can still identify the three regulatory

regimes, however, the asymmetry seen in the ecosystem to global heat flux “off” plot is exaggerated. Comparatively fewer flasks sit within the upper temperature limited regime when the ecosystem to global heat flux function is “off” and that the rate at which total population decreases as the average environmental effect becomes more positive is much larger in the ecosystem to global heat flux “off” scenario compared to when ecosystem to global heat flux “on”. Looking closer at this effect and those flasks within the upper temperature limited regime it can be seen that fewer flasks are found with an average environmental effect over +0.5 when ecosystem to global heat flux is “off”. It can also be seen when comparing the two plots for flasks with an average environmental effect between 0 and +0.5 there are both less flasks when the ecosystem to global heat flux function is “off” and those that do survive tend to have a lower population.

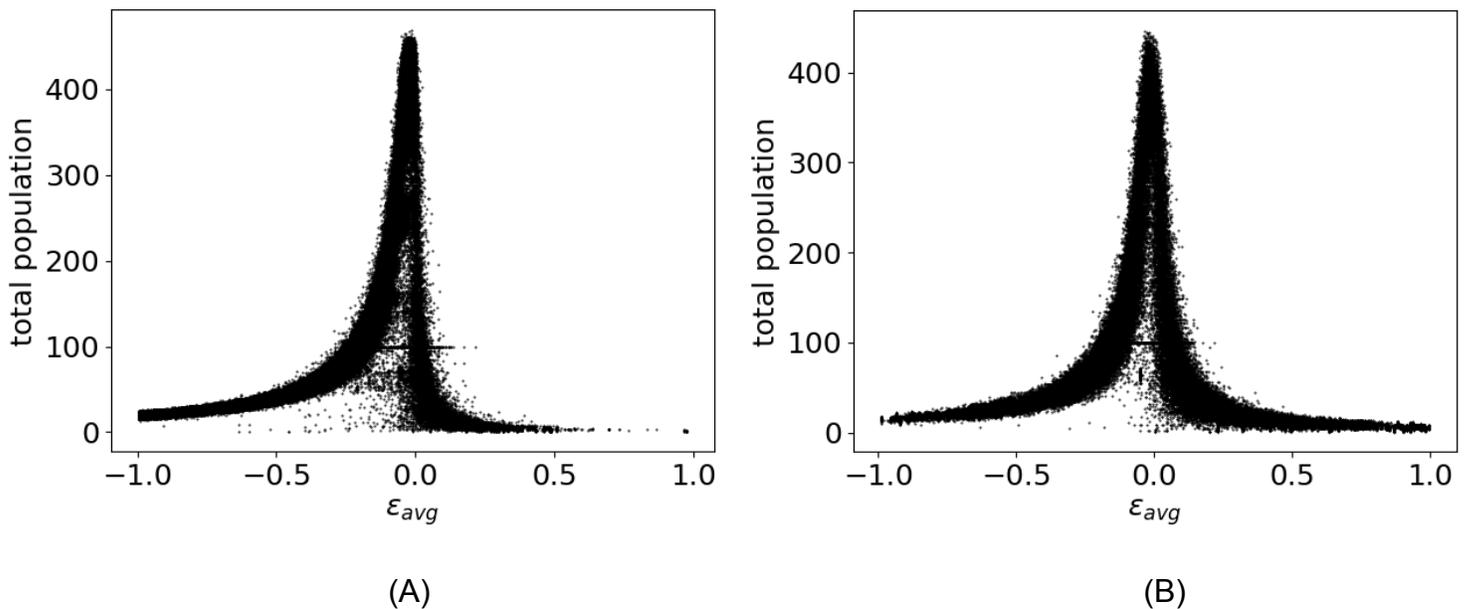


Figure 4: Average ecosystem flask population plotted against the average environmental effects per microbe of each ecosystem flask for all not extinct flasks. Plot (A) showing results for the ecosystem to global heat flux “off” and Plot (B) showing results for ecosystem to global heat flux “on”.

The effect of global temperature on the average population of non-extinct flasks and their average environmental effects per microbe.

The effect of Global temperature on the average population of each non-extinct flasks and their average environmental effects per microbe explored in Figure 5. Each plot shows the population of non-extinct flasks against their average environmental effects per microbe for varying values of I_a . Simulations were run with ecosystem to global heat flux “off” so the global temperature is always equal to I_a . Each plot is produced from an ensemble of 100 simulations with each simulation lasting 10,000 timesteps. Table 2 describes the values of I_a for each plot.

Plot	Temperature of global abiotic input (I_a)	Difference from ideal temperature
a	200	+50
b	175	+25
c	150	0
d	125	-25
e	100	-50

Table 2: Temperature of global abiotic input and difference from microbes ideal temperature for each plot in figure 5.

Plot A shows an asymmetry similar to earlier figures. It can be seen that when I_a is 50 units above A_{pref} those flasks with negative average environmental effects have larger populations than those with positive average environmental effects. With the highest populations being those with an average environmental effect that is negative but close to 0, this can be seen as the peak where the two curves meet sitting to the left of 0. In Plot A there are very few flasks that have an average environmental effect above +0.5. As I_a decreases and approaches A_{pref} , a number of changes occur. Firstly, the average environmental effect which incurs the highest population changes, this can be seen through the point at which the two curves meet moving towards 0. In plot B, where I_a is 25 above A_{pref} this point can be seen to be sat closer to 0 than in plot A, but it is still negative. Another change observed is a reduction in asymmetry, a general increase in population for flasks with positive average environmental effects can be seen and also an increase in the number of flasks that have an average environmental effect above +0.5.

In plot C, when I_a is equal to A_{pref} , we see complete symmetry. With the average environmental effect which incurs the highest population being centred on 0 and two symmetrical curves dropping away either side of this point. Plots D and E show I_a decreasing past A_{pref} , it can be seen that as this happens the peak at which the two curves meet now passes 0 into positive average environmental effect values. Along with this shift in the peak, we see a steepening of the curve for populations with negative average environmental effects, returning to the asymmetry seen in early plots but as a mirror image. This shows decreases in population for these flasks as their average environmental effect gets more negative. To summarise, as I_a moves from above to below A_{pref} we see a shift in the most successful average environmental effects and in the number of flasks within each temperature limited regime.

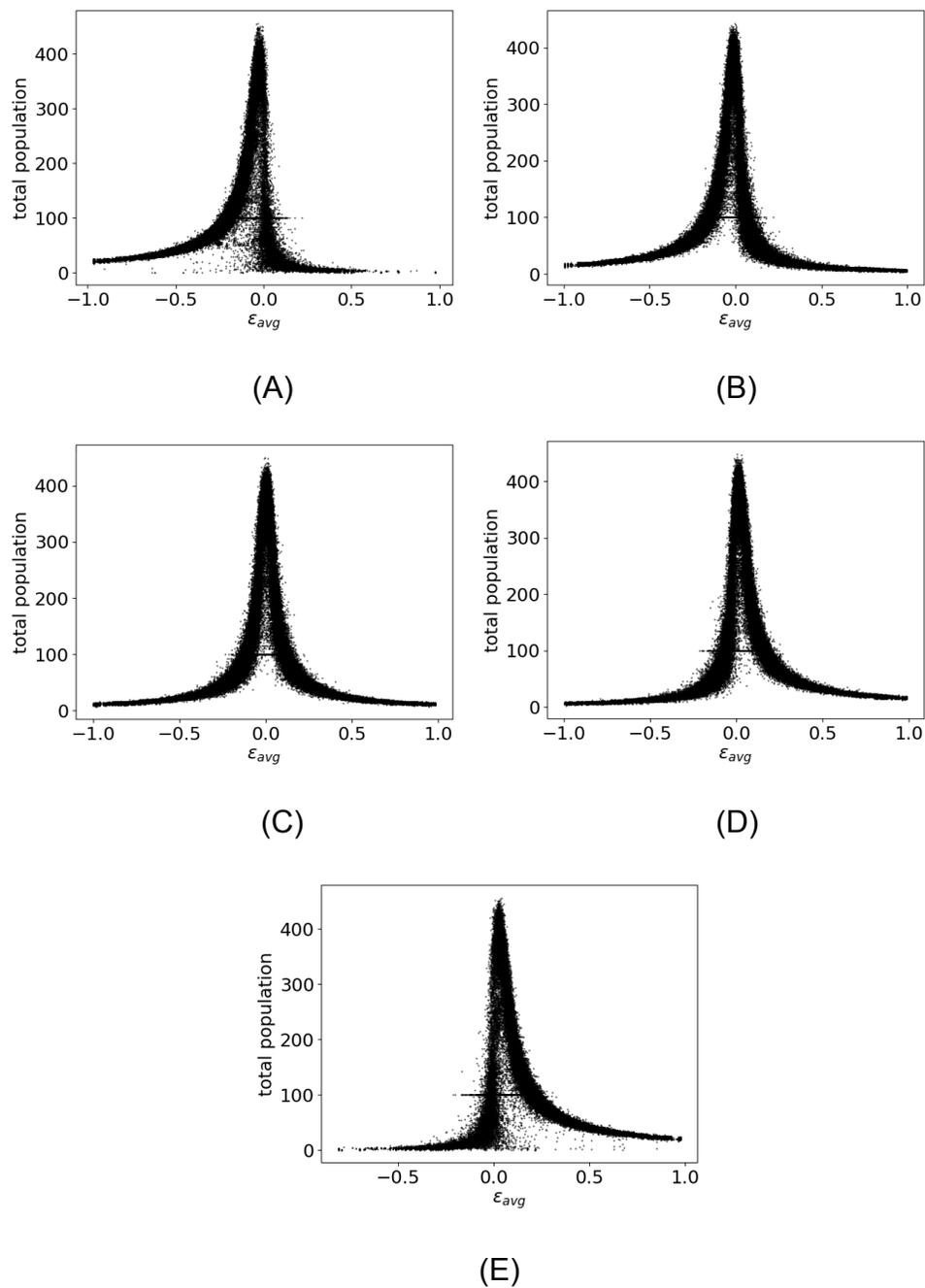


Figure 5: The average population of each non-extinct flask against their average environmental effects per microbe for varying values of I_a .

Discussion

This version of the flask model demonstrates not just that environmental regulation consistently emerges in a collection of flasks interacting with, and through, a shared global environment but also that, within these systems, interaction with a shared environment significantly decreases the probability of local extinctions occurring. It is this spatial layout, of nested ecosystem flasks within a global flask, that sets this model apart from previous flask models and allows emergent properties to be investigated at multiple scales.

Gaian models so far have explored how organisms interact with their environment and the emergence of environmental regulation. This was initially through spatial models where there are clear local environments to each organism and these interact with a global environment. (Watson and Lovelock, 1983; Downing and Zvirinsky, 1999) This allowed for an exploration of niche construction as a mechanism by which Gaian regulation works. Later versions of Daisyworld (McDonald-Gibson et al., 2008), 'Daisystat' (Dyke, 2010) and the flask model (Nicholson et al., 2017) removed the local environment and explored how organisms interact directly with a global environment. These models allowed us to see the emergence of double and single rein control as mechanisms for Gaian regulation.

This model aims to take a step back and look at not just how organisms interact with their environment but also at how ecosystems interact with and through a global environment. Here we see single rein control taking place in well-mixed ecosystems, forming a local environment specific to that ecosystem. This local environment then

interacts with a well-mixed global environment, and it is here where we see a form of higher level niche construction at play. Instead of individual organisms or groups of the same species altering their environment to create niches, we see whole communities forming feedbacks with their abiotic environment to create a form of ecosystem scale niche construction. With each community interacting with its environment to create a localised ecosystem environment, separate from the global. Within this environment they are able to maintain favourable conditions and create recycling loops. Some may do this better than others, with those that regulate better improving their chance of persistence.

However, as there is interaction with other ecosystems through the shared global environment, each ecosystem is not in complete control of its environment. Changes in the composition and interactions within one ecosystem can lead to changes in another. These ecosystem level interactions can lead to global scale properties that cannot be reduced to the properties of any of the component ecosystems, communities, populations or individual organisms. This model is novel in the sense that it allows us to view Gaia as a meta-ecosystem and to explore Gaia's global scale properties in a way that has previously not been done.

The first significant finding of this study was that when a collection of ecosystems are able to interact with a shared environment they will often alter the shared environment by pulling it closer to A_{pref} . This reaffirms past flask world findings (Williams and Lenton, 2007; Williams and Lenton, 2008; Williams and Lenton, 2010; Nicholson et al., 2017) that when organisms are able to affect the temperature of their environment through the by-products of their metabolism, a community will form that brings the environment closer to preferable conditions. The novel part of this finding is that even when you have multiple non-directly interacting ecosystems, in differing regulatory

regimes, a community of ecosystems evolves that acts on the whole to regulate the environment. From the results of this experiment and the existing theory on the evolution of regulation in natural systems we would predict that there are possibly a number of mechanisms behind this finding. Firstly, it seems as though a form of “selection by survival” (Doolittle, 2014) is occurring. Where those ecosystem flasks that have environment enhancing traits are more likely to survive, leading to a meta community (community of flasks) that has composition skewed towards flasks with environment enhancing traits, this can be seen in the skew in average environmental effects of microbes in Figure 4. It is also likely that single rein control (Nicholson et al., 2017) is not just occurring at population level within flasks but also at community level between flasks. Community level single rein control would be where whole communities found within ecosystems shrink and grow in reaction to global environmental changes caused by communities within other ecosystems. The result would be that global conditions are maintained even in the face of localised changes within ecosystems. The results in Figure 3.b suggest this, as one can see that even as ecosystems go extinct a relatively stable global temperature is maintained. This could be explained through surviving communities within flasks shrinking or growing to make up for the changes in global composition caused by ecosystem extinctions in other flasks. This would need further work to prove and could be done through perturbing single flasks within the system either through culling or changes in abiotic conditions. Changes in global conditions, population sizes, community compositions and local conditions within ecosystems could then be observed for signs of community scale single rein control.

This study went on to assess the difference in extinction rates and local ecosystem temperatures between communities of ecosystems when they are able to alter their shared environment and when they are not. It found that ecosystem extinction rates are reduced when ecosystems are able to alter the shared global environment and that

average local temperatures were found to be much closer to A_{pref} in this case. In the case where ecosystems could not alter their shared environment the average ecosystem temperature was found to be below A_{pref} and seemed to correlate with the ecosystem survival rate.

The results above can be understood through the differential survival and populations sizes between upper and lower temperature limited ecosystem flasks observed in figure 4.

In a scenario where I_a is greater than A_{pref} , ecosystems in the upper temperature limited regime are more likely to go extinct than those in lower temperature limited regimes. As their average environmental effects are to warm their environment they must maintain relatively low populations so as to not push their environment into an uninhabitable state. When at these low numbers they are at higher risk of extinction due to new mutations within the community or perturbations to flask inflow caused by external communities.

The difference in extinction rate between ecosystem to global heat flux “off” and “on” can be explained in this light. In the ecosystem to global heat flux “on” scenario the action of ecosystem flasks can bring the global temperature closer to A_{pref} , as seen in figure 3. As this occurs the temperature of inflow into all flasks is brought closer to A_{pref} , including those in the upper temperature limited regime. As seen in Figure 5, when I_a is brought down closer to A_{pref} this allows population size to increase in upper temperature limited flasks and the likelihood of their extinction to decrease.

Comparatively, in the ecosystem to global heat flux “off” scenario, global temperatures are unchanged by ecosystems flasks, meaning upper temperature limited flasks must maintain lower populations and therefore have a higher probability of extinction.

Differential survival between the temperature limited regimes can also help explain the difference in average mini flask temperatures between ecosystem to global heat flux “off” and “on” scenarios seen in Figure 3. The lower average mini flask temperatures and seeming correlation between average mini flask temperature and extinction rate can be explained through a greater number of upper temp limited flasks going extinct. With each upper temperature limited flask that goes extinct, the average environmental effects of the whole system moves towards lower temperature limited regimes, leading to a cooling effect as each extinction occurs and an average mini flask temperature below A_{pref} . In comparison, In the ecosystem to global heat flux “on” scenario, due to decreased probability of extinction in upper temperature limited flasks we see a more balanced number of ecosystems in each regime, leading to an average mini flask temperature close to A_{pref} .

Gaian metaecosystem dynamics

Stepping back, from the results of this experiment a form of meta ecosystem dynamics (Loreau, Mouquet and Holt, 2003) can be seen to be present. Meta ecosystem theory is a development of metapopulation (Levins, 1969) and metacommunity theory (Gilpin & Hanski, 1991), where a meta ecosystem is seen as a set of ecosystems connected by flows of energy and biotic and abiotic materials that as a whole form one large meta ecosystem. Meta ecosystem dynamics differ from meta population and meta community dynamics as it takes into account the flow of energy and materials between ecosystems as well as the movement of organisms. In the results of this study through the innate connection between temperature and community size we see a form of meta ecosystem dynamics emerge where ecosystems can affect one another's total

population and composition through interactions with an abiotic shared global environment. What we see emerge is a process by which optimum global temperature and community sizes are maintained and the probability of localised extinctions is greatly reduced in a collection of ecosystems.

Through single rein control local regulation emerges within ecosystem flasks and abiotic conditions are brought closer to those preferred by microbes. The effect of this localised regulations then “leaks” through the local to global heat flux into the global well mixed environment and leads to global abiotic conditions changing and moving closer to A_{pref} . This change in global conditions also creates more preferable inflow into all ecosystem flasks within the global environment.

With a local environment closer to A_{pref} caused by altered inflow from the global environment, any ecosystem flasks within a temperature limited regime that limits their population size to relatively small numbers can now grow and maintain higher populations. This makes these flasks less prone to chance extinction through mutations arising within the community or through changes to influx caused by other flasks in the system. This increase in populations in temperature limited populations causes feedback on the global environment and the above cycle continues.

This process makes the whole system more stable through creating more possible stable states available for a system to find itself in. It opens up both temperature limited regimes as a viable stable state where without inter flask interactions, one regime would have had a much lower survival rate. The results of more diverse possible states is that the environment is regulated more tightly and also a larger, more diverse population is maintained both within the ecosystem and global flasks. These meta ecosystems dynamics are visualised below in Figure 6.

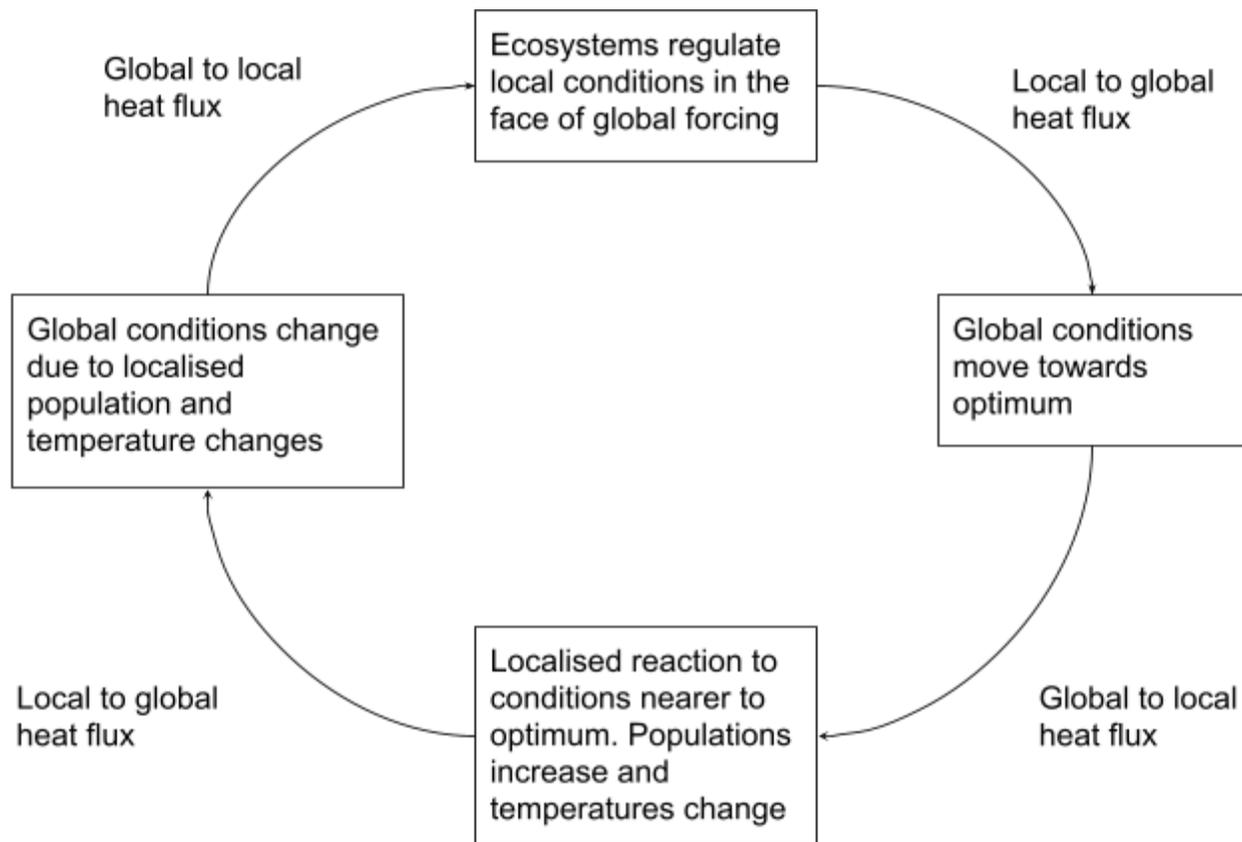


Figure 6: Meta-ecosystem dynamics maintaining population size and environment in the nested flask model

These emergent meta ecosystem dynamics could be seen as an ecosystem level mechanism by which Gaia maintains habitability. That is to say, as well as nutrient recycling and maintenance of habitable temperatures the system is also able to reduce the probability of perturbations causing extinctions through allowing for higher populations in certain temperature limited regimes.

Limitations

The spatial layout and structure of the model used in this study has limitations. By imposing clear ecosystem boundaries as flask containers we simplify the complexity and dynamic state of real world ecosystems. In reality, ecosystems have less clear boundaries that change as systems evolve and are often self defined (Banks-Leite & Ewers, 2001). Through simplifying to a flask structure we are likely to overlook many of the processes involved in ecosystem functioning and evolution. This will also lead to what could be seen as an oversimplification of meta ecosystem dynamics and how they emerge.

One limitation of this model is how the relationship between metabolic by-products and the environment are modelled. Within the flask model there is a direct effect on the temperature through each unit of biomass created. This is over simplifying a more complex relationship, the heat produced through respiration is not likely the by-product that mediates these life environment relationships. The most likely way in which organisms' metabolism affect the abiotic environment is through the alterations to environmental chemistry they make, through what they add and remove. This limitation has been approached by work of Nicholson and the Exogaia model (Nicholson et al., 2018), where she models simple planets with atmospheres, the composition of which affects the temperature of the planet. The life on these planets consume and excrete atmospheric chemicals. In Exogaia simulations environmental regulation emerges, suggesting that even though over-simplified this limitation does not prevent us from drawing inferences on life-environment feedbacks from our results.

The ecological interactions between microbes in this model could be seen as oversimplified. The ecosystems modelled could be seen as unrealistic as there is no energy flow between organisms modelled. The only ecological interactions between

organism are indirect and mediated through their interactions with their environment. This both limits the possible complexity within the ecosystems and also how energy flows through the system. If trophic levels were allowed to emerge in a model with similar rules of reproduction that are based on total biomass of an individual then there would likely be significant changes to the behaviour of the whole system.

Another limitation is the dynamics set up in the model. In this version of the nested model ecosystems can only interact with one another through the shared environment whereas both in reality and in previous multi flask models direct relationships can form between neighbours. The main problem caused through the assumption of separation is the inability for migration between flasks to occur. It has been shown in previous multi flask models (Williams and Lenton, 2008) that migration facilitates a multi level form of selection where communities that improve their environment are able to grow to large numbers and colonise those flasks containing environmentally degrading communities, who exist at smaller numbers. This form of evolution could very easily change the likelihood of localised extinctions and therefore alter the results of this study.

High rates of inflow and outflow to and from flasks is also a limitation of this and past flask models. Firstly, due to a high inflow rate any effects of destabilising mutants are felt very quickly and this allows communities to start to adapt and react to these effects quickly. In the real world there is often a delay between the growth in population of a destabilising mutant and the effects felt from such a mutant, making it harder for communities to adapt to deal with them. This can be seen in the evolution of oxygenic photosynthesis and the long delay until the great oxidation event (Summons et al., 1999) and this delayed onset of destabilisation is likely to be seen in the case of human emissions of greenhouse gases (Zeebe, 2013). Having rapid outflows also may increase the likelihood of regulation emerging as it means that once microbial metabolism decreases or halts then abiotic parameters are quickly brought back down

to the level of the inflow. This means that communities can recover quickly from the destabilising effects of microbes, which may not be the case in reality.

Future directions

The use of the nested flask model has allowed us to investigate life-environment feedback at the level of ecosystems and has displayed a form of meta ecosystem dynamics that increases population sizes and decreases the probability of localised extinctions. This work could be furthered through assessing how meta ecosystem dynamics affect previous flask world findings, such as probability of extinction at differing values of microbial temperature sensitivity and under differing perturbation types.

This model offers us the ability to better understand how systems interact with one another and the larger systems and the properties that emerge from them. The model could be extended to study how meta ecosystems evolve towards stability, specifically the role of sequential selection (Lenton, 2004) and entropic Gaian evolution (Arthur, 2019; Arthur & Nicholson, 2017). Sequential selection states that random replacement of collapsed systems over time alone enables the acquisition of stabilising mechanisms as unstable systems are likely to collapse and stable configurations tend to persist. This could be tested through allowing random reseedling after localised extinction events and observing for any changes this makes to the meta ecosystem compositions and stability. This would give a simple test to see the effects of selection by survival on ecosystem evolution.

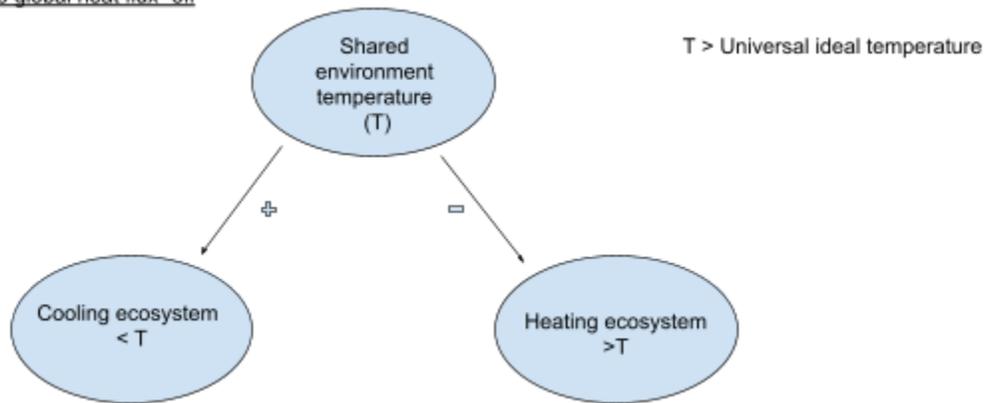
This model could also be extended to test and develop entropic hypotheses of Gaia through exploring them at a meta ecosystem level. The entropic Gaia hypothesis has been explored using the versions of the Tangled Nature Model (TNM) (Christensen et al., 2002) and is based on the observation that rather than total extinction, ecosystems collapse due to the breakdown of core interactions in a system. It also makes the assumption that reseeded after collapse is not random but it is based on what has been left behind and what has been laying in wait (dormant species). The entropic view of Gaia predicts that the evolution of a system is influenced by what patterns are there to what collapses and what is reborn over time and that the two are innately connected.

Over time and a number of ecosystem collapses, a cumulative process occurs where after each successive collapse there is a larger number and better quality choice of possible stable states for a system to find itself in. Through implementing TNM dynamics within ecosystem flasks and comparing this to the sequential survival test above we can start to see how important these entropic and cumulative effects are to the stability of natural systems and potentially start to assimilate existing theories on ecosystem evolution.

Conclusion

From the results of this study we can see a form of meta ecosystem dynamics emerge when ecosystems are able to interact with and through a shared abiotic environment. Feedbacks are formed that lead to tighter environmental regulation at a global scale and a decreased probability of ecosystem collapse. These feedbacks of ecosystems with and through the global shared environment are described below in Figure 7.

Ecosystem to global heat flux "off"



Ecosystem to global heat flux "on"

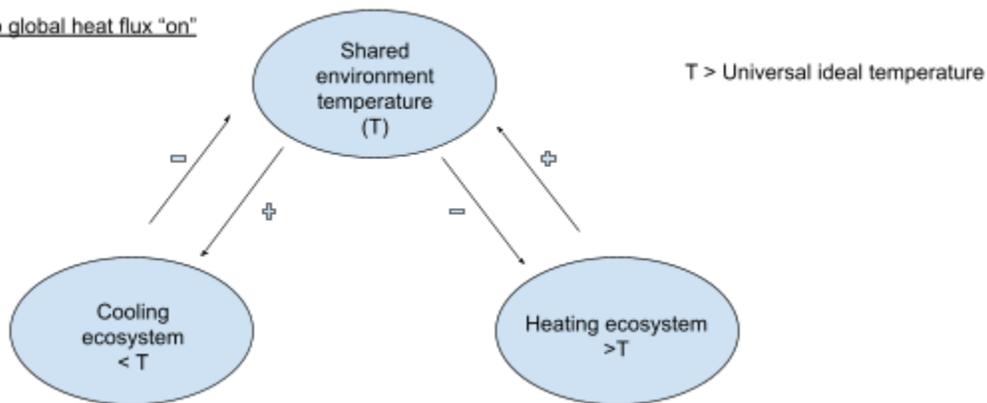


Figure 7: The feedbacks that emerge when ecosystems are able to interact with and through a shared environment in a case where shared environment temperature is greater than the universal Ideal temperature for microbes.

Through these feedbacks both temperature limited regimes are opened up as a viable stable state where, without interaction with, and through, a global environment, one regime would have had a much lower survival rate. The maintenance of population size and the number of possible stable states that ecosystems can find themselves in appears to be another string in Gaia's bow, apart from regulation of abiotic factors and nutrient recycling, in which habitability can be maintained in a living system.

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