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Exploring Ecosystems Health: Effects of Increments of Biodiversity and Trophic Complexity on the Stability of a Simple Gaian Ecosystem Model

Explorando Salud de Ecosistemas: Efecto de Incrementos en Biodiversidad y Complejidad Trófica Sobre la Estabilidad de un Modelo de Ecosistema Gaiano Simple

Erlwein, A.[a,b,c*]

[a] Instituto de Ingeniería Agraria y Suelos, Facultad de Ciencias Agrarias y Alimentarias, Universidad Austral de Chile.
[b] Centro Transdiciplinario de Estudios Ambientales y Desarrollo Humano Sostenible, CEAM, Universidad Austral de Chile.
[c] Núcleo TESES, Universidad Austral de Chile.

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**Corresponding author:*
Alfedro Erlwein
E-mail address:
aerlwein@uach.cl

ABSTRACT

The concept of ecosystem health is explored, deepening the analysis on the relationship between biodiversity and ecosystem stability, both as variables for health evaluation. Ecosystem stability is studied under a systemic approach in terms of resistance and resilience. According to some authors, when ecosystems´s models consider not only the effects of organisms on the environment but also feedbacks from the environment to the organisms, the interactions between biodiversity and ecosystem stability become positive or even synergic. To test this, the “Daisyworld” model is used to simulate the effects of diversity and trophic complexity increments on ecosystem stability. For this, the model was consecutively run with: 1st one species of daisy, 2nd two species of daisy, and 3rd two species of daisy and a herbivore. To study the stability of the system, three perturbations were introduced: 1st, 50% reduction on the daisy population, 2nd, 10% decrease on the solar radiation, and 3rd, 10% increase in the solar radiation regarding the initial value. From the execution of the model, it can be concluded that increments on biodiversity did result in more resistance but less resilience. Nevertheless, it is considered that the system becomes healthier, as its self-regulation is improved, and the total biomass (productivity) increased. However, increments in diversity or trophic complexity are themselves considered positive in evaluating the ecosystemic health.

RESUMEN

Se explora el concepto de salud ecosistémica, para lo cual se estudia la estabilidad entendida como resistencia y resiliencia sistémicas. De acuerdo a ciertos autores, cuando los modelos consideran, además de efectos de los organismos sobre el ambiente, retroalimentaciones entre el ambiente y los organismos, las interacciones entre diversidad y estabilidad podrían ser positivas o incluso sinérgicas. A modo de prueba se utiliza el modelo “El mundo de las Margaritas”, para simular el efecto de aumentos de biodiversidad y complejidad de la red trófica sobre la estabilidad de un ecosistema. Para ello el modelo se corre consecutivamente con: 1ra una especie de margarita (blanca), 2da dos especies de margarita (blanca y negra), y 3ra con dos especies de margarita y un herbívoro (predador de margaritas). Para estudiar la estabilidad del sistema se introducen 3 perturbaciones: 1ra: reducción en un 50% del número de margaritas, 2da: disminución en un 10% de la radiación solar respecto a un valor base y 3ra, aumento en un 10% de la radiación solar respecto a un valor base. De la ejecución del modelo se concluye que al aumentar la diversidad el sistema se hace más resistente pero menos resiliente. No obstante, se considera que el sistema se hace más saludable, al mejorar su autorregulación y al aumentar su biomasa (productividad). No obstante, el aumento del número de especies y su complejidad trófica son por sí solos factores utilizados para evaluar salud de ecosistemas, por lo que se concluye que el estado final del ecosistema en la modelación es más saludable.

Palabras clave: Biodiversidad, debate diversidad-estabilidad, salud de ecosistemas, “Mundo de las Margaritas”, sistemas complejos.

INTRODUCTION

Health, Diversity and Stability of Ecosystems

The value of holistic, ecologically-relevant approaches for measuring ecosystem conditions is well-established (Hallett *et al.*, 2016). Ecosystems are living systems, and because of it, they share some characteristics with other living systems. Among those are diversity, and community biomass or productivity. As in other living systems, the concept of health at the ecosystem level is a characteristic of the system as a whole.

A healthy ecosystem should be sustainable in the long term. Therefore, ecosystem health has become a useful approach in providing a way to assess ecosystems and their sustainability (Rapport, 1998; Harwell *et al.*, 2019). Health is a property of individuals, but also a property that emerge at the level of populations, communities, and ecosystems. In complex-interconnected systems, health is a quality that arises at a holistic level (Goodwin, 1997). That means, a quality that emerges not from a single component, but from the dynamic interactions of the different components. In other words, health is an emergent property of the whole system, like its behaviour or functionality, as it emerges from specific interactions between specific components of the system. The behaviour of a biological community is obviously more than just the sum of its constituent species (Begon *et al.*, 1990). In this way, the behaviour of the ecosystem is also more than just the sum of its constituent components.

However, the concept of ecosystem health has been debated for ages. Health seems to be a complex quality of living beings. And as quality, relevant problems emerge when it comes to quantify health in the search for indicators. Pimm (1991) claims that the "balance of Nature" is indeed more related to ecological stability and not necessarily health. As him, most well-known ecologists of biological communities do not use the term health. In fact, the term has received criticism and definitions have not found big consensus (Lu *et al.*, 2017)

Because of the former, health can be studied through the prism of complexity, studying the performance of the systems through time. This way, the problem can be studied through mathematics instead of philosophy of definitions. This is a great novelty of the complexity approach; its focus is more on the processes than in the parts, in other words, the focus is on the dynamic of the system.

In mathematical terms this behaviour is characteristically non-linear, that is, it behaves as quadratic, cubic or so functions, where changes tend to be amplified in time (Sole and Goodwin, 2000).

Although there is considerable debate about how to determine the characteristics of a healthy system, there is little debate about what is an unhealthy ecosystem. The definitions of ecosystem health have been related with the concepts of stress ecology, in which health is defined in terms of the system organization (including the diversity of biota and their balanced interactions), stability or resilience and vigour, as well as the absence of signs of ecosystem distress (Rapport *et al.*, 2001; Rapport *et al.*, 2002; Lu *et al.*, 2017).

Some common ecosystem health indicators are historical (historical abnormalities or ecosystem distress syndrome), or biological (indicator species, biological integrity, diversity and stability). Plesnik *et al.* (2011) propose a set of holistic ecosystem health indicators:

1. Vigour, organization, and resilience (V-O-R model).
2. Buffer capacity.
3. Diversity indexes (Shannon–Wiener index, Pielou Evenness Index, Margalef Index, Berger-Parker Index, etc.).
4. Size and connectivity of the ecological network.
5. Turnover rate of carbon/nitrogen.

Biodiversity vs stability: The diversity–stability debate

As it can be noticed, three aspects are commonly considered for defining health in ecosystems by most authors: biological diversity, stability (also indirectly as resilience or buffer capacity) and complexity (as food web levels and structure). However, more diversity or complexity not necessarily implies more stability (MacArthur, 1955). In fact, the relation between diversity and stability has been a major issue and a great source of discussion inside the field of ecology, the so called "diversity-stability debate" (McCann, 2000). Nevertheless, diversity and stability have been indeed used as indicators of ecosystems health (Rapport *et al.*, 1998; Costanza *et al.*, 1998; Hobbs, 1998). Its regard as ecosystems health indicators remains on its simple measuring.

The concept of stability can be understood as a set of two characteristics of the ecological system:

- Resilience: how fast the system returns to its equilibrium (initial condition or steady state).
- Resistance: how much the system changes when is disturbed.

As I mentioned before, stability in an ecosystem is strongly related with two factors:

- Diversity of the community.
- Connectance or connectedness; connectivity between members of a food web.

In the ecological search for the bases of stability, a debate has been going on what is the importance of diversity in the stability of a community. It was expected that a more diverse community would be also more stable. The evidence has tended to agree that diversity is positively related to ecosystem stability (McCann, 2000). In laboratories, ambitious experiments like Ecotron have shown that when diversity was increased, the stability (expressed as repeatability) also increases proportionally (McCann, 2000). Land evidence shown that resistance can be increased when diversity does it. Tilman and Downing (1994) showed that when diversity rises, the resistance to drought of the community also increases.

There are some factors that can control the diversity of some ecological communities. Those factors are called "diversity promoters". The diversity promoters can be positive, as the case of mutualism (allowing stable increases of diversity in the community), or negative as basically predation and disturbances. Those negative mechanisms interfere with the competitive exclusion principle, through wiping out individuals of the dominant species. The different diversity promoters involved in this research are explained in more detail next.

Predation

Defined as the consumption of an alive organism (prey) by another one (predator), it includes herbivory as well (Begon *et al.*, 1990). In terms of complex dynamics, predation turns to be more relevant in "Predator Controlled" communities. On them, there are some predators, called "key stone predators", that have a strong influence in the diversity of the whole community. This is possible because the preys of those predators, usually more than one species, have also a big impact on their community diversity, as they also depredate other species. Because of that, the key stone predator could be indirectly related with a lot of species of the community.

Disturbances

When the community is not mainly controlled by a predator, it is known as "Donor Controlled" community. On them, more important than predation are disturbances. In a forest ecosystem that has reached a climax state, for instance, the limit factor for non-dominant species to rise is the lack of light/space availability. Some disturbances can break the dominance of the climax's species (like big trees) to start a new ecological succession. Those disturbances have a stochastic distribution in time which make them less effective in the maintenance of diversity and stability on the community. Examples among the mentioned disturbances are:

- Trees falling
- Elephant's forest damage
- Fire
- Forest clear cut by man or animals (like beavers)
- Pests

For its mathematically study in classical ecology, diversity has been considered as been formed by two factors:

- Species richness: number of species present at a site.
- Species evenness: how even the individuals in the community are distributed among the species.

Species diversity indices consider both species richness and evenness. To measure diversity some indicators are used (normally known as diversity indices), in which richness and evenness (measured as equitability) are mathematically related. The most popular diversity index is the Shannon -Wiener diversity index H, which is defined as follows:

$$H = -\sum_{i=1}^{S} Pi \ln Pi$$

where:
S is the number of species.
Pi is the proportion of total individuals in the i th species.

Modelling a global self-organized ecosystem: Daisyworld model and climate regulation

Daisyworld (Lovelock, 1992) is a model that presents an interesting feedback between life and the environment. Those feedbacks are always present in nature, but they are normally not considered in classical population models (Harding, 1999). Without feedbacks between living beings and their environment, models are not located at ecosystem level, but at the level of biological communities. Gaian approach allows the study of the relation between complexity and resilience at the global ecosystem (Levin, 1999).

In the model, two species of daisies (one light and the other dark) are set to compete on a surface that receives light. In Daisyworld, that surface is thought to be the earth sphere that receives light from the sun. The novelty of it is that through the competition of both species of daisies under a classical natural selection scheme, a new quality emerges when their albedos are considered in the earth's global temperature: the system's equilibrium tends to go closer to the daisies optimum temperature. When sun luminosity is changed, as it has happened in geological history (Grotzinger *et al.*, 2007), the earth temperature of the model does not vary proportionally. Instead, the system is "attracted" to the optimum for the daisies to live. This self–regulation behaviour arises from within the system. The planetary self-regulation of global temperature is considered a particular example of the structural coupling between life and the global environment of the real world, so that the mathematical foundations of Daisyworld are increasingly being used in other Earth-system models (Harding, 1999; Wood *et al.*, 2008). The vision of the earth as a single self-organized system set by the emerging Earth-System Science, have become more accepted in the scientific community, being already part of currently usual climate science (McMullen and Jabbour, 2009; Steffen *et al.*, 2020). In addition, the earth climate regulation is nowadays considered among the most relevant ecosystem service of the earth-system, as it has direct influence over other services (Millennium Ecosystem Assessment, 2005; Masson-Delmotte *et al.*, 2018).

Finally, previous works in Daisyworld models have shown that increments of diversity and inclusion of herbivores in the model have given more stability to the system (Harding and Lovelock, 1996; Harding, 1999; Harding, 2001). This way, given the demonstrative models "Daisyworld" and "Predator-Prey", incorporated in the software Stella© (Hannon and Ruth, 1997), the hypothesis of this work was that including the herbivore in the Daisyworld set should increase the stability of this ecosystem as a result of its higher diversity, supporting a positive relation between biodiversity and ecosystems health. This research is an attempt to check such results in different, simpler platform, assuming that is a basic try on this complex topic. However, this attempt may allow to also get a simpler understanding of the feedback loops involved in global regulation mechanisms, besides eventually contributing to the strength of such focus of analysis of ecosystems.

MATERIALS AND METHODS

In order to explore the effects of diversity on the stability of ecosystems, two models developed by Hannon and Ruth (1997) for the software Stella© were coupled:

1) A version of Daisyworld model, conceptually considered as an ecosystem with only one trophic level (producers). On this way, Daisyworld was used as a grassland community model. The optimum temperature for both species is set at 25 °C, Celsius, following a Gaussian curve of growth as they move out of the optimum.

2) A version of a classical predator-prey model (Lotka-Volterra) adapted from an algae-herbivore set, conceptually considered as a second trophic level, given by the plant-herbivore relation in the food web.

The model was set to run from timelapse 0 to 2000, assuming one chronologic moth for every timelapse. Three perturbations (P) were applied to the system:

P1: As a disturbance, a 50% reduction in the daisy population (timelapse = 500).

P2: As an environmental change, a 10% reduction of the sunlight, in relation to the original level (timelapse = 1000).

P3: As a second environmental change, a 10% increment of the sunlight, in relation to the original level (timelapse = 1500).

Complexity is often defined in terms of the presence of more species, stronger inter-species interactions and greater connectance between species (Begon *et al.*, 1990). Therefore, the diversity of the community increases when adding another species of daisy and so with the addition of an herbivore species. However, the latter is not only an increase on diversity, but an increase on the complexity of the community structure, as it implies an increment of trophic levels in the structure of the foodweb (Begon *et al.*, 1990). Therefore, for the purpose of this research, the perturbations previously described were tested and compared on three diversity/complexity scenarios (S):

S1: one species of daisies (white daisy).
S2: two species of daisies (white and black daisy).
S3: two species of daisies and a grazing herbivore species acting as a predator.

The model was developed under the software Stella© version 7.0.1, and its diagram is shown in Figure 1.

For quantification of diversity, the Shannon-Wiener diversity index (H) was used. For the analysis of stability, resistance and resilience of the system, delay phase-space diagrams (X_n vs X_{n-1}) were used to study those aspects in terms of the system dynamics (to visualize the system´s behaviour) in the search of attractors for two variables of the model: world temperature and for the population of light daisies, both plotted for the 3 diversity/complexity scenarios.

RESULTS AND DISCUSSION

As it has already been studied in the classical Daisyworld models, global temperature regulation is a property that has emerged from the interactions of the two different species of daisies. This point is at the core of the interactions between species in a community, where stability emerges as a new property of such interactions, and not from individual species: diversity is a property of the community as a whole (Schultz, 2000). The results for the three diversity scenarios are shown in Table 1:

In Figure 2 the global temperature, global albedo, and sun luminosity are shown for the three diversity scenarios of the model, from lower to higher diversity-number of species and complexity of the food web. The effect of perturbations P (shown with arrows in the first chart) in the dynamics of the system can be observed through time. The variable world temperature reflects the ability of the ecosystem to self-regulate an environmental variable (as an ecosystem service). Although not very evident, if diversity/complexity is increased, a tendency to reduce the magnitude of the first fluctuation in response to the perturbation can be observed, revelling an increase in resistance of the system. However, the time to recover the steady state also increases, revelling a reduction in resilience. A specific analysis is given bellow, in the section *Attractors as a qualitative measure of stability*.

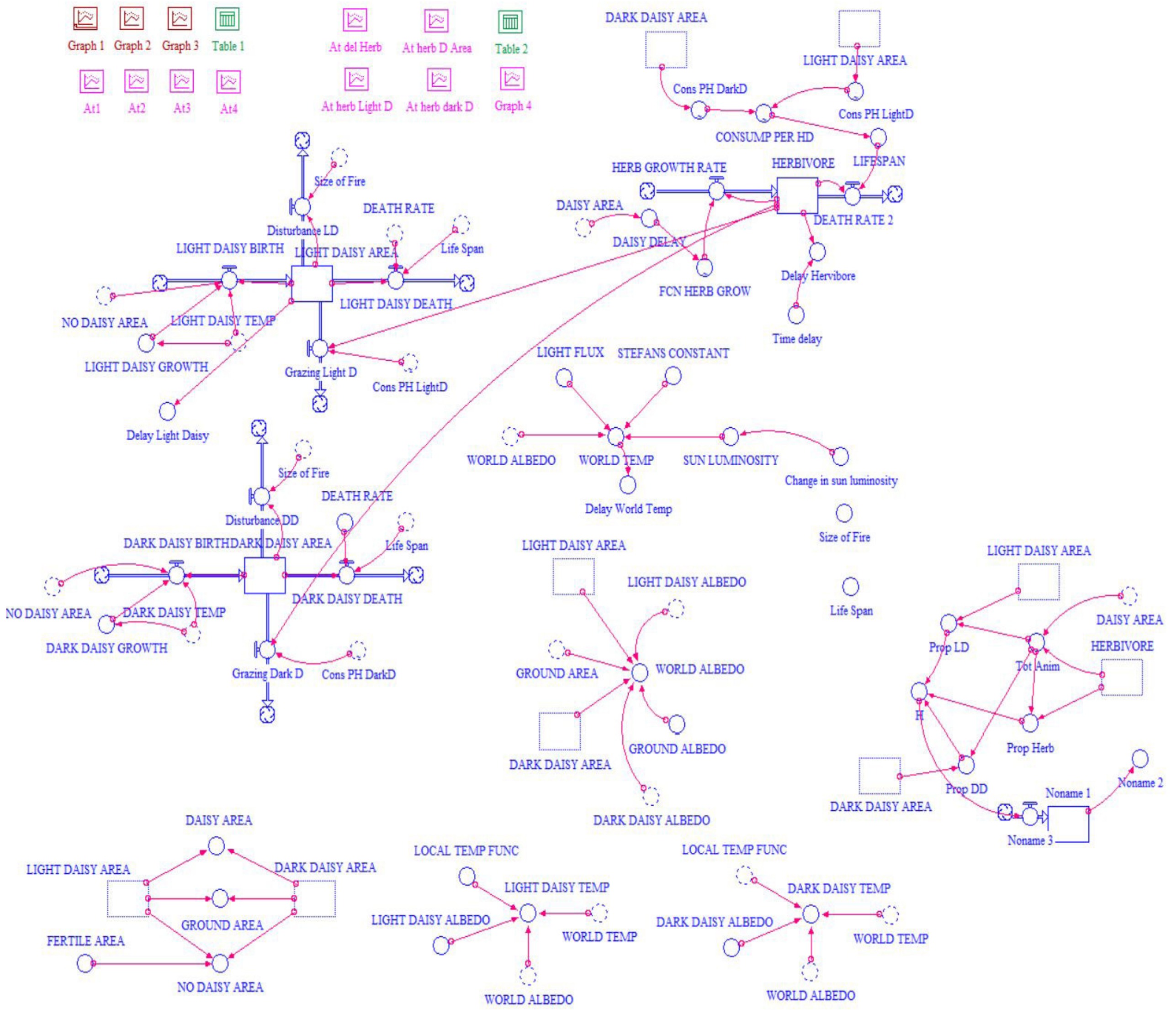


Figure 1. Diagram of the model used, coupling the submodels Daisyworld and plant-herbivore from Hannon and Ruth (1997) for the software Stella©.

Figura 1. Diagrama del modelo utilizado, acoplando los submodelos Mundo de las Margaritas y planta-hervíboro de Hannon y Ruth (1997) para el software Stella©.

Table 1. Shannon -Wiener diversity index, H, for the three diversity scenarios of the model.

Tabla 1. Índices de diversidad de Shannon -Wiener, H, para los tres escenarios de diversidad del modelo.

#			**H** (steady states at perturbations, P)		**H** (average)
Scenario	**Description**	**P1** (disturbance: 50% reduction in the daisy population)	**P2** (environmental change #1: 10% decrease in the solar radiation)	**P3** (environmental change #2: 10% increase in the solar radiation)	
S1	One daisy species	0.00	0.00	0.00	0.00
S2	Two daisy species	0.62	0.65	0.69	0.66
S3	Two daisy species and an herbivore species	0.74	0.79	0.87	0.80

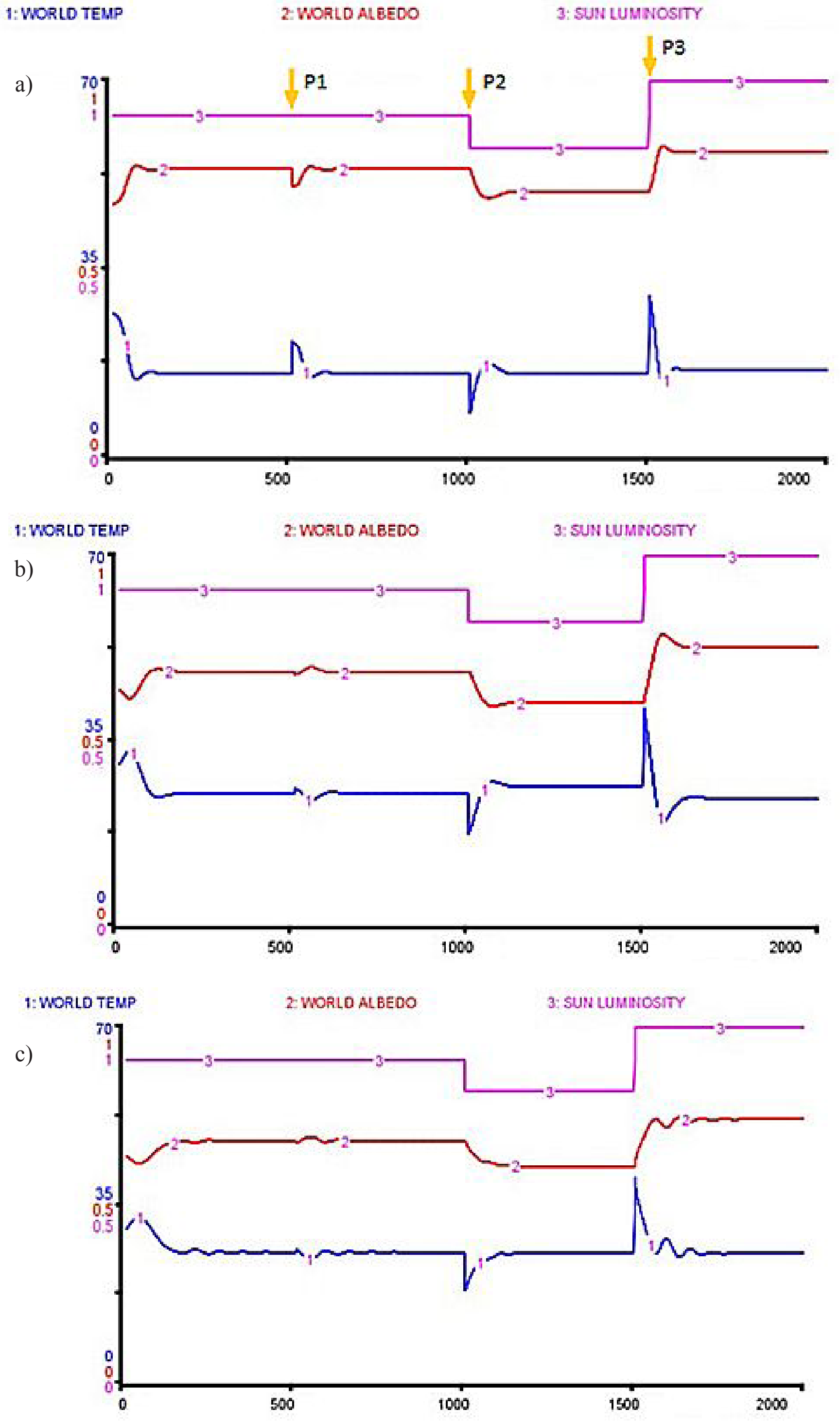


Figure 2. Global temperature, global albedo, and sun luminosity for the three diversity scenarios of the model, from lower to higher diversity-number of species and complexity of the food web. The effect of perturbations P (shown with arrows in the first chart) can be seen at time 500 (reduction of 50% of daisies population), 1000 (decrease in 10% of the sun luminosity) and 1500 (increase in 10% of the sun luminosity). a) One daisy species (light daisy), b) Two daisy species and c) Two daisy species and an herbivore species.

Figura 2. Temperatura global, albedo global y luminosidad solar para los tres escenarios de diversidad del modelo, desde menor a mayor diversidad – número de especies y complejidad de la red trófica. El efecto de las perturbaciones puede verse en los tiempos 500 (reducción de un 50% de la población de margaritas), 1000 (disminución en 10% de la luminosidad solar) y 1500 (aumento en 10% de la luminosidad solar). a) Una especie de Margarita (blanca), b) Dos especies de Margarita y c) Dos especies de Margarita y un herbívoro.

It is interesting to note that the property of changing the global temperature is a property of both species of daisies independently. In fact, just one species of daisy is enough to buffer the changes of temperature due to the sun luminosity changes. Nevertheless, the equilibrium in temperature when just one species of daisy is living never reaches the optimum for that species (set at 25 °C). When just the dark daisies are living, the global temperature stays around 34.5 °C, while when just the light daisies are living the global temperature stays around 15.5 °C. However, when the two species of daisies are living, the global temperature equilibrium stays between 23.71 and 25.98 °C. This effect is even stronger when an herbivore is added; the global temperature equilibrium stays between 25.28 and 25.52 °C, showing that in this case an increase of diversity and complexity reinforce the self-regulation (stability) of the system.

The previously shown data is related to the stability of a function: the ecosystem self-regulation. However, it is also possible to study the stability of its components, or, as it was mentioned, the conservation of its biomass. In Figure 3 it is shown the size of population of every daisy species, all daisies together (Daisy Area) and with an herbivore. The increase of total biomass of daisies (represented as Daisy Area) that the system can support is another emergent property of the interactions of the two species together. When both are present, the overall of daisies population stays at more than the double size that when just one species of daisy is present. However, adding the herbivore to the system reduce the total daisies area, although still stays higher than with one daisy species. On that it should be considered that the herbivore has no predator, so that its population remains at its maximum. It would be interesting to see the effect of adding a predator of herbivores (a carnivore) to the system, as it probably would reduce the population of herbivores, so that the population of daisies would therefore increase, although probably it would never get so high as if there were no predators (herbivores and carnivores) at all. At the same time, in the figure can be also seen the changes in the frequencies of both daisies in response to the solar luminosity. This last interplay of frequencies enhanced the temperature regulation as a self-regulating process.

Regarding the findings, and the fact that the more complex scenario did show more resistance, but less resilience, it is relevant to note that Harding (2001) obtained different results, gaining resistance but also resilience when biodiversity or complexity were increased in his model. Such different results could be explained by the fact that the predator-prey model used introduced an oscillatory dynamic in the general system, reducing its resilience. Here an important point must be added. Even though the oscillation can be easily avoided through adjustment of the model, it was left on purpose to resemble nature. Field data show that predator-prey populations in fact oscillate significantly (Blasius *et al.*, 2020). The dynamics of the predator-prey sub-model used is shown in Figure 4. Another explanation could be that this model was still not complex enough (as it has no carnivore) to stabilize the oscillatory behaviour of the model with herbivore. However, with the carnivore also more oscillation could also be added to the system. To know this, more research is needed.

Attractors as a qualitative measure of stability

To analyse resilience and resistance as stability variables, attractors of the system as a qualitative measure of its stability were explored. In this field, the more stable the system is, the more would tend to show a point attractor (Sole and Goodwin, 2000). Periodic attractors tend to be less stable than point attractors, but more stable than strange attractors, which in turn are more stable than no attractor at all. In the other hand, how resilient is the system can be seen through how fast and direct the system converges to the attractor. At the same time, how resistant is the system can be seen through the size of the attractor: the smaller the orbit developed by the system around the attractor is, the more resistant is the system, as it stays closer to its steady state. Regarding the system´s behaviour, delay-phase space diagrams (X_n vs X_{n-1}) show that their irregular form is basically due to the strong perturbations (Figure 5).

Regarding figure 5, when a second daisy is added, it can be observed that the world temperature steady state change from around 15 to 25 °C (which in fact is the optimum). In contrast, the attractor does not look more stable that the one of just one species of daisy. Nevertheless, when the herbivore is added, the attractor has just one ending point (is connected) and is narrower, which is a sign of a more stable system. Something similar happens with the light daisy attractor, as it tends to get more connected and smaller.

On the other hand, when the predator-prey relation is plotted in the phase-space diagram, more complex attractors emerge. When individual daisies are plotted against the herbivore, they show three point attractors, as part of the dynamics of self-regulation of the system (Figure 6).

However, it is interesting to note that when two species of daisies are plotted together against the herbivore, the system shows only one point attractor, which is more stable than the ones of individual daisies, revealing the emergent property of the interaction of the species of daisies (Figure 7a). A point attractor is formed, even though the attractor has three different starting points, produced by the perturbations in the model, and not by a complex behaviour. In this way, the herbivore-plant oscillation has been stabilised by the environmental feedbacks loops of the daisies, so that the system would get more stable as the complexity in-

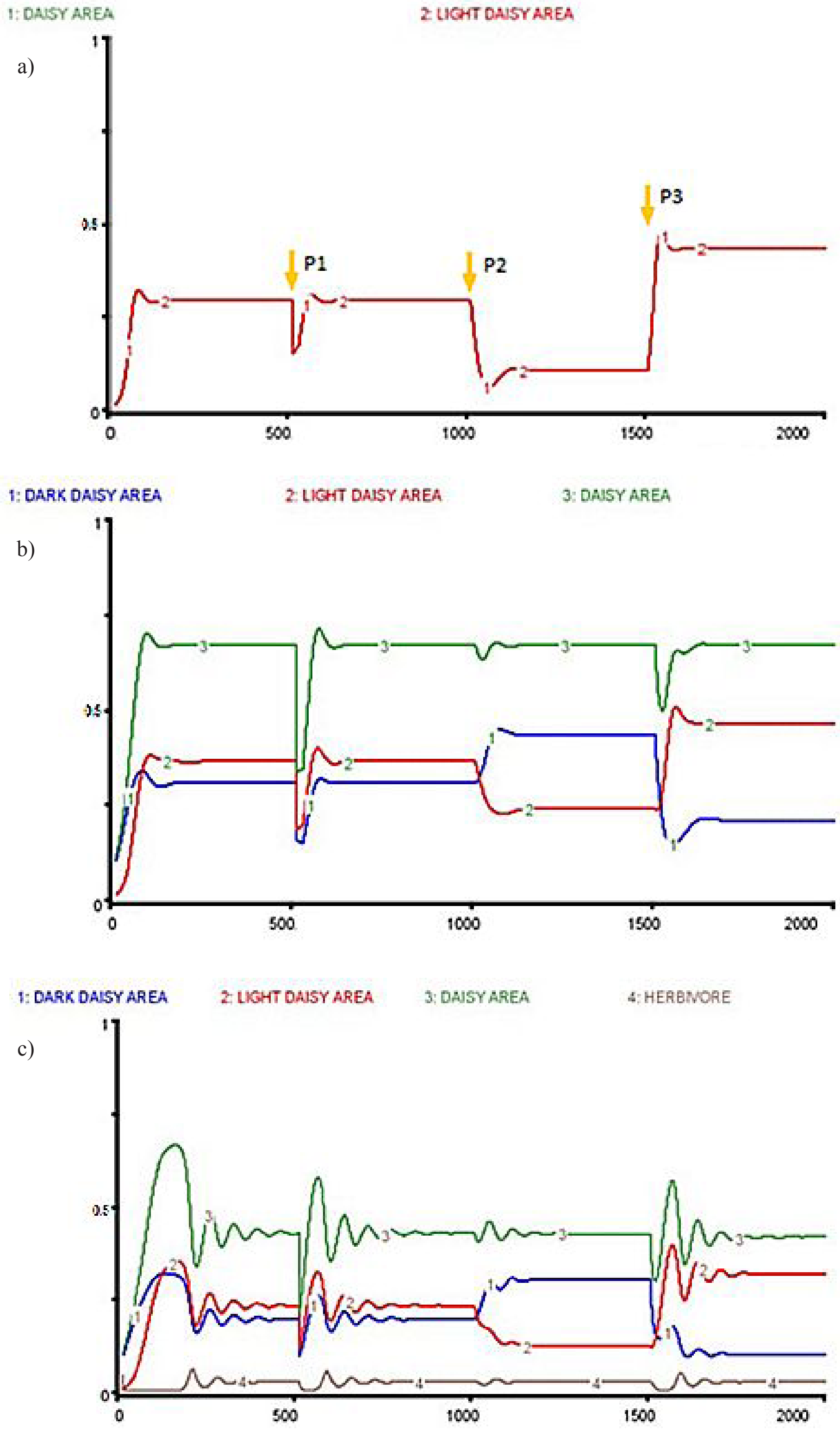
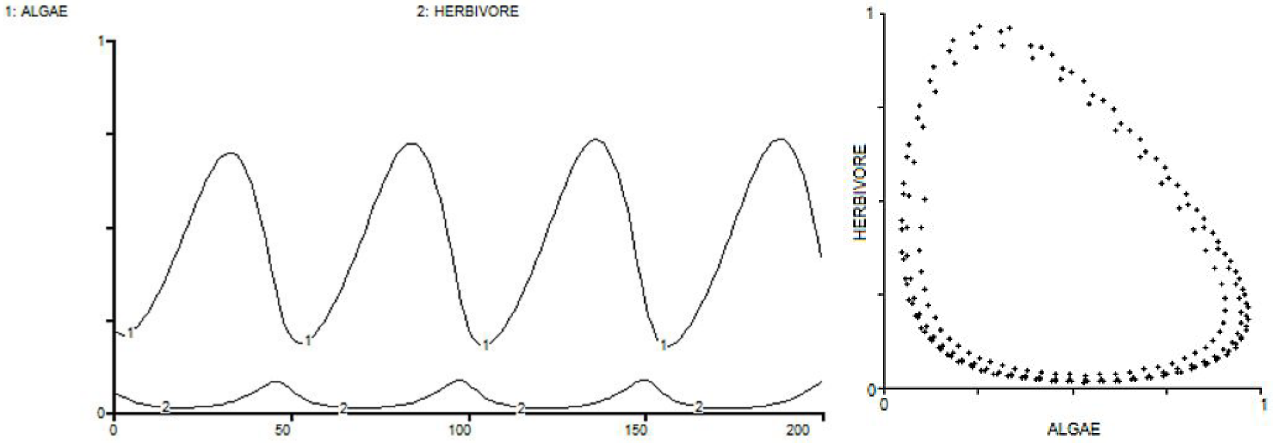


Figure 3. Population dynamics (expressed in terms of area) of both species of daisies independently, the sum of them (Daisy Area) and the herbivore, for the three diversity scenarios of the model. The timelapse of perturbations P are shown with arrows in the first chart. a) One daisy species (light daisy), b) Two daisy species and c) Two daisy species and an herbivore species.

Figura 3. Tamaños poblacionales (expresados en términos de área) de ambas especies de margarita por separado, del total de margaritas y del herbívoro, para los tres escenarios de diversidad del modelo. El lapso en que se producen las perturbaciones P se muestra con flechas en el primer diagrama. a) Una especie de Margarita (blanca), b) Dos especies de Margarita y c) Dos especies de Margarita y un herbívoro.

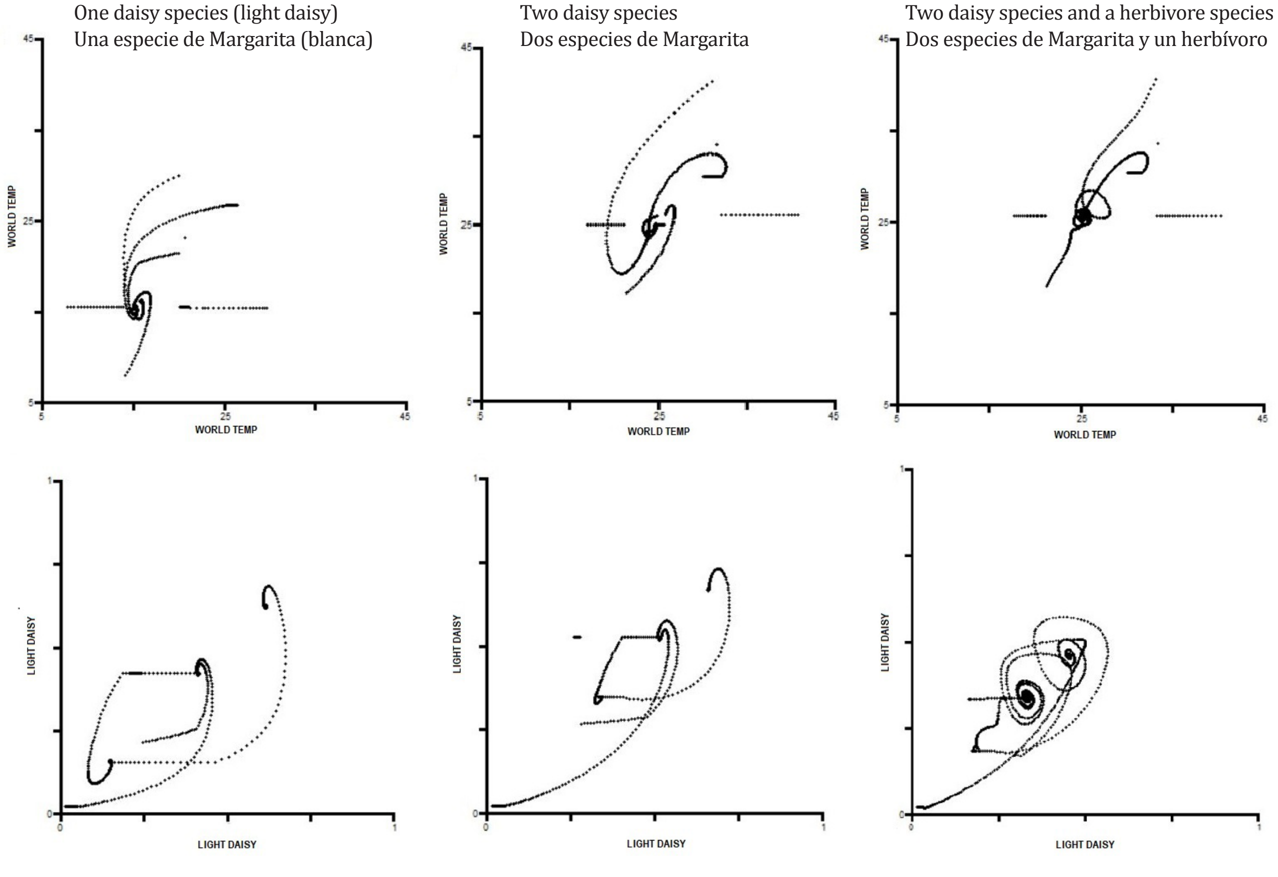


a)

b)

Figure 4. Oscillatory behaviour shown by the model "herbivore-algae" used for the inclusion of an herbivore to the model. a) Dynamics over elapsed time. b) Phase - space diagram of the same set, showing a periodic attractor.

Figura 4. Comportamiento oscilatorio presentado por el modelo "herbívoro-alga" usado para la inclusión de un herbívoro en el modelo de este trabajo. a) Dinámica en el tiempo. b) Diagrama de espacio-fase del mismo conjunto, mostrando un atractor periódico.


One daisy species (light daisy)
Una especie de Margarita (blanca)

Two daisy species
Dos especies de Margarita

Two daisy species and a herbivore species
Dos especies de Margarita y un herbívoro

Figure 5. Delay phase - space diagram (Xn v/s Xn-1) showing the attractors of the global temperature and light daisy population for the three diversity scenarios of the model.

Figura 5. Diagrama de espacio – fase de retraso (Xn v/s Xn-1) mostrando los atractores de temperatura global y población de margaritas blancas para los tres escenarios de diversidad del modelo.

creases. This stability can also be observed, in terms of a point attractor, in the delay phase-space of the herbivore (Figure 7b).

Finally, the fact that the increment on trophic complexity did not strengthen the resilience of the system may rise a discussion. The reasons for it can be many,

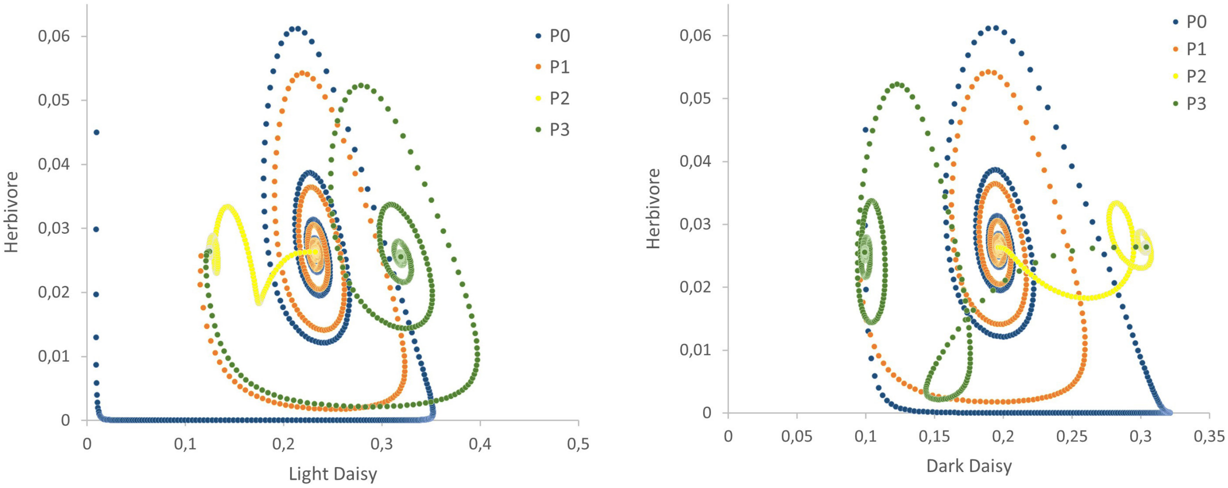


Figure 6. Phase - space diagram for light daisy v/s herbivore (a) and dark daisy v/s herbivore (b). The run after perturbations P are shown, being P0 the run before any perturbation. It is interesting to note that the diagrams of individual daisies show three point attractors.

Figura 6. Diagrama de espacio – fase para margarita blanca v/s herbívoro y margarita negra v/s herbívoro. Se muestran las ejecuciones después de las perturbaciones P, siendo P0 la ejecución antes de cualquier perturbación. Es interesante notar que los diagramas de margaritas individuales presentan 3 atractores de punto.

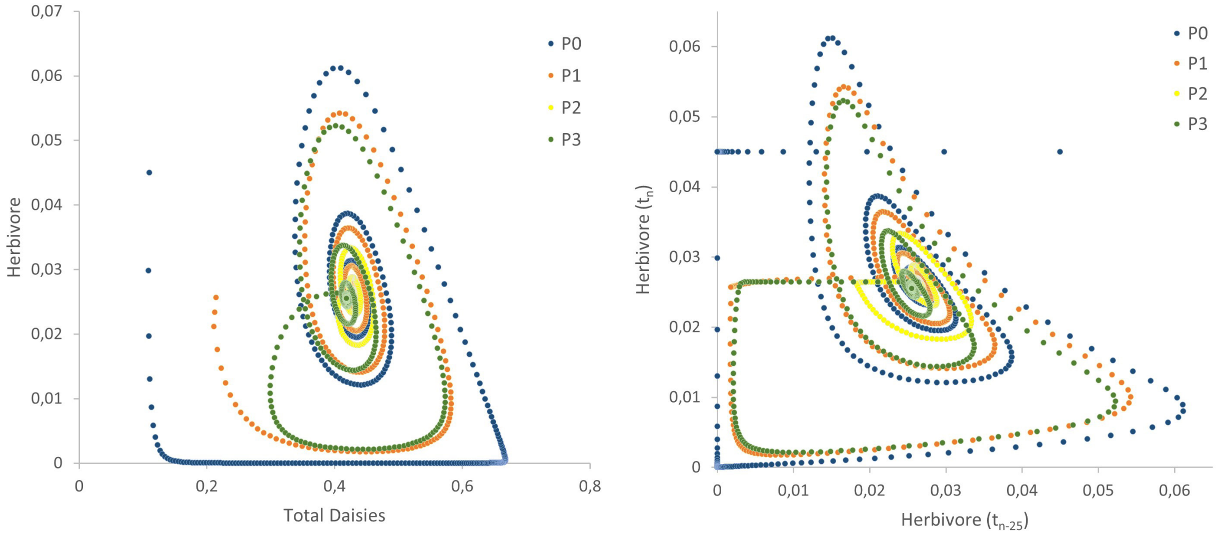


Figure 7. Phase - space diagram for: a) predator - prey (herbivore v/s total daises) in the run of the Daisy Word model, showing a point attractor. A single point attractor instead of three point attractors (Figure 6) reveals the emergence of a new property (emergent property) as higher stability from the interaction of both species of daisies. b) delayed herbivore (tn-25) v/s herbivore (tn) in the model, showing a point attractor.

Figura 7. Diagrama de espacio – fase para: a) predador - presa (herbívoro v/s margaritas) en la ejecución del "Mundo de las Margaritas", presentando un atractor de punto. Un solo atractor de punto en lugar de tres atractores de punto (Figura 6) revela la emergencia de una nueva propiedad (propiedad emergente) en términos de una mayor estabilidad a partir de la interacción de ambas especies de margaritas. b) herbívoro retardado (tn-25) v/s herbívoro (tn) en el modelo, presentando un atractor de punto.

from the mathematical bases of the model. In this way, results are strictly mathematical and cannot be projected into conclusions about natural ecosystems. However, cycles are frequently observed in nature, and oscillations of populations seem to be just part of the complex ecosystemic dynamics. In this way, new inclusions of diversity and trophic complexity could reduce more the resilience of the system through including more variability, or increase the resilience through the annulation of oscillations by the dynamics of the new components, strengthening the stability of the system as a whole. To find out that, more complex models of this kind are needed.

CONCLUSIONS

As conclusions, regarding the modelling analysed, it can be said that:

The addition of a second species of daisy does not necessarily increases the stability of the system but does contribute to the health of it in terms of welfare (as the system gets closer to the optimum temperature). Also, considering that diversity is used to measure ecosystems health, an increase of diversity, in a stable ecosystem, could be considered an increase on the ecosystem health too. Finally, the addition of a second daisy species does increase substantially the biomass of equilibrium, leading to a more productive ecosystem, factor that is also considered as an increment on ecosystem health.

The inclusion of an herbivore does not increase the stability of the system either (as the system gains resistance but loses resilience in relation to the previous runs) but does increase diversity as well.

The ecosystem with higher diversity (two species of daisies and an herbivore) might be considered healthier than the one with lower diversity (just one species of daisy), as the system gains resistance and productivity, reaches higher diversity and gets closer to the optimum temperature, although loosing resilience. This way, the hypothesis of this work is accepted.

Regarding the diversity-stability debate, the results of the presented model show, just as Lovelock and Harding showed previously, that higher levels of diversity might rise (and at least do not deteriorate) the ecosystem stability, through emergent properties (synergies) between the components of the system in a model that considers feedbacks between organism and their physical environment.

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