Theoretical approach to community structure: body size, density and energy

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Given the complexity of integrating and forecasting the interconnected effects of body size, population dynamics, and energy availability, theoretical approaches that link ecological and computational knowledge are required. Individual attributes, such as body size, exert influence and are, in turn, influenced by community structure. Distinguishing between the processes that generate population patterns and making predictions poses a challenge in theoretical ecology, drawing on concepts ranging from traditional natural philosophy to contemporary physical sciences. To address this challenge, our research proposes a computational model for conducting theoretical-exploratory simulations of a biological community, incorporating body size, density, and population dynamics based on the Metabolic Theory of Ecology principles. This community includes reproductive and non-reproductive individuals transitioning between feeding and reproductive areas. Accounting for seasonal limits and finite energy, we delineate the dynamic relationship between body size and population abundance. Additionally, we present a temporal simulation of allometric exponents describing the density pattern. The findings highlight the importance of considering energetic limitations to maintain the relationship between body size and population density and present the possibility of temporally modeling the allometric exponent of this demographic pattern.

Keywords: Body size, allometric relationships, density, energy, modeling.

1. Introduction

In recent decades, researchers have widely recognized the predictive influence of an individual's body size on demographic patterns [18, 25, 36, 37]. These studies report an allometric growth pattern emerges when different body dimensions grow at varying rates. Despite previous research, questions persist regarding the implications of allometric relationships between body size and various biological and demographic characteristics, aiming to deepen our understanding of this crucial phenomenon in evolutionary biology and ecology. Allometric relationships are described by the equation $Y = C_0 \cdot M^\alpha$, where Y represents a species characteristic, C_0 is a constant specific to the variable Y, and M represents body size. The dimensionless allometric exponent, denoted as α, can be interpreted as the slope of a straight line on a $\log(Y)$ versus $\log(M)$ graph. Allometric relationships, also known as power laws [33], allow the expression of fundamental ecological traits such as metabolism [6, 32], reproduction rate [30, 31], mortality rate [29],

and population abundance [28] concerning species body size. These functional relationships serve as simple and efficient predictors across a wide range of taxonomic groups [3, 4, 25–27].

Swiss botanist and physiologist Max Kleiber presented one of the earliest investigations into the relationship between body mass and a specific characteristic of individuals [24]. He suggested that the rate at which an organism generates energy from consumed calories to sustain itself is proportional to the body size raised to the power of $\alpha = 3/4$. Numerous studies have validated this exponent by compiling data from various types of organisms [30]. Building on Kleiber's proposition, the intrinsic population growth rate is proportional to the body size raised to the power of $\alpha - 1$. Similarly, it is reasonable to assume that lifespan is inversely related to the mortality rate, which is proportional to the body size raised to $\alpha - 1$ [21–23, 29]. In studies examining the relationship between body size and population density in herbivorous mammals, it has been observed that population density is proportional to body size raised to the power of $\alpha = -3/4$. It is important to note that the value of the exponent α is known to depend

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on various factors, including temperature, environmental conditions, metabolic activity, taxonomic group, and taxonomic level [18–20]. However, despite these influencing factors, a $\alpha = 3/4$ value represents a common expectation across a wide range of species.

Computational and mathematical modeling provides a means to establish connections among these allometric relationships [17]. To quantify and predict population density scaling in specific groups, researchers have employed consumer-resource models that describe interactions, including birth and death processes, to parameterize systems of differential equations [5, 13–16, 21]. These models exhibit varying levels of complexity, making it challenging to conduct a quantitative analysis of dynamics, especially in identifying which parameters drive the allometric pattern between density and body mass [11, 12]. These mathematical analysis tools may not be familiar to biologists or non-mathematical specialists. Therefore, it is crucial to develop simple models that facilitate scientific dialogue and enable accessible theoretical ecological analyses.

The main goal of this study is to bridge the gap between the natural language of ecosystems and computational language by representing the dynamics of biological communities without relying on systems of differential equations [13, 14, 16, 21]. Currently, numerical simulations in the field of computational science share similarities with laboratory experiments in terms of their assumptions and limitations [9, 10]. Integrating allometric relationships and biological processes, such as births, deaths, developmental stages (adults, juveniles), and extinctions, is proposed to capture demographic patterns accurately. Ribeiro and Pereira (2023) have reported on the different values of the allometric exponent in the Rubner and West-Brown-Enquist models [1]. Furthermore, this study posits that environmental conditions impact energy availability, potentially influencing the exponent value in relation to the metabolic adaptation of organisms. Therefore, we propose conducting a dynamic simulation in this context.

Our study is of a theoretical and exploratory nature and aims to develop a model for simulating the dynamics of a biological community to obtain its demographic pattern. The community comprises different species divided into reproductive and non-reproductive age groups, with dynamic transitions between feeding and reproductive zones. We explore two environmental scenarios: one with finite energy resources and another with seasonal fluctuations in energy availability. We are incorporating actual data and considering the dynamic conditions of the community and energy factors. As time passes, some species become extinct, and we introduce new ones to maintain the initial number of species. Our approach aims to contribute to ecological and evolutionary biology modeling by predicting the community structure and analyzing the allometric exponent of the demographic pattern, which describes the relationship between body size and density in a dynamic manner.

2. Materials and Methods

This study utilizes traditional programming language statements, such as *for*, *loops*, *switch* statements, and common conditionals, to capture the interactions occurring in a biological community and articulate the biological parameters and community dynamics. The simulation is implemented using PYTHON software, and detailed information on the code and implementation is provided in the Appendix A.

For the simulation, a community includes $n = 307$ species, the same number of species studied by John Damuth in 1981. An exponent α_i is chosen within the range of -1.15 to -0.35, and body masses (M_i) are randomly selected between 0 and 6, where the subscript i varies from 1 to n. With this data, the density (D_i) of species i is calculated as $D_i = k \cdot M_i^{\alpha_i}$, where k is constant [17, 22]. For each species, the metabolic rate (B_i) is calculated using the relationship $B_i = C_0 \cdot M_i^{3/4}$ [24]. Using the aforementioned information, the energy use per unit area of the population (E_i) is determined as the product of energy requirements and population density, expressed by the equation $E_i = C_0 \cdot M_i^{3/4} D_i$ [8]. Thus, the sum of energies from E_1 to E_n represents the total energy for the community.

Each species in the community is categorized into adults (in the reproductive stage) and juveniles (in the pre-reproductive stage). The cycle begins in the reproduction zone, where each species increases its population through reproductive events. During the transition to the feeding zone, the population decreases due to deaths associated with energy expenses during the journey. Upon arrival at the feeding zone, species acquire available energy in the order determined by their body sizes, with larger species feeding first, followed by smaller ones. The feeding dynamics are designed such that adults consume the available energy while juveniles acquire the remaining energy. Subsequently, a fraction of the juveniles that acquire the necessary nutrients transition into adults. Once this process is completed, the return journey begins, and due to the energy cost of transportation, only a fraction of the total number of individuals in the community returns to the reproduction zone. Each trajectory in the simulation is associated with a year on the temporal scale and is referred to as a "cycle" in the programming context.

Once all species have followed their trajectories, an evaluation is conducted to detect potential extinctions. When a species becomes extinct, a new species is randomly introduced, and the cycle begins anew with the same initial number of species. This process is illustrated in Figure 1. As part of our research proposal, we evaluate the allometric exponent annually and investigate whether it demonstrates a distinguishable pattern under different energy scenarios: infinite, temporally limited, and limited. By analyzing the dynamics of the allometric exponent over time, our goal is to gain valuable insights
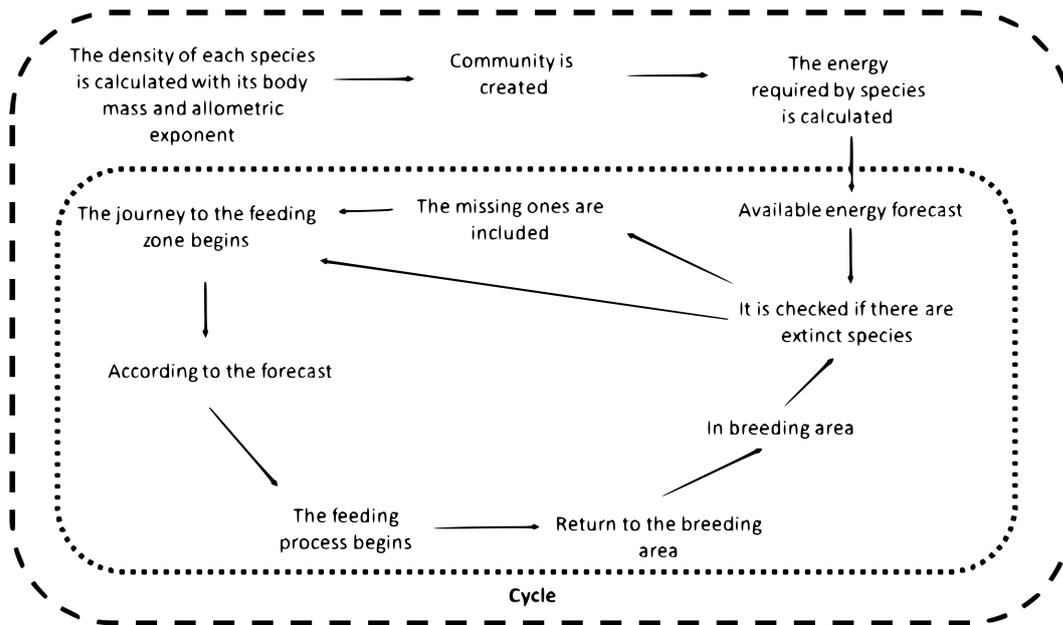
Figure 1: The flowchart illustrates the dynamic process of animal movement. The initial steps involve characterizing each species by its body mass, creating the community, and calculating the energy requirements for each species. Subsequently, the cycle begins, and the program executes the following steps: forecasting available energy, checking for extinct species, including any missing species, initiating the journey to the feeding zone, commencing the feeding process based on the forecast, returning to the breeding area, checking for extinct species in the breeding area, and restarting the cycle.

into the relationship between body size and population abundance in the context of varying energy availability.

An analytical description of the modeling process can be expressed through the continuous-time logistic model without distinguishing between adults and juveniles. In this model, the growth rate is represented as $r = r_0 \cdot M^\beta$ and the carrying capacity as $K = k_0 \cdot M^\gamma$. The system's dynamics are governed by the following differential equation:

$$\frac{dD_i}{dt} = r \cdot D_i \left[1 - \frac{D_i}{K}\right] := f(D_i) \tag{1}$$

This equation exhibits two equilibrium points, that is, where $dD_i/dt = 0$: when $D_i = 0$ or $D_i = K$. To analyze the behavior of the model around these points ($S = 0$ or $S = K$), we linearize the system to obtain a linear approximation:

$$\frac{dD_i}{dt} = f(D_i) \approx f(S) + f'(S) \cdot (D_i - S) \tag{2}$$

Since $f(S) = 0$, we can infer that

$$\frac{dD_i}{D_i - S} \approx f'(S)dt \Rightarrow \ln(D_i - S) \approx f'(S)t + C$$

Thus, we obtain the approximate solution:

$$D_i(t) \approx S - (D_i(0) - S) \cdot e^{f'(S) \cdot t} \tag{3}$$

Where $D_i(0)$ represents the initial population of species i. It is noteworthy that $f'(0) = r > 0$, implying

that $\lim_{t \to \infty} D_i(t) = \infty$; that is, an unstable equilibrium point. On the other hand, $f'(K) = -r < 0$, and thus $\lim_{t \to \infty} D_i(t) = K$; that is, a stable equilibrium point. Incorporating adults and juveniles through this analytical approximation requires adding more equations, which goes beyond the scope of this work. Please refer to the following works for more information on analytical extensions using this approach [13, 14, 21].

3. Results

We present a new algorithm that simulates community dynamics and focuses on exploring the body size-density relationship and the 3/4 rule through allometric relationships. The aim is to understand how these relationships influence the structure and configuration of biological communities. Figure 2a represents an initial community of animals where a negative relationship between body mass and density is observed. This means that as the size of the animals increases, the density of the community decreases. This may be due to larger animals requiring more resources and living space, leading to a less dense distribution of individuals in the area. It is important to note that in this initial community, energy is considered unlimited with no restrictions on energy resources. Subsequently, after 30 cycles, we arrive at Figure 2b, which describes the final configuration of the community. At this stage, a change in the initial pattern is observed. The blue line representing the linear fit shows a positive slope. This implies that community
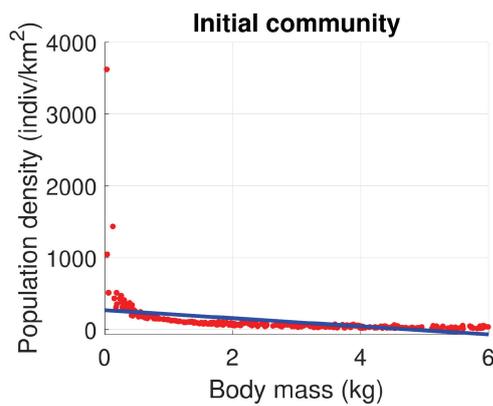
(a) Initial community configuration depicting the negative relationship between body mass and density.
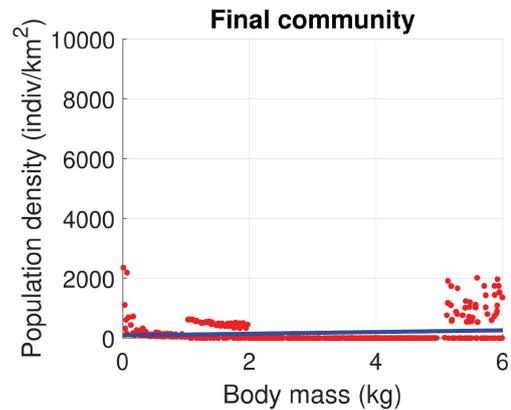
(b) Final community configuration after 30 cycles, demonstrating a shift from the initial pattern.

Figure 2: Analysis of the mass-density relationship in a dynamic community with **unlimited energy**. Figure (a) demonstrates an initial negative relationship; whereas size increases, density decreases. After 30 cycles, Figure (b) reveals a shift: an emerging positive relationship, with larger size correlated to higher density.
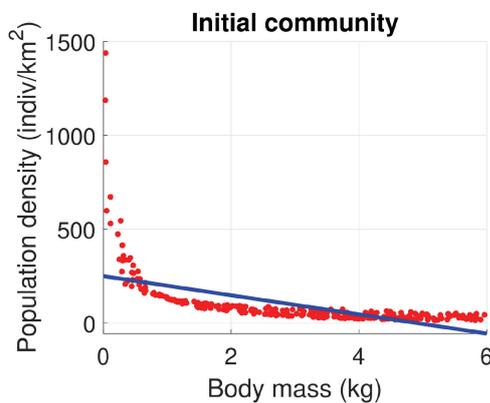
(a) Initial community configuration with a negative mass-density relationship.
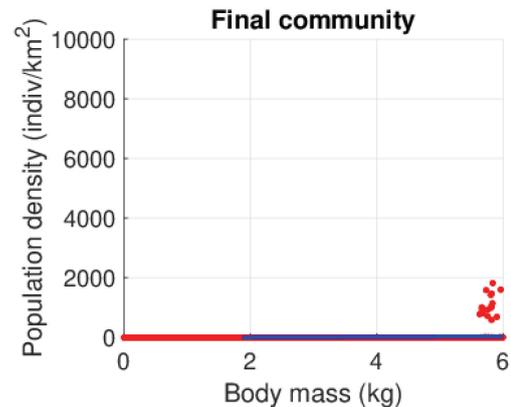
(b) Final community configuration after 30 cycles.

Figure 3: Analysis of the mass-density relationship in a community with **seasonal energy limitation**. Figure (a) illustrates an initial negative relationship, where density decreases as body mass increases. However, in Figure (b), after 30 cycles, a linear fit slope parallel to the body size axis is observed, indicating a constant density as body mass increases due to energy limitation. Despite this, Figure (b) shows the persistence and higher abundance of large species, contributing to species diversity in an environment with seasonally limited energy resources.

density also tends to increase as body size increases. Various factors may influence this change in the relationship between body mass and density in the community's final configuration. Although energy availability is unlimited, other resources such as space or specific ecological niches may have become limiting for smaller animals. This could increase intraspecific competition among smaller individuals, leading to a density redistribution within the community.

Figure 3(a) illustrates the initial negative relationship between body size and density in the community. As body size increases, density decreases. However, the slope of the linear fit is parallel to the body size axis during certain seasons due to energy limitations.

This suggests no significant decrease in density as body size increases. Despite this, larger species are identified with higher abundance in the community, indicating a low species diversity but the presence of large species. Figure 3(b) depicts the final configuration of the community after 30 cycles. Although the negative relationship between body size and density is maintained, the slope of the linear fit remains parallel to the body size axis, indicating that density does not significantly decrease with increasing body size. Despite this trend, the persistence of large species is observed in the community, contributing to species diversity in an environment with seasonally limited energy resources. These findings suggest that under conditions of seasonal

(a) Initial community configuration with a negative mass-density relationship.

(b) Final community configuration after 30 cycles.
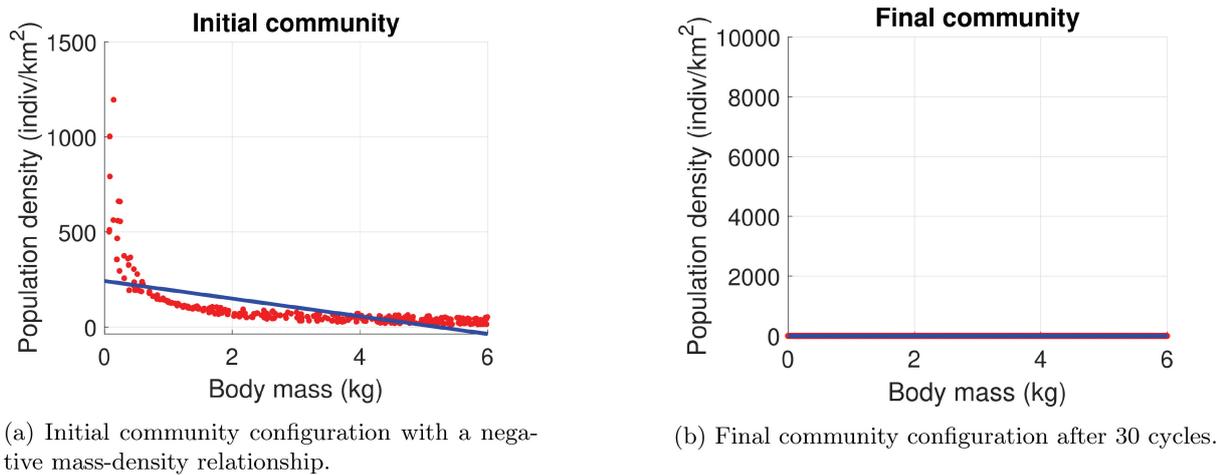
Figure 4: Analysis of the mass-density relationship in a community with **limited energy**. Figure (a) illustrates an initial negative relationship, where density decreases as body mass increases. However, in Figure (b), after 30 cycles, a linear fit slope parallel to the body size-axis is observed, indicating a constant density as body size increases due to energy limitation. Despite this, Figure (b) shows the persistence and higher abundance of large species, contributing to species diversity in an environment with seasonally limited energy resources.

(a) Unlimited energy.

(b) Seasonally limited energy.
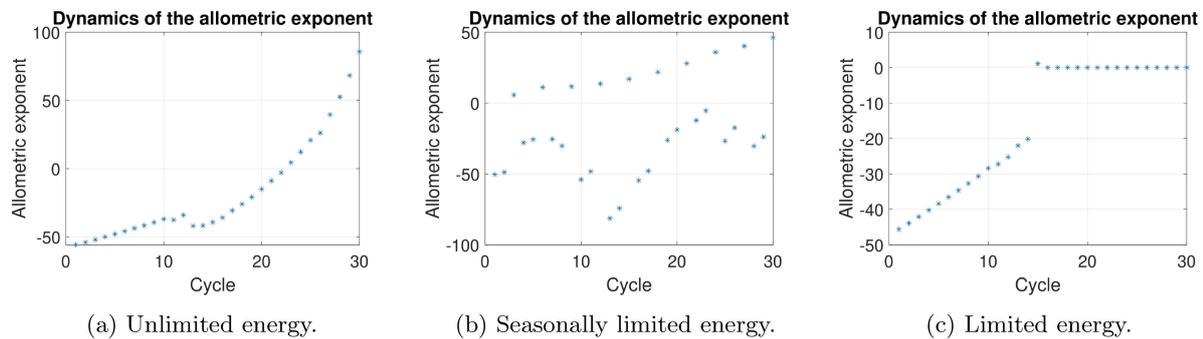
(c) Limited energy.

Figure 5: Dynamics of allometric exponents in different energy availability scenarios. The cases of unlimited energy, energy limitation by seasons and overall energy limitation are compared. The variation of these exponents is observed based on energy availability, indicating adaptations and adjustments in species' growth and developmental strategies in response to energy constraints.

energy limitation, large species may have a competitive advantage and persist in the community despite the negative relationship between body size and density. This parallels the era of dinosaurs, where large-sized species dominated despite limited resource availability [7].

Figure 4(a) shows that there is a negative relationship between the size of an organism and its density; larger organisms have a lower density. Figure 4(b) shows the final configuration of the community after energy limitation. The absence of any abundance above the zero-slope linear fit in Figure 4(b) indicates that larger species are not present in the community. This leads to a loss of diversity, which could be due to the fact that larger individuals are more vulnerable to energy limitations. As a result, the community is dominated by smaller species and has a lower variety of organisms. These findings emphasize the importance of energy availability in the conservation of biodiversity and the critical role that larger species play in ecosystems. Energy limitation

can significantly affect the structure and composition of the community, reducing diversity and the abundance of larger species.

On the other hand, Figure 5(a) demonstrates a scenario of unlimited energy, where a clear and ascending pattern of allometric exponent values is observed. Notably, from cycle 23 onwards, the slope becomes positive, indicating a higher abundance of larger species. This suggests that large species enjoy a competitive advantage and thrive in an environment with abundant energy resources, consequently influencing the overall community structure. Moving on to Figure 5(b), we observe a variable pattern of the allometric exponent, which can be attributed to seasonal energy limitations. As energy conditions fluctuate, species adapt by adjusting their growth and developmental strategies. This adaptation is reflected in the changing allometric exponent, highlighting the species' ability to respond to the constraints imposed by seasonal energy availability.

In Figure 5(c), an interesting pattern emerges, with an initial ascending trend of the allometric exponent that eventually stabilizes at zero. This pattern indicates that larger species tend to diminish in an energy-limited environment, resulting in a loss of diversity. The absence of large species can be attributed to their heightened vulnerability to energy constraints and the limited availability of resources. The insights gained from these dynamics of allometric exponents underscore the fundamental role of energy availability in shaping the growth, development, and diversity of species within a community. It is crucial to consider energy as a key factor in understanding ecological patterns and processes, as it significantly influences the dynamics and structure of biological communities.

4. Discussion

The body size of individuals exerts a significant impact on both the static and dynamic characteristics of biological communities [13, 14, 21, 26, 30]. This article presents an exploratory theoretical study that constructs a dynamic model of a community based on metabolic requirements and life history traits related to birth and mortality. We integrate parameters with the ecological meaning of the community using statements from a programming language, allowing the recreation of dynamics within a computational framework. It is demonstrated how, from an initial configuration of the body size-density relationship, the relationship is modified due to reproductive events, mortality during movements, and the availability of energy provided by the environment to satisfy the community's energy requirements.

Ecological patterns are modified due to infinite energy resources, seasonal energy availability, and limited energy resources. In a scenario with infinite energy availability (Figura 2), it is predicted that species with different body sizes can coexist. As resources become scarce, species abundances become more homogeneous, leading to a reduction in diversity (Figure 3 and Figure 4). In the case of seasonal energy availability, a configuration is observed where species with large body sizes can coexist, reminiscent of the era of dinosaurs. Conversely, the demographic pattern changes when energy is limited, decreasing species diversity. These findings are valuable for formulating ecological hypotheses, such as identifying the primary ecological dynamics affected by the body size-density pattern.

The patterns arising from the dynamics of allometric exponents contribute to establishing theoretical scenarios of potential extinctions and shaping hypotheses to evaluate species composition based on this stable pattern observed over decades. However, the controversy surrounding the exponent 3/4 necessitates a more detailed study to assess its temporal stability and implications for human well-being [22, 30]. When considering scenarios of unlimited resources or resources limited by season,

the patterns become more pronounced and allow for a greater variety of species. Within a specific range, these values establish that low- and high-energy species are distributed across a wide range of body sizes. Conversely, in the case of limited energy, the exponent value stabilizes at 0, suggesting a process of extinction. This occurs due to the programmed simulation allowing for the possibility of extinctions and the random incorporation of new species. However, after 30 cycles, a community with species differing in abundance is not generated.

The modeling and simulation conducted in this exploratory theoretical study have several limitations. Firstly, explicit predator-prey dynamics should be included, restricting our understanding of species interactions. Additionally, the values of the proportionality constants in the allometric relationships do not align with empirical data and have been arbitrarily chosen. A more detailed analysis could significantly enhance the accuracy of predicted demographic patterns. Another limitation is the absence of a description linking evolutionary and technological advancements with the energy requirements of species in the community. This needs to include a comprehensive understanding of how these factors would influence the dynamics and diversity of the community. Lastly, the computational speed is slow and could be improved through parallel computing techniques. This would reduce the simulation time and enable faster results.

Despite these limitations, the model fulfills a dual purpose. Firstly, it offers a straightforward means to incorporate allometric relationships, which connect various life history traits to community dynamics involving the movement of a community from a breeding zone to a feeding zone. Secondly, this study proposes a null model that necessitates specific programming techniques for its construction. This exploratory approach allows us to generate potential insights into questions such as: How do allometric relationships relate to and integrate into community dynamics? What is the origin and nature of the relationship between body mass and population density? These inquiries constitute challenging and enigmatic problems in Theoretical Ecology, which can be addressed by applying innovative computational algorithms.

5. Conclusion

The model offers a valuable framework for exploring ecological patterns. It demonstrates the impact of energy resource availability, whether infinite, seasonal, or limited, on species coexistence, abundance homogenization, and the potential for extinctions. The study highlights the importance of understanding the relationship between body size and population density and its influence on ecological dynamics. Moreover, integrating new algorithms with models described by differential equations, combined with the potential of current computing

technologies such as parallel computing and quantum computing, holds great promise for advancing our understanding of ecological systems. By taking advantage of these advanced computational capabilities, we can delve deeper into the complexities of ecological processes, resulting in a more complete and accurate description of dynamics. These technological advances offer exciting perspectives to explore intricate ecological phenomena and reveal new insights into ecosystem functioning.

Acknowledgements

Supplementary Material

The following online material is available for this article:
Appendix A

Data Availability

In this article, the data was theoretically generated, as described in the Materials and methods section.

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