



DOI 10.21685/2500-0578-2020-2-5

COMMENTARY ON "KEY ECOLOGICAL PARAMETERS OF IMMOTILE VERSUS LOCOMOTIVE LIFE" BY V. G. GORSHKOV AND A. M. MAKARIEVA

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Abstract. The stability and regulatory capacity of the Earth system to human induced change is an overarching present-day concern. The associated problems are of such large scale, spanning many scientific disciplines, that established methods in traditional fields are frequently proving inadequate. Professors Gorshkov and Makarieva have long taken unconventional approaches to large-scale ecological questions, and it was thus with enthusiasm that we greeted the request to comment on the collaboration published here [1].

Keywords: metabolic rate, population density, biotic regulation, biomass.

Acknowledgments. We are grateful for comments on an earlier draft from A. M. Makarieva and A. Aleinikov, and for funding from the Alexander von Humboldt Foundation to IH, and from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme to EG (grant agreement No. 682602).

For citation: Hatton I., Galbraith E. Commentary on "Key ecological parameters of immotile versus locomotive life" by V. G. Gorshkov and A. M. Makarieva. Russian Journal of Ecosystem Ecology. 2020;5(2). Available from: <https://doi.org/10.21685/2500-0578-2020-2-5>

УДК 574.4:581.5

КОММЕНТАРИЙ К СТАТЬЕ В. Г. ГОРШКОВА И А. М. МАКАРЬЕВОЙ «ФУНДАМЕНТАЛЬНЫЕ ЭКОЛОГИЧЕСКИЕ ПАРАМЕТРЫ НЕПОДВИЖНОЙ И ПЕРЕДВИГАЮЩЕЙСЯ ЖИЗНИ»

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Аннотация. Вопросы о том, насколько система Земли сохраняет устойчивость и регуляторную способность при обусловленных деятельностью человека изменениях, вызывают в настоящее время всеобщую обеспокоенность. Связанные с этим проблемы настолько масштабны и охватывают столь многие научные дисциплины, что методы, развитые в традиционных областях, часто оказываются несостоятельными. Профессоры Горшков и Макарьева уже давно применяли нестандартные подходы к масштабным экологическим проблемам, и поэтому мы с энтузиазмом приняли приглашение прокомментировать их опубликованную здесь совместную работу [1].

Ключевые слова: скорость метаболизма, плотность популяции, биотическая регуляция, биомасса.

Благодарности. Мы признательны за замечания по более раннему проекту от А. М. Макарьевой и А. А. Алейникова, а также за финансирование со стороны Фонда Александра фон Гумбольдта IH и Европейского исследовательского совета (ERC) в рамках программы Европейского Союза Horizon 2020 research and innovation programme to EG (грантовое соглашение № 682602).

As we had expected, we found this to be a thought-provoking work. The topics it touches on are wide-ranging, and rich with originality.

The simple approximations of life's basic characteristics on a per-area basis – with the idea of life as a thin 2 mm veneer over Earth's surface, half

autotrophic reaching out for sunlight, half heterotrophic balancing turnover – are simple and poetic. The notion that the wood layer is an "untouchable" component of the ecosystem, regulating temperature above and moisture below, all the while giving structural integrity to the biotic pump of the water cycle, breathes new vitality into inert timber. Although many biologists may take issue with some of the sweeping generalizations, we think there are promising aspects of their approach for addressing the broad questions tackled in this paper. One of these generalizations has been indispensable to our own work: that mass-specific metabolic rate is surprisingly constant across all of life. We devote the first part of our commentary to this topic.

The underlying framework of the paper is biotic regulation. Ultimately, it is the notion that the biosphere self-regulates. While we are sympathetic to the idea, we feel that biotic regulation needs to be better placed in the existing literature, and that claims of a genetic program underpinning these regulatory feedbacks needs to be treated cautiously, as we outline in the second part. We also question the use of several dichotomies that we think are not well-founded, and may not stand up to closer scrutiny. We devote the latter part of our commentary to these concerns.

Life's metabolic boundaries

For nearly a century, it has been known that within major groups such as mammals, whole-organism metabolic rate scales with body mass to a power significantly less than one, and typically near $3/4$ [2]. Therefore, on a per-gram basis, mass-specific metabolism decreases with body mass, scaling near $-1/4$. Although there were indications since the early 1960s that the same relationship may not extend all the way back to bacteria [3], these were rarely emphasized, nor were data available to properly examine such a broad scale relationship.

In 2008, Makarieva and Gorshkov published a remarkable paper with several collaborators that brought together the largest compilation of metabolism and body mass data assembled at the time [4] (see also [5]). These data, spanning over 3000 species from bacteria to large mammals, were drawn from an enormous number of published sources, many of them from the Russian literature. They showed unambiguously that across all of life, mass-specific metabolic scope is surprisingly constant, in contrast with what was widely assumed. They showed that instead of a $\sim 3/4$ scaling law in metabolism across all species on Earth,

metabolism scales nearer to unity, revealing on a mass-specific basis, strict energetic boundaries across all of life. When the authors thus make the dramatic claim that "the power of respiration per unit volume of living bodies is on average the same for all species of the biota and constitutes around 1 kW/m^3 ", it is based on extensive analysis.

Similar data are now available for other key ecological variables including abundance, growth and mortality. By pairing these variables with metabolism, we recently tested the most foundational assumptions of the Metabolic Theory of Ecology [6] across all eukaryotes [7]. Our findings are inconsistent with an underlying metabolic basis for all of the various $\sim 3/4$ scaling relations, as is widely assumed, given that across all species metabolism scales closer to one. On the other hand, maximum growth does scale near $3/4$ with mass across all species, as well as across different life-stages, and across whole-ecosystems of different biomes [7, 8, 9]. We propose that growth dynamics may be the fundamental basis for other $\sim 3/4$ scaling relations, including within-group metabolic relations.

In addition, our recent work showed reciprocal connections between the body mass scaling of metabolism and abundance [7]. Abundance mirrors changes in metabolism between major taxonomic groups, revealing a near inverse scaling (-1) across all species. We can transform these variables by body mass to get mass-specific metabolism (Fig. 1,A) and population-level biomass (Fig. 1,B). Their product gives the total population energy use per unit area (Fig. 1,C), which exhibits no trend with body mass. Population metabolism implies similar energetic boundaries across all life, and thus generalizes the 'energetic equivalence rule', first demonstrated in mammals [10]. All species thus appear to exist within common energetic bounds, on both a per-gram [4], and a per-area basis [7].

These findings, however, raise a possible inconsistency with Gorshkov and Makarieva's claim that large motile animals have a greater tendency for destabilizing their ecosystem through overconsumption. The near inverse scaling of abundance with body mass suggests that all species stand "elbow-to-elbow" in a similar way, relative to their size. Population metabolism (see Fig. 1,C) should be a good proxy for population consumption, and shows no systematic change from small to large species. Although this suggests that population consumption is similarly bounded across species, it does not tell us about community consumption, which depends on how community and functional group diversity varies

with body size. Since diversity tends to decrease with body size (and even log body size), it suggests a further diminishing of community con-

sumption among larger sized animal communities, and thus does not suggest any tendency for large animal overconsumption.

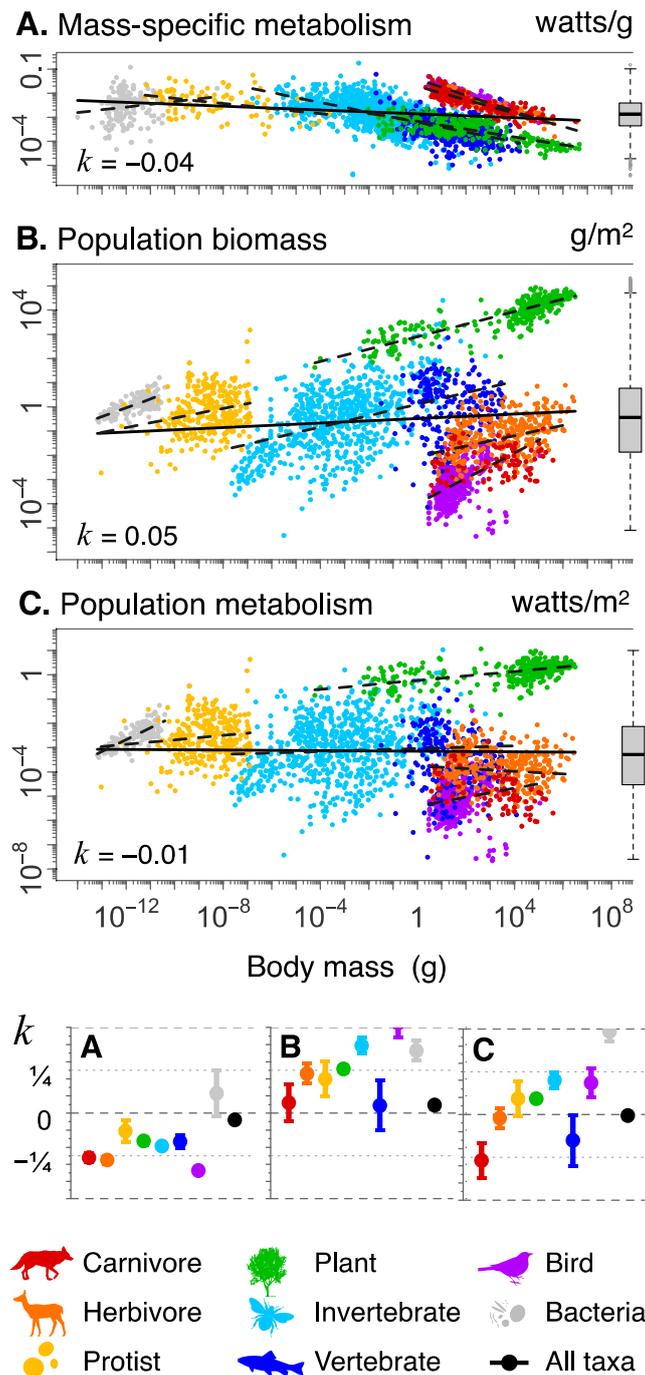


Fig. 1. Life's metabolic boundaries. Each point represents a species from bacteria to whales. In all plots, body mass is shown on the X-axis, and variables A–C on the Y-axis: A – mass-specific metabolism is notably constant across life's major groups, as was shown by Makarieva et al. [4]; B – population biomass also shows no systematic tendency to change with body mass, despite great variability; C – multiplying A and B gives total population energy use per unit area, revealing no trend with body mass, and implying an equivalence in energy use that spans all of life. Scaling exponents (k), and 95 % confidence intervals are shown for the groups listed (see [7])

Biosphere self-regulation

As we understand it, "biotic regulation" proposes that biota regulate their environment in a stable

state, near the optimum for life [11]. Taken to its logical conclusion, this implies the biosphere self-regulates to control environmental conditions for the benefit of life at large.

Very similar ideas enjoy a long history in Russian thought, going back to works of Piotr Kropotkin, Vladimir Kostitzin, and most of all Vladimir Vernadsky [12, 13]. James Lovelock, in formulating the Gaia hypothesis, was not aware of these prior works, though later acknowledged Vernadsky's precedent for many aspects of the hypothesis [14]. Both Lovelock and Vernadsky recognized that only living systems could so dramatically alter the stoichiometry in air, soil and sea from what might otherwise be expected [13, 15]. Both independently suggested that life on other planets could be tested by the ratios of their elements, which on Earth maintain such stability over long time scales, yet so far from thermodynamic equilibrium, that life must be playing a dominant role in regulating basic environmental factors. We find strong similarities between biotic regulation and the ideas of Vernadsky and Lovelock, although the latter are not explicitly cited. It is clear that Gorshkov and Makarieva have firmly advanced this broader field on many fronts [11, 16–18] and we think that placing biotic regulation in the broader context of previous work would serve to strengthen the paper's underlying framework.

Despite the persuasive evidence for life's role in global environmental cycles, the idea of biosphere self-regulation remains controversial, and is widely viewed as radical [19]. It is remarkable, and possibly counter-intuitive, to think that we, as individuals, might reside in a kind of living system much larger than anything we ever imagined. At the same time, it is distressing that we do not know the extent of the biosphere's regulatory capacity to buffer ever-growing human activity. For all of these reasons, biotic regulation and the related ideas that preceded it, should be vigorously pursued, but not assumed to be self-evident or well-established. To be taken seriously by a wide audience, they must be further investigated and carefully articulated.

Furthermore, we question whether biotic regulation necessarily requires a genetic component. The paper claims that "immotile organism biomass comprises time-invariable genetic information about how to keep the environment in a stable state". It seems questionable that any genetic information is time-invariable, and it is not clear how the stability of the environment would be genetically encoded. Similarly, the authors say that "... an efficient program of biotic regulation of the environment can be written into the genetic program of the immotile organisms". This requires the evolution of correlated activity of countless individuals, over diverse assemblages of species. Does biotic regulation necessarily require a genetic program?

The daisyworld model provides an illustration of how simple individual level competition can

translate into large scale regulation, absent any genetic information about the larger scale [20]. Two types of autotroph with different albedos (one black, one white) have different individual responses to temperature; black does well when it is cold by absorbing heat, and white does well when it is warm by reflecting sunlight. Because the large-scale absorption of sunlight is greater when black daisies are abundant, daisyworld will tend to gain heat when it is cold, and vice versa when it is warm. Therefore, the aggregate effect of this trait-pair to temperature at the individual level can broadly regulate the temperature of the environment, wherever it dominates. This scheme does not carry genetic information about the large-scale thermostat in which individuals take part.

Another pertinent model of large-scale regulation that appears to operate without a strict genetic component is that of the biotic pump [17, 18, 21]. The authors have previously proposed that forests, which can yield higher evaporation rates than standing water, can draw moist air deep into the continental interior, by lowering atmospheric pressure through condensation. The biotic pump appears to be a purely physical model for how living systems might mediate environmental conditions in a way that is beneficial for life, but does not appear to require a genetic program for its activity.

We have highlighted two models that we think exemplify biotic regulation that have no strict genetic basis. Of course, all life shares DNA, but if large-scale regulation is emergent from individual-level interactions or physical constraints, then the regulation is no more meaningfully genetic than it is any other shared aspect of living matter, be it macromolecular, cellular, metabolic etc. Any genetic program for large-scale regulation would need to be distributed across many species, which makes its evolution more difficult to account for, and should only be resorted to once simpler possible explanations have been exhausted.

False dichotomies?

There are a number of dichotomies in the paper that we believe may not apply across the time and length scales treated in this work. These dichotomies imply a qualitative change in some behavior that is thought to alter the stability of biotic regulation. Identifying break points between big vs. small, fit vs. not, moving vs. stationary, may describe localized processes, but broad generalizations about properties such as energy use or stability that range across many scales are more questionable. We focus on three dichotomies that we deem are not so "black and white", and one that we think requires greater emphasis.

Big vs. small animals

Body mass scaling laws show that many of life's most fundamental characteristics exhibit a scale-free regularity that spans all creatures big and small. Such characteristics include metabolism, abundance, growth and mortality. In all cases, there are no obvious qualitative changes in these characteristics at any particular size. While these scaling laws do show break points between major taxonomic or functional groups, these do not appear to coincide with the dichotomies raised.

We remain unconvinced that large animals necessarily pose any greater threat to the stability of ecosystems. The authors propose that large locomotor herbivores must destroy live biomass of the immobile ecosystem, however many herbivores do not destroy the plant, but merely crop it down. The "grazing optimization hypothesis", for example, posits that herbivores, even as large as elephants, actually enhance plant production, nutrient cycling, pollination and dispersal [22, 23]. Apparent acts of destruction at one scale can have larger temporal and spatial scale functions that may contribute to regulation and stability.

Decay vs. normal individuals

It is claimed that "decay individuals" possess mutated genetic information about the biotic regulation, and are thus competitively excluded from the population, while normal individuals are naturally selected. In addition to our previous question about a genetic program underwriting large-scale regulation, we question whether this distinction has predictive value, whether it is falsifiable, and ultimately whether "normal" and "decay" are only defined *a posteriori* based on whether morphs live or die. Can we, *a priori*, distinguish between these types, genetically or phenotypically, to gain mechanistic insight into biotic regulation?

Immobile vs. locomotive competition

The ability to move or not is an important distinction, but the claim that competitive ability can also be distinguished on this basis appears less certain. It is argued that immobile organisms compete more strongly with each other since they are deprived of free space and unable to escape competition. Although this is possible, it seems the opposite argument could also be made: immobile organisms may be less exposed to competition. The "priority effect" would posit that if an organism first establishes itself in a space, it inhibits immobile conspecifics from actively moving in to colonize, and could prevent competition for resources other than space [24]. Competitive interactions among sessile individuals are also limited to

nearest neighbours who may not be the same species with the same resource requirements. Locomotive individuals, on the other hand, often possess social behaviors to make competition more overt, including the patrol and defense of territory. We question the claim that locomotive species compete less strongly, and the inference that they therefore harbor a greater proportion of decay-individuals.

Terrestrial vs. aquatic systems

The paper discusses life on the planet in very general terms, which is part of its strength, but we feel it necessary to give greater emphasis to the distinction between terrestrial and aquatic systems. The 1 mm thick autotrophic layer, for example, only applies on land. The estimate of 13 Gt of phytoplankton reported in the author's Table 1 [25], extended over the 360 million km² of the ocean's surface amounts to an autotroph layer only ~0.04 mm thick. Thus the appealing symmetry of autotroph-to-heterotroph proportions reported on land does not apply to aquatic life. Although total terrestrial and aquatic net primary production are quite similar, the trophic pyramids and biomass distributions of heterotrophs over land and sea are entirely different.

Conclusion

Our view of this work is that it is creative and ambitious, but unfinished. We appreciated many of the salient calculations that might go towards a more holistic understanding of the biosphere's functioning. We view biotic regulation as a stirring fundamental question, which is also of great practical concern for understanding the regulatory capacity of the Earth system under prospects of global change. At the same time, we find aspects of the work that are in need of improvement or that appear to be unsupported. We have shown that there are boundaries on energy use in space that may apply across all of life, which does not appear consistent with large animals having a greater tendency to destabilize their ecosystem through overconsumption. We also believe the concept of biotic regulation needs to be better placed in the long history of similar thought, and its claimed genetic underpinning needs to be better characterized. While we are sympathetic to the author's goals and applaud their bold attempts at synthesis, we feel there are a number of areas, some of them central conclusions, that should not go unchallenged.

Reservations aside, we commend the authors on a highly stimulating work. Big ideas like these are in great need of further development, and we hope that Professor Gorshkov's collaborators will continue his legacy.

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