

Spatio-temporal eco-evolutionary dynamics of prey-predator systems with defended and undefended prey

Corresponding Author: Professor Dibakar Ghosh

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Attachments originally included by the reviewers as part of their assessment can be found at the end of this file.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

In this paper the authors consider an eco-evolutionary model of predator-prey dynamics with aposematic prey in a spatial scenario. The paper is well-written with a good underlying model and a lot of interesting content. The non-spatial version of the model is also considered, and this too has interesting results. Overall this is a good paper, based on a very worthwhile underlying idea for the research work, with sound analysis and conclusions. I do have a number of points that I would like the authors to address, however.

1. This paper has only Indian and UK authors, so I think that UK English would be the natural and preferable option, as opposed to US English currently used. This is up to the authors, of course (unless the journal has some rules on this).
2. On page 3 a and b are introduced at the start of Section II, but they do not appear subsequently, with epsilon taking on this role. Maybe the authors could drop any discussion of a and b here.
3. Four lines from the end of page 4 - $U+V+W+Z=1$. I see the basic logic, but this seems a bit odd. Why would an individual of each type occupy the same amount of space, why would they conflict with each other? It is not just individuals physically fitting into space, but about territoriality and competition for resources. In this context members of the same species would compete, but predators would thrive from the presence of prey. I think some justification/adjustment of this concept would be helpful.
4. Page 4 end of the first column/top of the next - without loss of generality - this phrase is not appropriate for this type of model. There are so many assumptions about the form of the different aspects of the model, that it is already somewhat specific, and in the context of numerical choices, the choice of the boundary value of 0.5 here can be significant - certainly not without loss of generality. I think it is fine what the authors do, just do not say this.
5. On the above subject, some functions are very specific and not so clear in motivation. Why the function in equation (4)? Not only is it specific, one of the assumptions underlying it seems questionable. Certainly $e_2 < e_1$ is fine, but why should $e_2 > e_1$? The consequences of consumption of toxic prey could be death or some serious incapacitation of much greater size than e_1 .
6. Equation (8) is just equation (7) repeated. Just refer to the previous equation. In general, there is also too much rewriting of similar equations, in addition to this identical pair. Please update the paper for succinctness/ logical presentation.
7. Table 1 - can you provide more explanation as to why this specific set of parameters is selected? Similarly, why the particular set of numbers 2/3 down column 2 on page 11 is picked?
8. In general there are lots of formulae; these seem to be generally implemented in a good way, but how biologically realistic are they? A lot more justification of choices made in this regard would help.
9. Can the authors comment on whether the results observed in their model occur in real populations, if there are novel

predictions in this regard, anything problematic?

10. On page 15 the authors say the study results "have far-reaching implications ...". They certainly make interesting predictions and suggestions for things to consider, but this statement is rather too grand for a specific model like this. Please reword.

Small points:

Page 1 column 1 line 7 consume the prey for

page 5 column 2 line 11 straightforward

Reviewer #2

(Remarks to the Author)

The authors propose a model that generates spatial eco-evolutionary dynamics within a predator-prey community. The study addresses important and timely questions regarding whether and how spatial patterns and evolutionary trajectories are coupled—which is recognized as key driver of ecosystem stability and resilience. I find the topic highly relevant and potentially impactful, and I appreciate the ambition of combining spatial ecology with evolutionary dynamics in a mechanistic framework.

That said, I believe the current manuscript leaves several fundamental questions insufficiently addressed, both in terms of clarity and biological framing. At this stage, I cannot recommend it for publication. However, I genuinely believe that with focused revisions, the manuscript could become a valuable contribution to the field. Below, I provide detailed feedback with the hope that it will help the authors improve both the clarity and the positioning of their work.

1. Presentation and Model Description

The presentation of the model and parameters is currently quite difficult to follow. For example, the explicit formulation in Eq. (5) is not clearly explained. Key components like the definition of p , used in ξ , γ , and η , are missing or unclear. Similarly, the role of η in Eq. (5) seems hidden within β_2 .

The confusion actually starts already in Eq. (1), where functions are written in shorthand (e.g., f rather than $f(x)$). This makes it unnecessarily difficult for readers to follow the equations and track where specific parameters enter the model. Clarifying this notation would greatly improve accessibility.

2. Calculations are overwhelming

The manuscript contains a large amount of detailed mathematical derivation in the main text (e.g., Eqs. 8–21). While I appreciate the authors' commitment to transparency, the density of these calculations interrupts the readability and flow of the paper. It's unlikely that most readers (or reviewers, under standard timelines) can check these calculations in detail. I suggest moving these derivations to a Supplementary Material and focusing the main text on conveying the intuition, mechanisms, and key consequences of the model. This would not only improve readability but also help highlight the biological relevance of the results.

3. Parameter Interpretability in Figures

Given the number of parameters involved, the figures would benefit from being more self-contained. For instance, including reminders of parameter meanings (either in captions or figure labels) would greatly enhance readability and comprehension.

4. Biological Framing – Use of "Aposematic"

The use of the term *aposematic* prey feels overstated in this context. While the introduction provides an informative overview of *aposematism*, a biological phenomenon tied specifically to visual signaling—the mathematical model is an abstraction, being only inspired by this phenomenon. The model actually may seem to capture broadly predator-prey attraction/repulsion. I recommend the authors carefully reconsider whether the term *aposematic* is appropriate for the title and framing. It may be more accurate to present the model as being inspired by *aposematism* and other mechanisms (callings, scent marks, etc). Otherwise, readers could reasonably expect the paper to make specific contributions to the study of *aposematic* signaling, which isn't the case here.

5. Timescales

The manuscript does not adequately explore how timescales—specifically the diffusion rates (D_u and D_v)—impact both the spatial dynamics and the evolutionary s . These parameters are held constant across the results (Table 1), yet diffusion fundamentally influences not only stability and steady states but also the pace and nature of spatial dynamics.

The current presentation misses the opportunity to clarify the role of spatial pattern in the eco-evolutionary feedback in the well-mixed baseline (e.g., $D_u = D_v = 0$). Comparing the well-mixed and spatially structured regimes would help elucidate how spatial constraints influence the co-evolutionary dynamics.

Additionally, the manuscript lacks discussion of the choice of diffusion-reaction ratio (i.e., Damköhler number). Providing intuition or analysis of the system's behavior in the limits of slow versus fast diffusion would significantly strengthen the study.

Minor issues:

The parameterization of Eq. (4) is not well justified. Is there an empirical or theoretical rationale for this choice? If so, providing a reference or explanation would be helpful.

Reviewer #3

(Remarks to the Author)

The manuscript entitled “Spatio-temporal eco-evolutionary dynamics of prey-predator interactions with aposematic prey” offers a compelling and timely contribution to the field of mathematical ecology and eco-evolutionary dynamics. The authors develop a novel three-species reaction-diffusion model to study interactions among non-defended prey, chemically defended aposematic prey, and predators in a spatially extended environment. The framework explicitly couples ecological processes (such as spatial diffusion and free-space mediated reproduction) with evolutionary strategies (namely, aposematism and associated toxicity costs), allowing the investigation of how evolutionary traits influence population persistence and spatial organization. The study stands out by integrating theoretical ecology, nonlinear dynamics, and empirical biological motivation into a unified modeling approach. Through a combination of linear stability analysis, bifurcation diagrams, and extensive numerical simulations, the manuscript provides a deep mechanistic understanding of species coexistence and the conditions that drive transitions between stable equilibria and complex spatio-temporal patterns.

One of the key points to mention about this manuscript lies in its originality and ecological grounding. The incorporation of aposematic defence—a biologically widespread and ecologically important trait—into a spatial eco-evolutionary model represents a novel and significant contribution. While classical predator-prey models typically omit such trait-mediated interactions or assume fixed strategies, this work captures the dynamic trade-off between defence and reproduction. The authors substantiate their modeling assumptions with real-world examples from diverse biological systems, including amphibians (e.g., *Oophaga pumilio*), snakes (*Micrurus fulvius*), and microbial communities (*Pseudomonas aeruginosa*), effectively anchoring the mathematical framework in observed ecological phenomena. Mathematically, the model is carefully constructed and analytically rich. The authors perform a detailed non-dimensionalization, derive biologically interpretable equilibrium points, and carry out a rigorous linear stability analysis. Their analysis of Turing instability conditions is particularly noteworthy, with a clear derivation of the instability thresholds and validation through spectral analysis. The bifurcation diagrams in the (κ, η) parameter plane reveal ecologically meaningful transitions between extinction, partial coexistence, and full species coexistence, highlighting the sensitivity of ecosystem dynamics to both ecological (resource availability) and evolutionary (toxicity level) factors.

The manuscript presents a suite of well-executed numerical simulations that illuminate how varying ecological and evolutionary parameters shape the spatio-temporal distribution of species. The transitions from spotted to striped to hole-like patterns with increasing intra-predator competition (μ) or space limitation (κ) are visually compelling and ecologically interpretable. The use of color-coded spatial snapshots, time-series portraits, and phase diagrams offers a holistic view of the system’s dynamics, making the results accessible to readers from both theoretical and empirical backgrounds. Overall, the manuscript excels in combining biological insight with theoretical modeling and computational experimentation. It contributes meaningful understanding to how eco-evolutionary feedbacks operate in spatially extended systems, with implications for biodiversity, community stability, and pattern formation in natural ecosystems. This manuscript makes a meaningful contribution to the field of eco-evolutionary dynamics and is suitable for publication after minor clarifications and cosmetic improvements, I would like put below:

1. I would like to ask the authors if they could identify or comment anything about any similarity with the idea of the aposematic prey, i.e., the transformation of prey species from the undefended form to the defended form, being similar to any known evolutionary dilemma, like the PD, SD or SH?
2. The authors have put the spatio-temporal distribution of the undefended prey in the 100 x 100 grid and pointed out different spatial patterns generated through numerical simulations, whereas they never have come up with any distribution of the defended prey or the predators, anywhere in the manuscript. It would be good if they had mentioned the other species in the manuscript and a little about the similar or dissimilar patterns generated for the other evolutionary species.
3. The colorbars used in the manuscript comes up with same range (0 to 1), whereas the upper bound of the total population and free space is assumed to be $1/\kappa$. Can they author mention how would the spatial distribution of species would look if they set the max range $1/\kappa$, other than the diagram, where they varied the parameter κ ?

So, overall this manuscript is suitable for publication after these minor clarifications.

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

I was about the original version of this paper, as were the other reviewers. In their response the authors have mainly done a good job in addressing my concerns and I am happy with all points apart from two, where more clarification is needed. These are my points 8 and 9.

My point 8. In general there are lots of formulae; these seem to be generally implemented in a good way, but how biologically realistic are they? A lot more justification of choices made in this regard would help.

The authors' response starts "Our model contains multiple functional forms that were chosen to capture key biological mechanisms while maintaining mathematical tractability. In the revised manuscript, we have expanded the justification for each major functional choice to clarify their biological basis: ...".

This would be a satisfactory response, except it is not clear to me what exactly has been changed in the paper and where.

My point 9. Can the authors comment on whether the results observed in their model occur in real populations, if there are novel predictions in this regard, anything problematic?

The authors' response starts "Our model is formulated in a generalized theoretical framework and the qualitative s have parallels in real ecological systems. A concrete example may be seen ..."

This is again a good response, except that I cannot see that the details have been included in the paper itself.

Reviewer #2

(Remarks to the Author)

Reviewer #3

(Remarks to the Author)

The authors have provided satisfactory responses to all the queries. Accordingly, I recommend the acceptance of the article

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Response of “Spatio-temporal eco-evolutionary dynamics of prey-predator interactions with aposematic prey”

Editor’s comment: We hope to receive your revised paper within six weeks; please let us know if you aren’t able to submit it within this time so that we can discuss how best to proceed. If we don’t hear from you, and the revision process takes significantly longer, we will close your file. In this event, we will still be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Physics or published elsewhere in the meantime.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further. We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

Response: We thank you for your email from 11th July 2025, regarding our manuscript COMMSPHYS-25-0793 and the attached reports of the three referees. We are grateful to the referees for their constructive comments. We have made every effort to incorporate their suggestions. In our point by point response to the referees’ comments, we detail the changes made and provide appropriate explanations. In the revised manuscript, the changes to the text are indicated by blue text. We look forward to your final positive decision.

Reviewer #1: (Remarks to the Author):

In this paper the authors consider an eco-evolutionary model of predator-prey dynamics with aposematic prey in a spatial scenario. The paper is well-written with a good underlying model and a lot of interesting content. The non-spatial version of the model is also considered, and this too has interesting results. Overall this is a good paper, based on a very worthwhile underlying idea for the research work, with sound analysis and conclusions. I do have a number of points that I would like the authors to address, however.

1. This paper has only Indian and UK authors, so I think that UK English would be the natural and preferable option, as opposed to US English currently used. This is up to the authors, of course (unless the journal has some rules on this).

Response: In the previous version, combination of the US and UK English were present. Now, we have maintained the consistency throughout the manuscript.

2. On page 3 a and b are introduced at the start of Section II, but they do not appear subsequently, with ϵ taking on this role. Maybe the authors could drop any discussion of a and b here.

Response: We thank the reviewer for pointing this out. In an earlier draft, the parameters a and b were introduced as generic representations of predator energetic gain from undefended prey and energetic loss from defended prey, respectively. However, in the present formulation, this role is captured more via, the toxicity parameter ε and the resulting conversion efficiency $e_2(\varepsilon)$ in Eq. (4). Since a and b are no longer used in the model equations or subsequent analysis, we have removed a and b from the start of Section II to avoid redundancy and improve clarity. The discussion now proceeds directly from the biological setup where we introduce ε as the relevant trait variable.

3. Four lines from the end of page 4 - $U+V+W+Z=1$. I see the basic logic, but this seems a bit odd. Why would an individual of each type occupy the same amount of space, why would they conflict with each other? It is not just individuals physically fitting into space, but about territoriality and competition for resources. In this context members of the same species would compete, but predators would positively thrive from the presence of prey. I think some justification/adjustment of this concept would be helpful.

Response: We thank the reviewer for this insightful observation. The constraint $U + V + W + Z = 1$ is not intended to suggest that predators and prey occupy identical physical space or compete directly for territory. Rather, it represents a coarse-grained approximation of a finite ecological capacity—such as limited resources, energy throughput, or reproductive space—within which all species coexist. We acknowledge that, in reality, species exert different pressures: predators typically require larger territories but occur at lower densities, while prey can be more abundant and clustered. Moreover, predators depend positively on prey availability, so their interaction is not a matter of direct spatial competition.

The purpose of the normalization is therefore not to model individual-level spatial exclusion but to bound the total ecological load or biomass. An increase in prey biomass, for example, reduces the ecological “room” for predators only indirectly—by drawing on shared resources like nutrients or reproductive space—rather than by physically displacing them. To avoid misunderstanding, we have clarified in the manuscript that the normalization condition enforces a global ecological constraint and does not imply identical spatial footprint, equal physical size, or universal competition among species. Positive trophic interactions are already incorporated through the nonlinear growth and functional response terms, while the normalization simply ensures finite system capacity.

This modeling device, commonly used in eco-evolutionary frameworks (e.g., Gokhale & Hauert, *Theoretical Population Biology* 2016; van Baalen & Rand, *Journal of Theoretical Biology* 1998), reduces dimensionality and captures trade-offs: growth in one population indirectly limits others due to shared dependence on finite ecological resources. Accordingly, the revised text (p. 4) now emphasizes that the constraint refers to an abstract carrying capacity rather than direct spatial exclusion.

4. Page 4 end of the first column/top of the next - without loss of generality - this phrase is not appropriate for this type of model. There are so many assumptions about the form of the different aspects of the model, that it is already somewhat specific, and in the context of

numerical choices, the choice of the boundary value of 0.5 here can be significant - certainly not without loss of generality. I think it is fine what the authors do, just do not say this.

Response: We agree that the phrase “without loss of generality” is not appropriate in this context, especially given the specific assumptions made in the model and the potential sensitivity of the system to parameter choices such as the boundary value of 0.5. We have removed this phrase from the manuscript and revised the surrounding text to reflect that the choice of threshold is a modeling assumption made for analytical clarity and does not imply generality across all eco-evolutionary systems.

5. On the above subject, some functions are very specific and not so clear in motivation. Why the function in equation (4)? Not only is it specific, one of the assumptions underlying it seems questionable. Certainly $e_2 \leq e_1$ is fine, but why should $e_2 \leq -e_1$? The consequences of consumption of toxic prey could be death or some serious incapacitation of much greater size than e_1 .

Response: The function defined in Eq.(4) was designed to model a biologically realistic trade-off in predator response to defended (toxic) prey. Specifically, it smoothly interpolates between beneficial and harmful energetic outcomes, depending on the toxicity level $\varepsilon \in [0, 1]$. The functional form, based on a scaled inverse hyperbolic tangent, ensures that the predator’s conversion efficiency from defended prey biomass remains bounded within the interval $(-e_1, e_1)$. This maintains analytical tractability and numerical stability and prevents biologically unrealistic outcomes such as unbounded mortality or explosive dynamics.

The justification for enforcing $e_2(\varepsilon) > -e_1$, while possibly restrictive in extreme cases, stems from our intention to capture the sublethal consequences of toxin ingestion, which are well-documented in empirical studies of aposematic systems (e.g., poison frogs, butterflies, and toxic beetles). In such systems, predators often learn to avoid poisonous prey due to adverse but non-fatal experiences, and the defensive value of aposematism evolves as a result of these sublethal deterrence effects rather than instantaneous death. Therefore, we interpret the negative part of the function $e_2(\varepsilon)$ not as literal predator mortality, but as an “effective reduction in reproductive output” due to toxin exposure, which could represent energy loss, illness, avoidance behavior, or even opportunity cost.

To incorporate the negative effect of consuming highly toxic aposematic prey, we define the conversion efficiency from defended prey biomass to predator biomass, e_2 , as a transition term of the form $s(x; k) = \tanh(kx)$, where x is a centered driver variable and $k > 0$ controls the steepness of the transition. As $k \rightarrow \infty$, S approaches a step function. Accordingly, we define

$$e_2(\varepsilon) = e_1 \tanh\left(k\left(1 - \frac{\varepsilon}{0.5}\right)\right),$$

which ensures $e_2(0) = e_1$, $e_2(1/2) = 0$, and $e_2(1) = -e_1$, consistent with the biological constraints. To encode an arbitrarily steep but bounded transition, we re-parameterize the steepness as

$$k = \tanh^{-1}\left(1 - \frac{\varepsilon}{e_1}\right),$$

so that $k \rightarrow \infty$ as $\varepsilon \rightarrow 0$. Substituting this expression for k into the definition of $e_2(\varepsilon)$ and taking the sharp-switch limit $\varepsilon \rightarrow 0^+$ yields

$$e_2 = \lim_{\varepsilon \rightarrow 0} e_1 \tanh \left[\left(1 - \frac{\varepsilon}{0.5} \right) \tanh^{-1} \left(1 - \frac{\varepsilon}{e_1} \right) \right].$$

As shown in Fig. 1 (below), the function is structured such that $e_2(\varepsilon)$ transitions from a positive value (when $\varepsilon < 0.5$) to a negative value (when $\varepsilon > 0.5$), reflecting the idea that low toxicity might provide some nutritional value, whereas higher toxicity imposes increasingly stringent fitness penalties. Moreover, the functional ensures that defended prey with moderate toxicity levels induce a graded response from the predator, avoiding abrupt behavioral shifts unless empirically justified. This modeling choice captures a broad range of predator responses across eco-evolutionary systems—especially when prey defense mechanisms are costly but not necessarily lethal. Nevertheless, we acknowledge that more extreme outcomes are plausible in some ecological contexts. Our framework allows for such extensions by modifying the scaling in the hyperbolic tangent or replacing it with other sigmoid-like functions, should empirical data demand stronger penalties. For now, we opt for a formulation that balances biological realism with analytical control and interpretability.

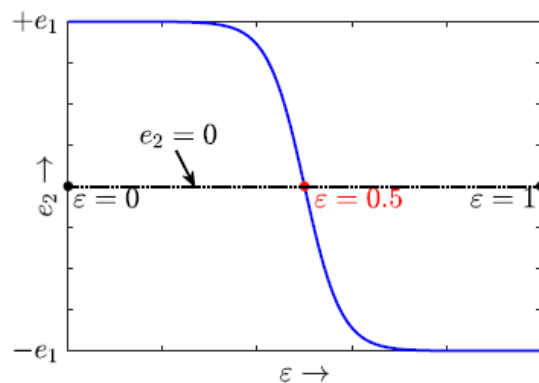


Figure 1: Variation of e_2 concerning the level of toxicity of defended prey, $\varepsilon \in [0, 1]$. For $\varepsilon < 0.5$, $0 < e_2 < e_1$: Consumption of defended preys with low level of toxicity gives positive impact to the growth of predators. For $\varepsilon > 0.5$, $-e_1 < e_2 < 0$: Ingestion of aposematic preys with high level of toxicity induces a negative effect to the reproduction of predators.

6. Equation (8) is just equation (7) repeated. Just refer to the previous equation. In general, there is also too much rewriting of similar equations, in addition to this identical pair. Please update the paper for succinctness/ logical presentation.

Response: We agree that Eq. (8) is a direct repetition of Eq. (7) and that such repetition does not add clarity. In the revised manuscript, we have removed Equation (8) and now simply refer to Eq. (7) where needed. We have also reviewed the rest of the manuscript to reduce unnecessary rewriting of similar equations, ensuring a more succinct and logically structured presentation of the mathematical model.

7. Table 1 - can you provide more explanation as to why this specific set of parameters is selected? Similarly, why the particular set of numbers 2/3 down column 2 on page 11 is picked?

Response: The parameter set in Table-I was selected to ensure that the system operates in a biologically meaningful regime where the three species (undefended prey, defended prey, and predators) can coexist and where diffusion-driven instabilities can emerge. The chosen values balance ecological realism — based on typical ranges observed in predator–prey systems involving defended prey (e.g., toxicity rates, carrying capacities, and predator mortality) — with mathematical tractability, ensuring that the interior equilibrium point is feasible and stable in the absence of diffusion, yet unstable under the diffusion conditions analyzed.

In general, all model parameters can all varied within ecologically reasonable ranges, given in earlier discussion. However, the particular values in Table-I were selected to demonstrate the eco-evolutionary mechanisms under study while keeping the numerical results directly comparable across different pattern-forming regimes.

8. In general there are lots of formulae; these seem to be generally implemented in a good way, but how biologically realistic are they? A lot more justification of choices made in this regard would help.

Response: Our model contains multiple functional forms that were chosen to capture key biological mechanisms while maintaining mathematical tractability. In the revised manuscript, we have expanded the justification for each major functional choice to clarify their biological basis:

- The predator–prey interaction terms are based on well-established functional response formulations (e.g., Holling type II and trait-mediated modifications), which capture saturating consumption rates observed in empirical systems.
- The toxicity–conversion relationship in Eq. (4) is chosen to represent a smooth trade-off between nutritional benefit and toxin-induced fitness costs, consistent with experimental observations in aposematic prey–predator systems (e.g., poison frogs, lady beetles, monarch butterflies).
- The diffusion and coupling terms follow standard spatial ecology frameworks, ensuring that movement and dispersal processes remain ecologically plausible while allowing for analytical treatment of stability and pattern formation.

We have updated the text to explicitly link each functional form to its ecological interpretation and relevant literature. This should improve the reader’s understanding of the biological realism of our assumptions while retaining the general applicability of the model.

9. Can the authors comment on whether the results observed in their model occur in real populations, if there are novel predictions in this regard, anything problematic?

Response: Our model is formulated in a generalized theoretical framework and the qualitative outcomes have parallels in real ecological systems. A concrete example may be seen in tropical butterfly communities involving *Heliconius* and *Dismorphia*. *Heliconius* butterflies are

chemically defended and exhibit bright warning coloration (aposematism). Dismorphia butterflies, which are harmless, mimic Heliconius to avoid predators (Batesian mimicry). Predators quickly learn that the warning colors of Heliconius indicate unpalatability or harm, leading them to avoid both Heliconius and their mimics. As Heliconius populations grow, predator avoidance of these patterns strengthens, further benefiting Heliconius. However, over time, predators may learn to distinguish between the model and the mimic, causing Dismorphia to suffer increased predation and population decline. This dynamic illustrates how increasing aposematism in defended prey can indirectly reduce the survival of undefended prey — consistent with the patterns described in our model.

Our model also makes novel predictions, such as specific ranges of prey toxicity and predator response parameters where defended and undefended prey can coexist with predators in stable spatial mosaics, and conditions where defended prey can indirectly stabilize predator–prey cycles. These outcomes are biologically plausible and testable in empirical systems, such as controlled mesocosm experiments or microbial predator–prey setups where defense traits and spatial heterogeneity can be manipulated. While some assumptions (e.g., a shared ecological capacity $U + V + W + Z = 1$) are idealized, they allow for tractable analysis without qualitatively altering the central eco-evolutionary mechanisms.

10. On page 15 the authors say the study results “have far-reaching implications ...”. They certainly make interesting predictions and suggestions for things to consider, but this statement is rather too grand for a specific model like this. Please reword.

Response: According to the referee’s suggestion, we have implemented your suggestions in the revised manuscript.

Small points: Page 1 column 1 line 7 consume the prey for page 5 column 2 line 11 straight-forward

Response: We are extremely grateful to the reviewer for pointing out the above interesting comments/suggestions which are vital to enhance the readability of the manuscript. We have implemented these changes in the revised manuscript.

Reviewer #2(Remarks to the Author):

The authors propose a model that generates spatial eco-evolutionary dynamics within a predator-prey community. The study addresses important and timely questions regarding whether and how spatial patterns and evolutionary trajectories are coupled—which is recognized as key driver of ecosystem stability and resilience. I find the topic highly relevant and potentially impactful, and I appreciate the ambition of combining spatial ecology with evolutionary dynamics in a mechanistic framework. That said, I believe the current manuscript leaves several fundamental questions insufficiently addressed, both in terms of clarity and biological framing. At this stage, I cannot recommend it for publication. However, I genuinely believe that with focused revisions, the manuscript could become a valuable contribution to the field. Below, I provide detailed feedback with the hope that it will help the authors improve both the clarity and the positioning of their work.

Response: We thank the reviewer for highlighting these issues of clarity. We have endeavoured to modify the manuscript based on their comments.

1. Presentation and Model Description: The presentation of the model and parameters is currently quite difficult to follow. For example, the explicit formulation in Eq. (5) is not clearly explained. Key components like the definition of p , used in ξ , γ , and η , are missing or unclear. Similarly, the role of η in Eq. (5) seems hidden within β_2 . The confusion actually starts already in Eq. (1), where functions are written in shorthand (e.g., f rather than $f(x)$). This makes it unnecessarily difficult for readers to follow the equations and track where specific parameters enter the model. Clarifying this notation would greatly improve accessibility.

Response: In the revised manuscript, we have substantially improved the presentation of the model and its parameters. Specifically: we have expanded the explanation accompanying Eq. (5) to explicitly define all quantities. The parameter p is basically κ in the transformation below Eq. (5) and it was our typographical error. After non-dimensionalize the eco-evolutionary model, the parameters d_1 , d_2 change to ξ and γ , respectively. The toxicity rate of defended prey is represented by $\eta = \eta(\varepsilon)$. β_2 is the Conversion efficiency from defended prey biomass to predator biomass; it depends on the toxicity level, *i.e.*, on $\beta_2 = \beta_2(\eta)$.

We have revised the notation in the model equations to remove shorthand forms such as f in place of $f(x)$, ensuring that dependencies on state variables are explicit. We have also revised the model formulation and trust that it is now easier to understand how specific parameters enter the model. These changes make the mathematical formulation more transparent and make it more accessible to readers less familiar with the notation style.

2. Calculations are overwhelming: The manuscript contains a large amount of detailed mathematical derivation in the main text (e.g., Eqs. 8–21). While I appreciate the authors' commitment to transparency, the density of these calculations interrupts the readability and flow of the paper. It's unlikely that most readers (or reviewers, under standard timelines) can check these calculations in detail. I suggest moving these derivations to a Supplementary Material and focusing the main text on conveying the intuition, mechanisms, and key consequences of the model. This would not only improve readability but also help highlight the biological relevance

of the results.

Response: We appreciate your suggestion, and have moved the linear stability analysis part (Eqs. 8-21 in the old version) to the appendix. We believe that this change has improved the readability of the paper.

3. Parameter Interpretability in Figures: Given the number of parameters involved, the figures would benefit from being more self-contained. For instance, including reminders of parameter meanings (either in captions or figure labels) would greatly enhance readability and comprehension.

Response: In line with the referee's suggestion, we have modified the figure captions.

4. Biological Framing – Use of “Aposematic”: The use of the term aposematic prey feels overstated in this context. While the introduction provides an informative overview of aposematism, a biological phenomenon tied specifically to visual signaling—the mathematical model is an abstraction, being only inspired by this phenomenon. The model actually may seem to capture broadly predator-prey attraction/repulsion. I recommend the authors carefully reconsider whether the term aposematic is appropriate for the title and framing. It may be more accurate to present the model as being inspired by aposematism and other mechanisms (callings, scent marks, etc). Otherwise, readers could reasonably expect the paper to make specific contributions to the study of aposematic signaling, which isn't the case here.

Response: We agree that while the model draws conceptual inspiration from aposematism, it is formulated as a general framework for predator–prey interactions where one prey type imposes a cost (e.g., via toxicity, chemical deterrents, or behavioral defense) and another prey type remains undefended. The specific visual signaling component of aposematism is not explicitly modeled, and thus the framework can also encompass other deterrence or attraction/repulsion mechanisms, such as chemical cues, acoustic signals, or scent marking. In the revised manuscript, we have adjusted the framing to clarify this broader scope. The introduction now states that the model is inspired by aposematism and other defense mechanisms rather than being a direct model of aposematic signaling, and we have revised the text to ensure the term “aposematic prey” is used only when referring to the biological inspiration, not as the sole interpretation of the defended prey in the model.

We changed the title by replacing “aposematic prey” by “defended and undefended prey”. Now the new title becomes “Spatio-temporal eco-evolutionary dynamics of prey-predator systems with defended and undefended prey”.

5. Timescales: The manuscript does not adequately explore how timescales—specifically the diffusion rates (D_u and D_v)—impact both the spatial dynamics and the evolutionary outcomes. These parameters are held constant across the results (Table 1), yet diffusion fundamentally influences not only stability and steady states but also the pace and nature of spatial dynamics. The current presentation misses the opportunity to clarify the role of spatial pattern in the eco-evolutionary feedback in the well-mixed baseline (e.g., $D_u = D_v = 0$). Comparing the well-mixed and spatially structured regimes would help elucidate how spatial constraints influence the co-evolutionary dynamics. Additionally, the manuscript lacks discussion of the

choice of diffusion-reaction ratio (i.e., Damköhler number). Providing intuition or analysis of the system's behavior in the limits of slow versus fast diffusion would significantly strengthen the study.

Response: We acknowledge that the values of the diffusion coefficients can significantly influence the spatial dynamics in reaction-diffusion systems. However, in our study, we have primarily focused on understanding how the spatial distribution of each population responds to variations in key ecological and evolutionary parameters—specifically, the predator mortality rate (μ), the inverse carrying capacity (κ), and the toxicity level of the defended prey (η). These parameters were chosen because they directly control the biological interactions and evolutionary pressures shaping the system.

While the diffusion coefficients were held fixed for most simulations, we explored their role in certain cases. In particular, we observed that for lower values of diffusion coefficients—specifically, $D_u = 0.01, D_v = 0.01$; the system exhibits a variety of spatial states, with five distinct types of spatial organization emerging. When the diffusion coefficients were increased to $D_u = 0.04$ and $D_v = 0.04$, the system yields spot or hexagonal-like and roll patterns (see Fig. 2 below); however, smooth transitions as seen in the experiments given in our manuscript did not appear in this case at this rate for mobility. We did not include this figure in the manuscript but would be happy to do so.

For a particular case, i.e., $D_u = D_v = 0.0$ and $D_W = 1.0$, only predator mobility is present. The spatio-temporal behavior for this case is included in Appendix-B.

While, the effect of the diffusion-reaction ratio is not studied in this work, we view it as an interesting future problem. We discuss this point in the conclusion section.

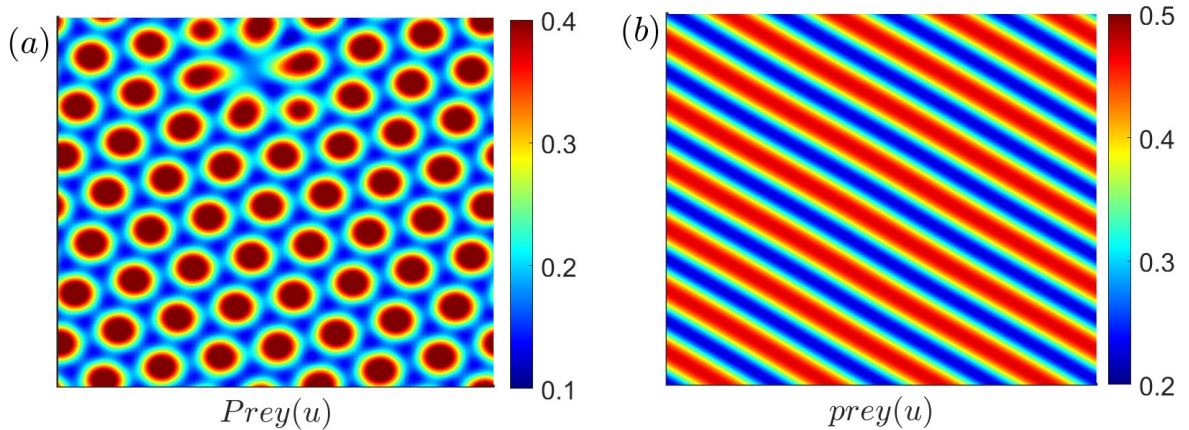


Figure 2: The spatio-temporal distribution of undefended prey (u) for $D_u = D_v = 0.04$ at (a) $\mu = 0.89$ and (b) $\mu = 0.95$.

Minor issues: The parameterization of Eq. (4) is not well justified. Is there an empirical or theoretical rationale for this choice? If so, providing a reference or explanation would be helpful.

Response: The function defined in Equation (4) was designed to model a biologically realistic trade-off in predator response to defended (toxic) prey. Specifically, it smoothly interpolates between beneficial and harmful energetic outcomes, depending on the toxicity level

$\varepsilon \in [0, 1]$. The functional form, based on a scaled inverse hyperbolic tangent, ensures that the predator's conversion efficiency from defended prey biomass remains bounded within the interval $(-e_1, e_1)$. This not only maintains analytical tractability and numerical stability but also avoids biologically unrealistic outcomes such as unbounded mortality or explosive dynamics.

The justification for enforcing $e_2(\varepsilon) > -e_1$, while possibly restrictive in certain extreme cases, stems from our intention to capture sublethal consequences of toxin ingestion, which are well-documented in empirical studies of aposematic systems (e.g., poison frogs, butterflies, and toxic beetles). In such systems, predators often learn to avoid poisonous prey due to adverse but non-fatal experiences, and the defensive value of aposematism evolves through these sublethal deterrence effects rather than instantaneous death. Therefore, we interpret the negative part of the function $e_2(\varepsilon)$ not as literal predator mortality, but as an “effective reduction in reproductive output” due to toxin exposure, which could represent energy loss, illness, avoidance behavior, or even opportunity cost.

To incorporate the negative effect of consuming highly toxic aposematic prey, we define the conversion efficiency from defended prey biomass to predator biomass, e_2 , as a transition term of the form $s(x; k) = \tanh(kx)$, where x is a centered driver variable and $k > 0$ controls the steepness of the transition. As $k \rightarrow \infty$, S approaches a step function. Accordingly, we define

$$e_2(\varepsilon) = e_1 \tanh\left(k\left(1 - \frac{\varepsilon}{0.5}\right)\right),$$

which ensures $e_2(0) = e_1$, $e_2(1/2) = 0$, and $e_2(1) = -e_1$, consistent with the biological constraints. To encode an arbitrarily steep but bounded transition, we re-parameterize the steepness as

$$k = \tanh^{-1}\left(1 - \frac{\varepsilon}{e_1}\right),$$

so that $k \rightarrow \infty$ as $\varepsilon \rightarrow 0$. Substituting this expression for k into the definition of $e_2(\varepsilon)$ and taking the sharp-switch limit $\varepsilon \rightarrow 0^+$ yields

$$e_2 = \lim_{\varepsilon \rightarrow 0} e_1 \tanh\left[\left(1 - \frac{\varepsilon}{0.5}\right) \tanh^{-1}\left(1 - \frac{\varepsilon}{e_1}\right)\right].$$

As shown in Fig. 3 below, the function is structured such that $e_2(\varepsilon)$ transitions from a positive value (when $\varepsilon < 0.5$) to a negative value (when $\varepsilon > 0.5$), reflecting the idea that low toxicity might still provide nutritional value, whereas higher toxicity imposes increasingly stronger fitness penalties. Moreover, the form ensures that defended prey with moderate toxicity levels induce a graded response from the predator, avoiding abrupt behavioral shifts unless empirically justified. This modeling choice thus captures a broad range of predator responses across eco-evolutionary systems—especially when prey defense mechanisms are costly but not necessarily lethal. Nevertheless, we fully acknowledge the reviewer's point that more extreme outcomes are plausible in some ecological contexts. Our framework allows for such extensions by modifying the scaling in the hyperbolic tangent or replacing it with other sigmoid-like functions, should empirical data demand stronger penalties. For now, we opt for a formulation that

balances biological realism with analytical control and interpretability.

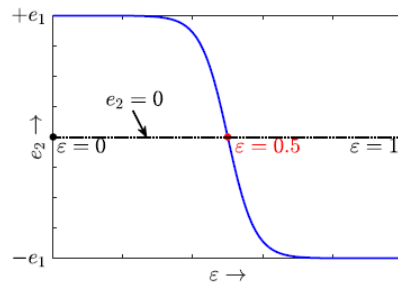


Figure 3: Variation of e_2 concerning the level of toxicity of defended prey, $\varepsilon \in [0, 1]$. For $\varepsilon < 0.5$, $0 < e_2 < e_1$: Consumption of defended preys with low level of toxicity gives positive impact to the growth of predators. For $\varepsilon > 0.5$, $-e_1 < e_2 < 0$: Ingestion of aposematic preys with high level of toxicity induces a negative effect to the growth of predators.

Reviewer #3 (Remarks to the Author):

The manuscript entitled “Spatio-temporal eco-evolutionary dynamics of prey-predator interactions with aposematic prey” offers a compelling and timely contribution to the field of mathematical ecology and eco-evolutionary dynamics. The authors develop a novel three-species reaction-diffusion model to study interactions among non-defended prey, chemically defended aposematic prey, and predators in a spatially extended environment. The framework explicitly couples ecological processes (such as spatial diffusion and free-space mediated reproduction) with evolutionary strategies (namely, aposematism and associated toxicity costs), allowing the investigation of how evolutionary traits influence population persistence and spatial organization. The study stands out by integrating theoretical ecology, nonlinear dynamics, and empirical biological motivation into a unified modeling approach. Through a combination of linear stability analysis, bifurcation diagrams, and extensive numerical simulations, the manuscript provides a deep mechanistic understanding of species coexistence and the conditions that drive transitions between stable equilibria and complex spatio-temporal patterns.

One of the key points to mention about this manuscript lies in its originality and ecological grounding. The incorporation of aposematic defence—a biologically widespread and ecologically important trait—into a spatial eco-evolutionary model represents a novel and significant contribution. While classical predator-prey models typically omit such trait-mediated interactions or assume fixed strategies, this work captures the dynamic trade-off between defence and reproduction. The authors substantiate their modeling assumptions with real-world examples from diverse biological systems, including amphibians (e.g., *Oophaga pumilio*), snakes (*Microcrurus fulvius*), and microbial communities (*Pseudomonas aeruginosa*), effectively anchoring the mathematical framework in observed ecological phenomena. Mathematically, the model is carefully constructed and analytically rich. The authors perform a detailed non-dimensionalization, derive biologically interpretable equilibrium points, and carry out a rigorous linear stability analysis. Their analysis of Turing instability conditions is particularly noteworthy, with a clear derivation of the instability thresholds and validation through spectral analysis. The bifurcation diagrams in the (κ, η) parameter plane reveal ecologically meaningful transitions between extinction, partial coexistence, and full species coexistence, highlighting the sensitivity of ecosystem dynamics to both ecological (resource availability) and evolutionary (toxicity level) factors.

The manuscript presents a suite of well-executed numerical simulations that illuminate how varying ecological and evolutionary parameters shape the spatio-temporal distribution of species. The transitions from spotted to striped to hole-like patterns with increasing intra-predator competition (μ) or space limitation (κ) are visually compelling and ecologically interpretable. The use of color-coded spatial snapshots, time-series portraits, and phase diagrams offers a holistic view of the system’s dynamics, making the results accessible to readers from both theoretical and empirical backgrounds. Overall, the manuscript excels in combining biological insight with theoretical modeling and computational experimentation. It contributes meaningful understanding to how eco-evolutionary feedbacks operate in spatially extended systems, with implications for biodiversity, community stability, and pattern formation in natural

ecosystems. This manuscript makes a meaningful contribution to the field of eco-evolutionary dynamics and is suitable for publication after minor clarifications and cosmetic improvements, I would like put below:

Response: We thank the reviewer for the constructive comments and appreciate the work for publication in *Communications Physics*.

1. I would like to ask the authors if they could identify or comment anything about any similarity with the idea of the aposematic prey, i.e., the transformation of prey species from the undefended form to the defended form, being similar to any known evolutionary dilemma, like the PD, SD or SH?

Response: We thank the reviewer for this thought-provoking question. The transformation of prey from an undefended form to a defended form in our model is conceptually similar to strategic shifts seen in classical evolutionary game theory, with the exact correspondence depending on the relative magnitude of defense costs and predator pressure. In our framework, the defended prey type invests in a costly trait (e.g., chemical toxicity, morphological defense, deterrent signaling) that reduces predation risk but imposes an energetic or reproductive penalty. Undefended prey, by contrast, avoid this cost but remain more vulnerable to predators. This sets up a social dilemma at the ecological level.

When the defense cost is moderate and the benefit of reduced predation is partially shared with the undefended prey (through reduced overall predator density), defended prey effectively “cooperate” by providing a public good (lower predation risk) from which undefended prey “free-ride.” In this regime, neither strategy dominates, and coexistence between defended and undefended types is possible — analogous to the SD dilemma’s stable mixed equilibrium.

If the defense cost is large relative to the benefit (e.g., strong reproductive penalty, low predator pressure), both prey types would be better off in the absence of defense. However, because predation pressure persists, the undefended prey always outperform defended prey in direct competition, leading to selection against defense. Here, the costly trait is lost despite potential group-level benefits — mirroring the PD’s tragedy of cooperation collapse.

If the benefit of defense is very high but only realized when most individuals adopt it (e.g., predators avoid the prey species only when the defended type is common enough to reinforce the learned avoidance), then mutual defense is the optimal strategy. However, if initial defended prevalence is low, the strategy is unstable, and the system may revert to undefended dominance. This corresponds to SH’s coordination problem, where both “all defended” and “all undefended” are equilibria, with one being risk-dominant depending on initial conditions.

From an eco-evolutionary perspective, our model thus spans a continuum of evolutionary dilemma structures depending on parameter regimes: low defense costs and high shared benefits yield SD-like dynamics; high costs produce PD-like collapse; and threshold-dependent predator learning produces SH-like coordination effects. The “aposematic prey” scenario in our work is a biologically grounded example of these underlying game-theoretic dilemmas, with predator avoidance learning and toxicity cost shaping where in this continuum a given system may lie. We have added a short discussion in the revised manuscript to highlight these correspondences,

as they provide a conceptual bridge between aposematism-inspired predator–prey models and the rich body of theory on evolutionary games.

2. The authors have put the spatio-temporal distribution of the undefended prey in the 100 x 100 grid and pointed out different spatial patterns generated through numerical simulations, whereas they never have come up with any distribution of the defended prey or the predators, anywhere in the manuscript. It would be good if they had mentioned the other species in the manuscript and a little about the similar or dissimilar patterns generated for the other evolutionary species.

Response: We have checked the spatial patterns for the defended prey and the predator using the same methodology and the patterns are same for all three species.

3. The colorbars used in the manuscript comes up with same range (0 to 1), whereas the upper bound of the total population and free space is assumed to be $1/\kappa$. Can they author mention how would the spatial distribution of species would look if they set the max range $1/\kappa$, other than the diagram, where they varied the parameter κ ?

Response: The prey density values predominantly lie within the range $[0, 1]$, which allows clear visualization of spatial patterns when using a standard colorbar. However, when we re-scale the colorbar to represent $1/\kappa$, density differences are visually compressed, particularly near the upper bound (around 1). As a result, the contrast between regions of varying prey density is diminished, making the patterns less discernible in the corresponding figures.

So, overall this manuscript is suitable for publication after these minor clarifications.

Response of “Spatio-temporal eco-evolutionary dynamics of prey-predator systems with defended and undefended prey”

Editor’s comment: Your manuscript titled “Spatio-temporal eco-evolutionary dynamics of prey-predator systems with defended and undefended prey” has now been seen again by our referees, whose comments appear below. In light of their advice I am delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Physics.

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. At the same time we ask that you edit your manuscript to comply with our journal policies and formatting style in order to maximise the accessibility and therefore the impact of your work.

Response: We sincerely thank the Editor for the positive assessment of our manuscript and for the opportunity to revise it for Communications Physics. We are pleased to inform you that we have carefully addressed all the remaining concerns raised by Reviewer 1. In particular, we have expanded the manuscript to clearly explain the biological justification of our functional forms and to highlight the connections of our results to empirical systems and their novel predictions. These additions were made at appropriate points in the text to improve clarity and accessibility, as suggested by the reviewer.

We have also revised the manuscript to ensure compliance with the journal’s formatting style and policies. We believe that these final changes have further strengthened the presentation of our work, and we hope that the revised version will now be suitable for publication in Communications Physics.

Reviewer #1: (Remarks to the Author):

I was positive about the original version of this paper, as were the other reviewers. In their response the authors have mainly done a good job in addressing my concerns and I am happy with all points apart from two, where more clarification is needed. These are my points 8 and 9.

My point 8. In general there are lots of formulae; these seem to be generally implemented in a good way, but how biologically realistic are they? A lot more justification of choices made in this regard would help. The authors’ response starts “Our model contains multiple functional forms that were chosen to capture key biological mechanisms while maintaining mathematical tractability. In the revised manuscript, we have expanded the justification for each major functional choice to clarify their biological basis: ...”. This would be a satisfactory response, except it is not clear to me what exactly has been changed in the paper and where.

Response: We thank the reviewer for pointing out the need to make the biological rationale behind our functional forms clearer and easier to locate. In the revised manuscript, we have added a dedicated paragraph that provides the biological justification for functional forms. This new subsection gathers together the explanations that were previously dispersed across the model description and expands on them with explicit references. We detail the ecological and evolutionary basis for each functional choice, such as the trade-off between defense and reproduction in defended prey, the use of the Beverton–Holt recruitment function for prey reproduction, the Holling type II functional response for predation, and the smooth hyperbolic tangent formulation for predator conversion efficiency from defended prey. We believe this focused section makes the biological motivation of our modeling framework much clearer, and we are grateful for the reviewer’s suggestion that led to this improvement.

My point 9. Can the authors comment on whether the results observed in their model occur in real populations, if there are novel predictions in this regard, anything problematic? The authors’ response starts ”Our model is formulated in a generalized theoretical framework and the qualitative outcomes have parallels in real ecological systems. A concrete example may be seen ...” This is again a good response, except that I cannot see that the details have been included in the paper itself.

Response: We again thank the reviewer for this important comment and for encouraging us to more clearly connect our theoretical results to real populations. In the revised manuscript, we have now added a dedicated explanatory paragraph in the Discussion (end of Section V) discussing the connections to empirical systems and predictions. In this new paragraph, we explicitly highlight empirical parallels, such as toxin-mediated predator–prey oscillations in amphibians and microbes, trophic downgrading in marine food webs, and diffusion-driven refugia observed in vegetation and coral reef ecosystems. We also outline novel predictions of our framework, including thresholds in prey toxicity (η) that govern predator persistence, the role of habitat fragmentation (κ) in shaping coexistence regimes, and the stabilizing influence of predator competition (μ) on prey persistence. We believe these additions directly address the reviewer’s concern and significantly improve the manuscript by clarifying its biological relevance and predictive value.

Reviewer #2(Remarks to the Author):

The authors fully addressed my concerns. I have not found any other issue with the current version, so I am recommending it for publication.

Response: We sincerely thank the reviewer for recommending the manuscript for publication in Communications Physics.

Reviewer #3 (Remarks to the Author):

The authors have provided satisfactory responses to all the queries. Accordingly, I recommend the acceptance of the article

Response: We sincerely thank the reviewer for the acceptance of our manuscript.

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So, overall this manuscript is suitable for publication after these minor clarifications.