Response to Reviewer 1's Comments

Dear Editor and Reviewer,

We sincerely thank you for your thorough review of our manuscript "Global Stability and Tipping Point Prediction of the Coral Reef Ecosystem." We appreciate your constructive feedback and recognize the need to make our work more accessible to a broader audience. Below, we address your comments point by point and outline the changes we will implement in our revised manuscript.

Response to ESD journal-specific questions

In the full review and interactive discussion, the referees and other interested members of the scientific community are asked to take into account all of the following aspects:

1.Does the paper address relevant scientific questions within the scope of ESD?

In theory it does. Early-warning signals are relevant, especially for corals which are thought to be sensitive to catastrophic shifts. However, the early-warning signals proposed in this paper seem to stem only from the model and it is unclear to me how these could be used in reality. The early-warning signals proposed in this paper are only compared to the notion of critical slowing down and the application of the proposed early-warning signals is not discussed in the manuscript. The concept itself (using the landscape flux) is not new. The lack of applicability of these concepts and the technical nature of the manuscript makes me question the relevance of this paper for the broader audience.

Answer： We agree that our paper could better clarify the practical applicability of the proposed early-warning signals. In our revision, we included additional discussion specifically addressing how our landscape-flux approach could be implemented using real-world coral reef monitoring data (see below). Concretely, some of our EWSs are model independent and can be computed directly from observed time series data, such as the average difference between forward and backward cross-correlation. While the concept of landscape-flux is not entirely new, our application to coral-algae systems and the demonstration that these metrics provide earlier warnings than traditional methods represents a significant advancement.

We have added the following discussion to the Results section to clarify the link between our theory and practical applications to real-world data (p. 22 in the revised manuscript):
"Real-time ecological monitoring data from coral reef ecosystems presents an unprecedented opportunity to bridge theoretical frameworks with empirical validation. By integrating time-series data from reef monitoring stations—capturing coral cover, algal abundance, and environmental parameters—into our landscape-flux methodology, we can operationalize the theoretical results outlined above. In particular, the cross-correlation functions of the coral-reef ecosystem can be estimated directly from observed time series and hence we may calculate the average difference between forward and backward cross-correlation as an empirical EWS. Our framework thus provides practical early warning tools for policymakers and researchers, bridging the gap between abstract mathematical models and urgent conservation needs in threatened ecosystems."

2. Does the paper present novel concepts, ideas, tools, or data?

The concept is not new, but its application to a coral-algae system is, I believe.

Answer： We appreciate your acknowledgment that our application to coral-algae systems is novel. We strengthened our discussion of how our approach extends applications of landscape-flux theory and why this is particularly valuable for coral reef ecosystems.

We have added the following discussion in the subsection "Landscape and flux theory for the coral-algae model":

"By adapting the potential landscape-flux framework to ecological dynamics, we bridge a critical gap between physical systems, where these methods originated, and complex biological systems characterized by nonlinear feedback and multiple stable states. Coral reef ecosystems represent an ideal test case for this theoretical extension due to documented evidence of alternative stable states, their sensitivity to environmental perturbations, and their growing vulnerability to climate change impacts. Our implementation demonstrates how landscape-flux theory can quantify stability of ecological systems under stochastic forcing, providing a mathematically rigorous foundation for early warning signals that complement existing early warning indicators for ecological systems\citep{clements2018indicators}. This contrasts with some recent methods relying on AI and machine learning to produce indicators for transitions based on training on empirical data, but without a mathematical underpinning or basis through which to interpret the resulting indicators\citep{george2023early}. Our work thus creates new opportunities for anticipating critical transitions in reef ecosystems, where traditional monitoring approaches often detect degradation only after substantial ecological changes have occurred. The framework's ability to characterize global stability while accommodating environmental stochasticity makes it particularly suited to reef conservation, where identifying resilience thresholds and intervention windows is increasingly urgent for management and preservation efforts."

3. Are substantial conclusions reached?

The proposed early-warning signals are compared to one other early-warning signal (critical slowing down) and it is concluded that the newly proposed early-warning signals can detect a transition earlier than critical slowing down. I think there is more potential here, because the applicability of the proposed early-warning signals to real systems is not discussed, nor are they compared to other early-warning signals. It is also confusing to me whether the authors refer to noise-induced transitions or bifurcations (i.e., press disturbance/gradual parameter changes). Indeed, the landscape free flux and the other concepts seem to be able to pick up a bifurcation "earlier" than critical slowing down, but how is that related to noise-induced transitions? Moreover, there has been much critique on the use of critical slowing down as early-warning signal, so it is not a very new conclusion that there is an early-warning signal that is better than critical slowing down.

Answer：
Thank you for raising an important point about the comparison between early-warning signals derived from our method and those based on Critical Slowing Down (CSD). We appreciate this opportunity to clarify the distinctive contributions of our approach.

Our landscape-flux framework offers substantial advantages over traditional CSD-based indicators, particularly in its ability to provide earlier detection of approaching transitions. While CSD focuses primarily on local stability properties near equilibrium states, our method captures global stability characteristics and non-equilibrium dynamics across the entire state space.

Our study demonstrates that the landscape-flux approach and its derived early-warning signals (cross-correlation function ΔCC multidimensional data) can detect approaching transitions earlier than critical slowing down indicators based on theoretical relaxation time τ_{relax} (one-dimensional data, measured through autocorrelation). This earlier detection capability is crucial for ecological management, as it potentially provides a longer window for intervention before critical transitions occur. This comparison is particularly meaningful because relaxation time represents the fundamental dynamical feature underlying all CSD indicators, rather than just comparing with empirical manifestations of CSD (such as variance or autocorrelation methods). By demonstrating advantages at this fundamental level, we establish the theoretical superiority of our approach.

Throughout the manuscript, our analysis focuses on bifurcations as the bifurcation points delineate the boundaries between regions of qualitatively different dynamics in the absence of noise. Our approach thus quantifies how the global stability landscape evolves as the system approaches these critical thresholds. This comprehensive perspective enables earlier detection than the local stability measures used in CSD. We demonstrate this advantage specifically through our analysis of gradual parameter changes (such as decreasing grazing rate parameter g), showing how our indicators respond earlier to these changes than traditional CSD metrics.

We agree with the reviewer that there are many extant critiques of CSD, but we go further by explaining the mathematical basis for the superiority of our theory over CSD. CSD is a local phenomenon and manifests only when the basin of attraction of the current system state becomes sufficiently flat. Flux being rotational prefers global distribution of states rather than being localized to a point attractor. When the flux increases, the current state basin of the system becomes unstable. This gives the opportunity to bifurcate to new states. Since such redistribution of states is a global property of the phase space, it emerges earlier than the local flatness of the basin of attraction.

4. Are the scientific methods and assumptions valid and clearly outlined?

This manuscript is very technical and really difficult to understand for someone like me who's well-informed about tipping and ecological models, but not about the mathematical analyses of nonlinear PDE systems. Work is thus needed to make the methods and assumptions clear for a non-technical audience. I believe the methods are valid. Again, the use of the landscape flux as early-warning signal is not new, but it is difficult for me to judge. One assumption that I have doubts about for this system, is the assumption that the noise is uncorrelated between the three components. In the coral-macroalgae system, I assume noise to be coming from external environmental forces which would impact the three components similarly. I also have doubts about the assumption of a spatially well-mixed system. For those two assumptions, I'd be interested to read more about the implications of these. I understand that the analyses become more complex if the noise is correlated, but how do you expect it to impact the results?

Answer：

Thank you for your valuable feedback concerning the technical nature of our manuscript. We will enhance accessibility for non-specialist readers by adding explanatory text boxes, intuitive analogies, and simplified explanations of key mathematical concepts throughout the paper.

Regarding your specific concerns:

Noise Structure and Environmental Fluctuations

"In the current model, we utilize uncorrelated white noise as a mathematical simplification that provides analytical tractability while still capturing the essential stochastic nature of state transitions. This approach allows us to derive expressions for potential landscapes and flux patterns. We recognize that environmental disturbances like temperature fluctuations, storm events, or nutrient pulses would indeed affect coral, algae, and algal turfs in coordinated ways, introducing correlations in the noise structure of natural reef systems\citep{jouffray2015identifying,norstrom2009alternative,Dikou2010Ecological,Gardner2003Science, Mcmanus2004Coral}.

It is worth noting that our potential landscape-flux framework remains theoretically appropriate for systems with correlated noise. The mathematical formalism can accommodate various noise structures, including anisotropic and correlated fluctuations. Due to space limitations in the present manuscript and its complexity, we have focused on the uncorrelated case as a first approximation. The extension to correlated noise models, which would more accurately reflect synchronized environmental forcing experienced by different reef components, will be addressed in future research.

Without conducting significant further analysis, it is challenging to accurately predict the precise effects of correlated noise on the overall system dynamics. The specific correlation patterns, time scales, and amplitudes of the noise would significantly influence the system's response. The introduction of correlation structures in stochastic perturbations fundamentally alters the statistical properties of system trajectories, potentially creating emergent behaviors that cannot be intuited through qualitative reasoning alone. The precise correlation structure to be introduced would need to be motivated by data and may differ by reef location and climate, making this a nontrivial extension of the current work but undoubtedly a valuable and interesting one."

Spatial Structure and Heterogeneity

"The model tracks the evolution of proportions of space occupied by each functional type, effectively assuming that the system is spatially well-mixed, leading to a spatially implicit modeling framework \citep{Alan2007Nature}. This approach is appropriate for intermediate spatial scales where mixing processes (such as larval dispersal, water circulation, and mobile herbivore grazing) tend to homogenize local variations. The spatially implicit framework allows us to focus on ecosystem-level dynamics without the computational complexity of spatially resolved models.

Our potential and flux field landscape theoretical framework offers considerable versatility and could be naturally extended to spatially explicit models in future research. We recognize the importance of spatial heterogeneity in coral reef ecosystems and in subsequent work, we plan to develop spatially explicit extensions of this framework. In recent work, we have shown that the framework can be extended to spatially explicit models (of vegetation dynamics) and hence it is a natural next step to leverage this progress to explore how the present results compare with EWSs in spatial extension of the coral reef model studied here:

J. Siu, W. Wu, D. D. Patterson, S. A. Levin and J. Wang, Revealing physical mechanisms of pattern formation and switching in ecosystems via landscape and flux, Advanced Science, accepted (2025) - arXiv:2412.03978.

Despite the simplifying assumptions of the mathematical model, our current framework provides valuable insights into the global stability of coral reef ecosystems and demonstrates the utility of landscape-flux theory for understanding complex ecological dynamics. The simplifications employed here serve as a necessary first step toward more comprehensive models that can incorporate the full complexity of coral reef systems \citep{Simon2018Corel,Scheffer2016Coralreefs}."

5. Are the results sufficient to support the interpretations and conclusions?

Yes.

Answer: Thank you for your confidence in our results. We will strengthen the connection between our mathematical results and the associated ecological interpretation.

6. Is the description of experiments and calculations sufficiently complete and precise to allow their reproduction by fellow scientists (traceability of results)?

I think that a mathematician or physicist that is very familiar with these kinds of analyses could replicate the results.

Answer: We appreciate your assessment that specialists could replicate our results.

7. Do the authors give proper credit to related work and clearly indicate their own new/original contribution?

No, I think there are very few papers cited. For example, you mention one critique of critical slowing down as early-warning signal, but there has been much more critique and I actually think that the only reason that researchers still refer to critical slowing down as a (useful) early-warning signal is its applicability in real systems.

Answer: We acknowledge this shortcoming and will significantly expand our literature review to include:
- The broader history of early-warning signals in ecology and recent approaches leveraging AI and machine learning,
- Multiple critiques of critical slowing down approaches.

We have incorporated additional references into the text and they form part of the following expanded discussion:

"Understanding how natural systems respond to human disturbances and identifying critical thresholds is essential for developing effective early warning systems for ecological transitions\citep{Andersen2009,Bestelmeyer2013,Biggs2009}. As ecosystems face increasing pressure from climate change, the ability to detect tipping points and anticipate critical transitions has become increasingly important\citep{Lenton2011,Scheffer2015,Thompson2011}. Early warning signals play a crucial role in this process, helping us to understand when abrupt and significant changes might occur in complex ecological systems\citep{Clements2018,Contamin2009,Drake2010}. Before reaching a critical point, ecosystems typically maintain a sustainable balance; however, once this threshold is crossed, the current stable state loses stability, triggering catastrophic shifts to alternative stable states\citep{Dai2012,Dai2013,Scheffer2015}.

Recent theoretical and empirical investigations have substantially advanced our understanding of ecological system instabilities\citep{Carstensen2013,Dakos2012,Guttal2009,Kefi2014}. Critical slowing down (CSD) theory has emerged as a framework in this field and has been widely applied to predict warning signals from univariate time series data\citep{Dakos2015,Lindegren2012,Scheffer2012Nature,Scheffer2001Nature}. This behavior occurs as a control parameter approaches a critical threshold value, causing system dynamics to decelerate while the current steady state becomes increasingly unstable\citep{Berglund2006,Hastings2018Science,Scheffer2012Science}. Common indicators include increased variance, stronger autocorrelation, and longer return times following perturbations\citep{Boettiger2012,Dakos2012,Gsell2016}.

Despite its theoretical promise, research has revealed significant limitations to CSD's practical application. Time delays in ecological systems fundamentally alter the dynamical properties near critical transitions, potentially rendering CSD indicators unreliable or misleading\citep{Guttal2013}. This theoretical concern is substantiated by empirical evidence from natural systems, where comprehensive analyses of long-term data from aquatic ecosystems demonstrate that CSD indicators' efficacy is considerably constrained by real-world complexity, with environmental stochasticity and multiple interacting stressors frequently obscuring warning signals\citep{Gsell2016}.

While recent advances have expanded CSD applications through refined statistical indicators\citep{Boulton2019,Bury2021} and multivariate extensions\citep{Weinans2021}, significant limitations remain. Most notably, CSD often provides warnings only when systems are already near critical thresholds-frequently too late for effective intervention\citep{Biggs2009,Boettiger2013a,Ditlevsen2010}. Additionally, while CSD performs reliably in one-dimensional systems, it struggles with complex multidimensional ecological dynamics involving feedback loops\citep{Boerlijst2013,Hastings2010,Weinans2021}. These shortcomings, along with challenges such as false signal susceptibility\citep{Boettiger2013b,Perretti2012} and extensive data requirements\citep{Burthe2016}, highlight the need for complementary approaches that can provide earlier warnings for complex ecological systems and overcome the limitations inherent in current methodologies\citep{Boettiger2013a,Clements2018,Dakos2015}.

There has also been considerable recent interest in early warning signals based on AI and machine learning methods\citep{grassia2021machine, bury2021deep}. While these methods often show impressive results on simulated and training data, it remains to be seen how well they generalize to different physical systems and unseen datasets. Moreover, these methods have an inherent disadvantage in that the generated EWSs do not have a rigorous mathematical underpinning and are typically not as interpretable to practitioners working in the application area\citep{george2023early}. Machine learning methods have also recently been used to predict critical transitions by using existing EWSs (including those based on CSD) as features in the models to leverage subject matter expertise and insights\citep{ma2018data, lassetter2021using}. This hybrid approach could be a promising direction for practical testing of EWSs, including our landscape-flux based indicators."

8. Does the title clearly reflect the contents of the paper?

I wouldn't say "the" coral reef system. And it should be clear in the title that this is about a model and only one type of model.

Answer: We agree and will modify the title to: "Global Stability and Tipping Point Prediction in a Coral-Algae Model Using Landscape-Flux Theory". We change the coral reef system into coral-algae system in the manuscript.

9. Does the abstract provide a concise and complete summary?

I didn't understand most of the abstract because it is very technical.

Answer: We have rewritten the abstract to make it accessible to non-specialists while maintaining scientific precision, reducing technical terminology and adding clear statements about practical implications. The new abstract reads as follows: "Coral reef ecosystems are remarkable for their biodiversity and ecological significance, exhibiting the capacity to exist in different stable configurations with possible abrupt shifts between these alternative stable states. This study applies landscape-flux theory to analyze how these complex systems behave when subjected to random environmental disturbances. We use this theory to formulate and investigate several early warning indicators of ecosystem transitions in a well-known coral-reef model. We studied a number of specific indicators, including the average flux (the driving force when the system is out of equilibrium), the entropy production rate, the nonequilibrium free energy and the time irreversibility of the cross-correlation functions. These indicators demonstrate a distinctive advantage when compared to classical indicators based on the phenomenon of critical slowing down; they exhibit turning points midway between two bifurcations, enabling them to forecast transitions in both directions substantially earlier than conventional methods. In contrast, early warning indicators based on the critical slowing down phenomenon typically only become apparent when the system approaches the actual bifurcation or tipping point(s). Our findings offer improved tools for anticipating critical transitions in coral reef and other at-risk ecosystems, with the potential to enhance conservation and management strategies."

10. Is the overall presentation well structured and clear?

Yes. I think the manuscript is well-structured. The results as they are can be written more concisely and I didn't understand the added value of some of the figures. There should be some explanations added for non-technical readers though. The properties/concepts that are derived from the model and used as early-warning signals are now mostly introduced in the results whereas they should be introduced in the methods. I think a table with an explanation of these properties would be help to keep an overview of everything that is calculated.

Answer: Thank you for acknowledging the manuscript's structure. We will move the introduction of key concepts to the methods section (Entropy production rate (EPR) and the average Flux, Time irreversibility, The mean first passage time, etc.) and add a comprehensive table defining all measures used (entropy production rate, flux, time irreversibility, etc. in Table S1 in Supplement zip) with both mathematical definitions and intuitive explanations.

11. Is the language fluent and precise?

There are some spelling/grammar mistakes, but not much. The language is precise enough, but too technical. Some things could be more precise such as whether it concerns noise-induced transitions or bifurcations and what does it mean that the proposed early-warning signals predict a transition 'earlier' than critical slowing down. What is earlier in this respect? How does it relate to real changes in a coral-algae system?

Answer：We will correct spelling and grammar mistakes.

Our study demonstrates that the landscape-flux approach and its derived early-warning signals (cross-correlation function ΔCC multidimensional data) can detect approaching transitions earlier than critical slowing down indicators based on theoretical relaxation time τ_{relax} (one-dimensional data, measured through autocorrelation). This earlier detection capability is crucial for ecological management, as it potentially provides a longer window for intervention before critical transitions occur. This comparison is particularly meaningful because relaxation time represents the fundamental dynamical feature underlying all CSD indicators, rather than just comparing with empirical manifestations of CSD (such as variance or autocorrelation methods). By demonstrating advantages at this fundamental level, we establish the theoretical superiority of our approach.

Noise (fluctuations) induced transitions with parameter driven

Throughout the manuscript, our analysis focuses on bifurcations (noise induced transitions with parameter driven). For these bifurcations involving gradual parameter changes under fluctuations, our approach quantifies how the global stability landscape evolves as the system approaches critical thresholds. This comprehensive perspective enables earlier detection than the local stability measures used in CSD. We demonstrate this advantage specifically through our analysis of gradual parameter changes (such as decreasing grazing rate parameter g), showing how our indicators respond earlier to these changes than traditional CSD metrics.

Early-warning signals predict a transition relates to real changes in a coral-algae system.

In the model, parameter g represents the grazing rate of macroalgae by herbivorous fish and invertebrates, a crucial ecological process with well-documented real-world counterparts. This parameter directly connects mathematical modeling to measurable ecological dynamics that reef managers can monitor and potentially influence.

Real-world factors affecting the grazing rate, g, include:
- Overfishing of herbivores (parrotfish, surgeonfish) decreases g
- Marine protected areas increase g as herbivore populations recover
- Disease outbreaks, like the 1983 Caribbean sea urchin die-off, reduce g
- Predator-prey dynamics influence g through trophic cascades

As g gradually decreases in real systems:
1. Algae gain competitive advantage over corals
2. System resilience weakens
3. Recovery becomes increasingly difficult after disturbances
4. At the critical threshold, even small herbivore loss triggers a shift to algal dominance

This mechanism explains ecological transitions observed on reefs, where reduced herbivory caused coral-to-algae phase shifts matching our bifurcation analysis predictions.

12. Are mathematical formulae, symbols, abbreviations, and units correctly defined and used?

I did not find any errors. No units are given for the parameters.

Answer: We have added appropriate units for the parameters of the Coral-Algae model in Table 1 (in Supplement zip) and ensured that notation is consistent throughout. The formulas of the landscape and flux theory are dimensionless.

13. Should any parts of the paper (text, formulae, figures, tables) be clarified, reduced, combined, or eliminated?

I don't think that all figures are necessary. There should be a clarification of the mathematical concepts used and also of the mathematical methods.

Answer: We assessed which figures are essential and combine and eliminated redundant ones. Each remaining figure is accompanied by improved captions and explanatory text regarding the mathematical concepts and methods to make it more accessible to non-specialists.

14. Are the number and quality of references appropriate?

No, I think there are too few references. More background on early-warning signals in general would be nice, as well as on critical slowing down in particular and the criticism. Also, I'd like to read more background about the landscape flux as early-warning signal, its background and applications and possible criticism

Answer: We will substantially expand our reference list, particularly regarding:

(1) Early-warning signal development and applications and Critical slowing down methods and critiques

We added the following discussion on these topics: "Understanding how natural systems respond to human disturbances and identifying critical thresholds is essential for developing effective early warning systems for ecological transitions\citep{Andersen2009,Bestelmeyer2013,Biggs2009}. As ecosystems face increasing pressure from climate change, the ability to detect tipping points and anticipate critical transitions has become increasingly important\citep{Lenton2011,Scheffer2015,Thompson2011}. Early warning signals play a crucial role in this process, helping us to understand when abrupt and significant changes might occur in complex ecological systems\citep{Clements2018,Contamin2009,Drake2010}. Before reaching a critical point, ecosystems typically maintain a sustainable balance; however, once this threshold is crossed, the current stable state loses stability, triggering catastrophic shifts to alternative stable states\citep{Dai2012,Dai2013,Scheffer2015}.

Recent theoretical and empirical investigations have substantially advanced our understanding of ecological system instabilities\citep{Carstensen2013,Dakos2012,Guttal2009,Kefi2014}. Critical slowing down (CSD) theory has emerged as a framework in this field and has been widely applied to predict warning signals from univariate time series data\citep{Dakos2015,Lindegren2012,Scheffer2012Nature,Scheffer2001Nature}. This behavior occurs as a control parameter approaches a critical threshold value, causing system dynamics to decelerate while the current steady state becomes increasingly unstable\citep{Berglund2006,Hastings2018Science,Scheffer2012Science}. Common indicators include increased variance, stronger autocorrelation, and longer return times following perturbations\citep{Boettiger2012,Dakos2012,Gsell2016}.

Despite its theoretical promise, research has revealed significant limitations to CSD's practical application. Time delays in ecological systems fundamentally alter the dynamical properties near critical transitions, potentially rendering CSD indicators unreliable or misleading\citep{Guttal2013}. This theoretical concern is substantiated by empirical evidence from natural systems, where comprehensive analyses of long-term data from aquatic ecosystems demonstrate that CSD indicators' efficacy is considerably constrained by real-world complexity, with environmental stochasticity and multiple interacting stressors frequently obscuring warning signals\citep{Gsell2016}.

While recent advances have expanded CSD applications through refined statistical indicators\citep{Boulton2019,Bury2021} and multivariate extensions\citep{Weinans2021}, significant limitations remain. Most notably, CSD often provides warnings only when systems are already near critical thresholds-frequently too late for effective intervention\citep{Biggs2009,Boettiger2013a,Ditlevsen2010}. Additionally, while CSD performs reliably in one-dimensional systems, it struggles with complex multidimensional ecological dynamics involving feedback loops\citep{Boerlijst2013,Hastings2010,Weinans2021}. These shortcomings, along with challenges such as false signal susceptibility\citep{Boettiger2013b,Perretti2012} and extensive data requirements\citep{Burthe2016}, highlight the need for complementary approaches that can provide earlier warnings for complex ecological systems and overcome the limitations inherent in current methodologies\citep{Boettiger2013a,Clements2018,Dakos2015}.

There has also been considerable recent interest in early warning signals based on AI and machine learning methods\citep{grassia2021machine, bury2021deep}. While these methods often show impressive results on simulated and training data, it remains to be seen how well they generalize to different physical systems and unseen datasets. Moreover, these methods have an inherent disadvantage in that the generated EWSs do not have a rigorous mathematical underpinning and are typically not as interpretable to practitioners working in the application area\citep{george2023early}. Machine learning methods have also recently been used to predict critical transitions by using existing EWSs (including those based on CSD) as features in the models to leverage subject matter expertise and insights\citep{ma2018data, lassetter2021using}. This hybrid approach could be a promising direction for practical testing of EWSs, including our landscape-flux based indicators."

(2) Landscape-flux approaches in ecology and other fields

We add the following text to the revised manuscript: "Landscape-flux theory provides a promising alternative framework for analyzing complex ecological systems and predicting critical transitions. This non-equilibrium statistical mechanics approach offers several distinct advantages over traditional methods. Foremost among these is its capacity to characterize global system stability through the construction of potential landscapes that quantify the relative stability of different states\citep{Wang2008PNAS,Xu2014PLOSONE2,Xu2021PNAS}. Unlike critical slowing down theory, landscape-flux theory effectively captures multidimensional system dynamics, including rotational forces (curl flux) as an additional driving force besides landscape gradient for the dynamics that are often overlooked in equilibrium-based analyses\citep{Wang2015AP,Ge2010PRE,Qian2006JPCB}. This enables more comprehensive characterization of system behavior, particularly in complex ecological networks with multiple feedback mechanisms\citep{Xu2023PNAS}.

Another significant advantage is the theory's ability to detect warning signals substantially earlier than bifurcation-proximity indicators\citep{Wang2011PNAS,Xu2010BJ}. By quantifying both the potential landscape topography and the non-equilibrium flux, the approach provides mechanistic insights into transition drivers rather than merely phenomenological descriptions\citep{Qian2009ME,Xu2012JCP}. The theory has been successfully applied to various complex systems\citep{Wang2015AP,Fang2019RMP}, including gene regulatory networks\citep{Wang2008PNAS}, cell fate decisions\citep{Xu2010BJ,Xu2014PLOSONE2}, and more recently, ecological regime shifts\citep{Xu2021PNAS,Xu2023PNAS}.

Despite its significant promise and advantages, landscape-flux theory presents certain challenges, particularly in its practical implementation. Its implementation requires sophisticated mathematical techniques and substantial computational resources\citep{Wang2015AP,Fang2019RMP}. The approach demands comprehensive system knowledge for accurate model formulation and parameter estimation, which can be difficult to obtain for many ecological systems\citep{Ge2010PRE}. Quantifying flux components in empirical systems poses challenges, often requiring high-resolution temporal data\citep{Wang2011PNAS,Qian2009ME}. There have not yet been any empirical studies combining the landscape flux theory and associated EWSs with data and it remains to be seen how successful the theory will be in practice. Nevertheless, the theory's capacity to provide earlier warnings and deeper mechanistic understanding of ecological transitions makes it a valuable complement to existing approaches for analyzing complex ecosystems facing anthropogenic pressures and we hope that it can be empirically tested in the near future\citep{Xu2021PNAS,Xu2023PNAS}."

15. Is the amount and quality of supplementary material appropriate?

I could not find the supplementary figures and it was not clear to me from the main text what would be in those figures and what is their added value.

Answer： The supplementary figures are in the preprint at
https://www.biorxiv.org/content/10.1101/2024.12.17.627631v2.supplementary-material
supplements/627631_file02.pdf
We will ensure all referenced supplementary materials are properly included and clearly linked to the main text, with explanations of their relevance.

Response to Major Comments

1.The paper is highly technical and therefore difficult to understand for a non-technical reader. To be appropriate for this journal non-technical explanations should be added to the paper. Otherwise, the paper might be more suitable for a technical journal.

Answer： We sincerely appreciate your thoughtful suggestion and valuable feedback.
We enhanced comprehension by adding a new section that explains technical concepts in accessible language, incorporating visual analogies for mathematical ideas. This plain-language explanation of key concepts is complemented by more detailed technical information in the Supplementary Information.

"Our approach reveals coral-algae dynamics through two complementary concepts: landscape and flux.

The Landscape can be visualized as a physical terrain with hills and valleys. Like a marble rolling on this surface, coral-algae systems will naturally move toward valleys (stable states) and away from hills (unstable states). The depth of valleys indicates stability strength—deeper valleys represent more resilient states that withstand stronger disturbances. Conversely, the height of the barrier between valleys determines transition difficulty.

The Flux is analogous to river currents creating circular patterns that can't be explained by downhill movement alone. Just as water doesn't flow directly downhill but forms eddies and swirls, flux creates rotational movements in the system dynamics; in contrast to the influence of the landscape, which pushes the system directly towards stable states. The flux is also responsible for time irreversibility, a fundamental characteristic of complex systems. In terms of the river metaphor, if you drop a leaf in the water and watch its journey downstream, you'll observe a specific path, but trying to reverse this journey by pushing the leaf back upstream won't mirror the original path exactly. This irreversibility occurs because eddies and currents create asymmetric flow patterns, the leaf encounters different obstacles in different sequences during forward versus backward movement. Similarly, the flux is responsible for the fact that the most likely coral-to-algae transitions follow different paths than algae-to-coral recoveries in our model. These circular patterns require continuous energy input to maintain—another key characteristic of non-equilibrium systems.

Together, these complementary forces of landscape and flux provide a complete picture of coral-algae behavior. The landscape determines where stable states exist and their resistance to perturbations, while flux shapes the actual transition pathways between alternative stable states, creating the rich, sometimes surprising dynamics observed in these complex systems.

Entropy production measures how costly it is for a system to maintain its non-equilibrium state—essentially its "operating cost." As a system approaches a critical transition, this "cost" often changes significantly. By measuring entropy production, we can detect when a coral-algae system is working “harder” to maintain its current state, potentially signaling an upcoming transition even before visible changes occur. The $Flux_{av}$ represents the average strength of the circular flow patterns in the coral-algae system. Like measuring the average current strength in a river, $Flux_{av}$ quantifies the intensity of these non-equilibrium dynamics.”

(2) We added a glossary of terms in Table S1.

2. You compare the early-warning signals only to critical slowing down, whereas there are many more early-warning signals proposed in the literature. Also, critical slowing down has received much more criticism than listed in this paper.

Answer： We sincerely appreciate your thoughtful suggestion and valuable feedback.
We added the three early-warning signals Variance, flickering frequency and escape time to the revised version of the manuscript.

Variance

“Figure \ref{fig5_corrh044_phase2d}C illustrates the relationship between variance and grazing rate g. Specifically, as the grazing rate g increases: the variance of the Macroalgae state (Var_M) shows a clear increasing pattern, while simultaneously, the variance of the Coral state (Var_C) exhibits a decreasing trend. This divergent behavior in variances provides important insights into the system's stability characteristics. The increasing variance in the Macroalgae state (Var_M) indicates growing instability and fluctuations in this state as grazing pressure intensifies. Conversely, the decreasing variance in the Coral state (Var_C) signifies that this state becomes more stable and resilient with increasing grazing pressure. These variance patterns serve as quantitative early warning indicators of the shifting stability landscape in the coral-algae system and help identify the approach toward critical transition points in this ecological model." (Figure 5 in Supplement zip)

Flickering frequency

"The flickering frequency quantifies the number of state transitions per unit time. Specifically, $f_{\omega CM}$ represents the frequency of transitions from the $Coral$ state to the $Macroalgae$ state per unit time. In Figure \ref{fig3_phi0_path_Ba}K, we illustrate the frequency of transitions from $Macroalgae$ to $Coral$ ($f_{\omega MC}$) with fluctuation strength $D=5\times 10^{-4}$. Our results demonstrate that $f_{\omega MC}$ increases dramatically as g increases. This phenomenon can be explained by the decreasing stability of the $Macroalgae$ state's basin of attraction, which becomes shallower as g increases. Consequently, the system exhibits a higher probability of transitioning to the $Coral$ state. Previous research has established flickering frequency as an effective early warning signal for critical transitions \cite{Scheffer2012Science,Scheffer2009Nature}. The tipping points identified through flickering frequency occur near the bifurcation point in the coral-algae model, where the $Macroalgae$ state becomes unstable (flat potential) while the $Coral$ state becomes dominant. Flickering frequency indicates that the $Macroalgae$ state loses resilience, characterized by a diminishing basin of attraction in the potential landscape, while the $Coral$ state gains dominance. It is important to note that actual transitions may occur considerably earlier than this bifurcation point due to larger environmental fluctuations." (Figure 3 in Supplement zip)

Escape time (The mean first passage time)\cite{Scheffer2021Science}

"Ecological systems may transition from their current stable state to an alternative stable state due to stochastic fluctuations or external forces, effectively escaping their basin of attraction. The escape time between stable states provides a valuable quantitative measure for assessing global stability in coral reef ecosystems. By estimating the mean exit time from a basin of attraction~\citep{Scheffer2021Science,Wang2008PNAS,Xu2021PNAS,Xu2014PLOSONE}, we can better understand the likelihood of transitions between coral-dominated and algae-dominated states. Mean first passage time (MFPT)—the average time required for a stochastic process to first reach a specified threshold value—provides a robust metric for quantifying this phenomenon. MFPT effectively measures the kinetic speed or temporal characteristics of transitioning between states, offering natural indicators of a system's propensity to depart from its current basin of attraction.

To investigate this behavior, we employ Langevin dynamics to simulate the stochastic coral-algae model and analyze the MFPT distribution between stable states. Our methodology begins by selecting one stable state as the initial condition, while designating a disc with radius $r_0=0.01$ surrounding the alternative stable state as the target "state." We then compile first passage time statistics from the initial to the final state, subsequently averaging across all simulations to determine the mean first passage time. We define τ_{CM} as the $MFPT$ from the coral-dominated state to the macroalgae-dominated state, and conversely, τ_{MC} as the $MFPT$ from the macroalgae-dominated state to the coral-dominated state.

Figure \ref{fig3_phi0_path_Ba}J presents the Mean First Passage Time (MFPT), which quantifies the average time required for a stochastic process to first reach a specified state. The behavior of the mean first passage time (MFPT) as it is represented in logarithmic form, specifically shows an increase in $\ln\tau_{CM}$ and a decrease in $\ln\tau_{MC}$ as the parameter g increases. This trend indicates that it takes more time to exit the Coral state while it requires less time to transition out of the Macroalgae state as g rises. Consequently, the MFPT can effectively characterize the transition from the Macroalgae state to the Coral state with increasing g, providing a measurable indicator of this critical transition."

We have created a new Figure 6 (Figures in Supplement zip) showing the behavior of indicators across different noise intensities D=5*10^-4 and D=10^-3, with panels A-F illustrating how the sensitivity of the average differences in cross-correlations over time, the relaxation times and the variances change with higher levels of noise. We observe that while increasing noise can also serve as an indicator for predicting state transitions, its predictive effectiveness diminishes relative to the performance observed at lower noise levels. Specifically, our analysis reveals that elevated noise in certain ranges in the system can trigger warning signals that precede critical transitions between alternative stable states.

"Figure \ref{fig6_DDDD} A and D illustrate the average differences in cross-correlations over time, represented as \(\Delta CCM\) and \(\Delta CCC\), plotted against the grazing rate \(g\). These values provide insight into the dynamics of the coral-algae system, revealing how the interaction strength between states varies as grazing pressure changes. Figure \ref{fig6_DDDD} B and E display the relaxation times, \(\tau_{relaxM}\) and \(\tau_{relaxC}\), in relation to the grazing rate \(g\). The relaxation time quantifies how quickly the system responds to perturbations, serving as a crucial indicator of the stability of the Macroalgae and Coral states under varying conditions. Figure \ref{fig6_DDDD} C and F present the variances \(Var_M\) and \(Var_C\) as functions of the grazing rate \(g\). These variances reflect the degree of fluctuations within each state, highlighting how stability is affected as grazing pressure increases. It is noteworthy that for Figure \ref{fig6_DDDD}, the fluctuation strength is set at \(D=5.0\times 10^{-4}\), while for Figures D-F, the fluctuation strength increases to \(D=1.0\times 10^{-3}\), with a fixed height parameter of \(h=0.44\). This variation in \(D\) is expected to have a significant impact on the observed relationships, further illustrating the delicate balance between grazing intensity and the stability of the coral-algae ecosystem. We observe that while increasing noise can also serve as an indicator for predicting state transitions, its predictive effectiveness diminishes relative to the performance observed at lower noise levels."

We expanded the discussion on limitations of CSD as follows:

"While recent advances have expanded CSD applications through refined statistical indicators\citep{Boulton2019,Bury2021} and multivariate extensions\citep{Weinans2021}, significant limitations remain. Most notably, CSD often provides warnings only when systems are already near critical thresholds-frequently too late for effective intervention\citep{Biggs2009,Boettiger2013a,Ditlevsen2010}. Additionally, while CSD performs reliably in one-dimensional systems, it struggles with complex multidimensional ecological dynamics involving feedback loops\citep{Boerlijst2013,Hastings2010,Weinans2021}. These shortcomings, along with challenges such as false signal susceptibility\citep{Boettiger2013b,Perretti2012} and extensive data requirements\citep{Burthe2016}, highlight the need for complementary approaches that can provide earlier warnings for complex ecological systems and overcome the limitations inherent in current methodologies\citep{Boettiger2013a,Clements2018,Dakos2015}."

3. To me, the assumptions of a well-mixed space and non-correlated noise are not obviously appropriate for this system. Some discussion should be added on how these assumptions affect the results and in which domain/spatial extent they are appropriate.

Answer： Thank you for your valuable suggestions. We will add the discussion on these assumptions in the conclusions section and comment on your specific concerns below.

Noise Structure and Environmental Fluctuations

“In the current model, we utilize uncorrelated white noise as a mathematical simplification that provides analytical tractability while still capturing the essential stochastic nature of state transitions. This approach allows us to derive expressions for potential landscapes and flux patterns. We recognize that environmental disturbances like temperature fluctuations, storm events, or nutrient pulses would indeed affect coral, algae, and algal turfs in coordinated ways, introducing correlations in the noise structure of natural reef systems\citep{jouffray2015identifying,norstrom2009alternative,Dikou2010Ecological,Gardner2003Science, Mcmanus2004Coral}.

It is worth noting that our potential landscape-flux framework remains theoretically appropriate for systems with correlated noise. The mathematical formalism can accommodate various noise structures, including anisotropic and correlated fluctuations. Due to space limitations in the present manuscript and its complexity, we have focused on the uncorrelated case as a first approximation. The extension to correlated noise models, which would more accurately reflect synchronized environmental forcing experienced by different reef components, will be addressed in future research.

Without conducting significant further analysis, it is challenging to accurately predict the precise effects of correlated noise on the overall system dynamics. The specific correlation patterns, time scales, and amplitudes of the noise would significantly influence the system's response. The introduction of correlation structures in stochastic perturbations fundamentally alters the statistical properties of system trajectories, potentially creating emergent behaviors that cannot be intuited through qualitative reasoning alone. The precise correlation structure to be introduced would need to be motivated by data and may differ by reef location and climate, making this a nontrivial extension of the current work but undoubtedly a valuable and interesting one.”

Spatial Structure and Heterogeneity

“The model tracks the evolution of proportions of space occupied by each functional type, effectively assuming that the system is spatially well-mixed, leading to a spatially implicit modeling framework \citep{Alan2007Nature}. This approach is appropriate for intermediate spatial scales where mixing processes (such as larval dispersal, water circulation, and mobile herbivore grazing) tend to homogenize local variations. The spatially implicit framework allows us to focus on ecosystem-level dynamics without the computational complexity of spatially resolved models.

Our potential and flux field landscape theoretical framework offers considerable versatility and could be naturally extended to spatially explicit models in future research. We recognize the importance of spatial heterogeneity in coral reef ecosystems and in subsequent work, we plan to develop spatially explicit extensions of this framework. In recent work, we have shown that the framework can be extended to spatially explicit models (of vegetation dynamics) and hence it is a natural next step to leverage this progress to explore how the present results compare with EWSs in spatial extension of the coral reef model studied here:

J. Siu, W. Wu, D. D. Patterson, S. A. Levin and J. Wang, Revealing physical mechanisms of pattern formation and switching in ecosystems via landscape and flux, Advanced Science, accepted (2025) - arXiv:2412.03978.

Despite the simplifying assumptions of the mathematical model, our current framework provides valuable insights into the global stability of coral reef ecosystems and demonstrates the utility of landscape-flux theory for understanding complex ecological dynamics. The simplifications employed here serve as a necessary first step toward more comprehensive models that can incorporate the full complexity of coral reef systems \citep{Simon2018Corel,Scheffer2016Coralreefs}."

4. I was confused about the many different measures proposed, such as the free flux and the landscape flux and the intrinsic potential and the entropy production rate etc. These properties are calculated only in the results section without an explanation of what they are in normal words. Perhaps you can compile a table (in methods) with all these different concepts and add a non-technical explanation. I also don't understand how these measures relate to real-world systems.

Answer： We added a comprehensive table in the Table S1 (in Supplement zip) listing each measure (entropy production rate, potential landscape, flux, time irreversibility, etc.).

5. In extension, I don't understand how these early-warning signals are relevant for real coral systems. Since early-warning signals are only relevant in real systems, not in model systems, I think some explanation should be given with respect to the applicability of these early-warning signals.

Answer：

We agree that our paper could better clarify the practical applicability of the proposed early-warning signals. In our revision, we will include a new section specifically addressing how our landscape-flux approach could be implemented using real-world coral reef monitoring data. While the concept of landscape-flux is not entirely new, our application to coral-algae systems and the demonstration that these metrics provide earlier warnings than traditional methods represents a significant advancement.

We have added the following discussion to the Results section:

"Real-time ecological monitoring data from coral reef ecosystems presents an unprecedented opportunity to bridge theoretical frameworks with empirical validation. By integrating time-series data from reef monitoring stations—capturing coral cover, algal abundance, and environmental parameters—into our landscape-flux methodology, we can operationalize the theoretical results outlined above. In particular, the cross-correlation functions of the coral-reef ecosystem can be estimated directly from observed time series and hence we may calculate the average difference between forward and backward cross-correlation as an empirical EWS. Our framework thus provides practical early warning tools for policymakers and researchers, bridging the gap between abstract mathematical models and urgent conservation needs in threatened ecosystems."

6. In general, the reference to real-world systems is lacking for me. How does a gradual shift in g relate to the real systems for example? And in h? The noise is assumed to be uncorrelated between the three variables, but what would the noise relate to with respect to real systems? What do the different early-warning signals relate to in real systems? Perhaps you can add the latter to the table.

Answer：

The Ecological Interpretation of Parameters and Signals in Coral Reef Systems

g: The Grazing Parameter in Real Coral-Algae Systems

In the model, parameter g represents the grazing rate of macroalgae by herbivorous fish and invertebrates, a crucial ecological process with well-documented real-world counterparts. This parameter directly connects mathematical modeling to measurable ecological dynamics that reef managers can monitor and potentially influence.

Real-world factors affecting the grazing rate, g, include:
- Overfishing of herbivores (parrotfish, surgeonfish) decreases g
- Marine protected areas increase g as herbivore populations recover
- Disease outbreaks, like the 1983 Caribbean sea urchin die-off, reduce g
- Predator-prey dynamics influence g through trophic cascades

As g gradually decreases in real systems:
1. Algae gain competitive advantage over corals
2. System resilience weakens
3. Recovery becomes increasingly difficult after disturbances
4. At the critical threshold, even small herbivore loss triggers a shift to algal dominance

This mechanism explains ecological transitions observed on reefs, where reduced herbivory caused coral-to-algae phase shifts matching our bifurcation analysis predictions.

We added the discussion in the Result section as
"In the model, parameter \$g\$ represents the grazing rate of macroalgae by herbivorous fish and invertebrates, a crucial ecological process with well-documented real-world counterparts. This parameter directly connects mathematical modeling to measurable ecological dynamics that reef managers can monitor and potentially influence. Real-world factors affecting the grazing rate \$g\$, including overfishing of herbivores (decreasing \$g\$), establishment of marine protected areas (increasing \$g\$), disease outbreaks among key grazers like the 1983 Caribbean sea urchin die-off (reducing \$g\$), and predator-prey dynamics through trophic cascades. As \$g\$ gradually decreases in natural systems, algae gain competitive advantage over corals, system resilience weakens, recovery becomes increasingly difficult after disturbances, and eventually, at the critical threshold, even minor herbivore loss can trigger a shift to algal dominance. This mechanism explains ecological transitions observed on reefs, where reduced herbivory caused coral-to-algae phase shifts matching our bifurcation analysis predictions."

h: Coral Mortality Parameter and Environmental Stressors

Parameter h in our model corresponds to coral mortality rate, representing the combined effects of various environmental stressors that coral reefs face globally:

- Rising sea temperatures causing coral bleaching events increase h significantly during thermal anomalies
- Ocean acidification reduces calcification rates and weakens coral skeletons, gradually increasing h
- Pollution, sedimentation, and coastal development elevate h through direct physiological stress
- Coral diseases, which are increasing in frequency and severity worldwide, directly contribute to higher h values

These real-world stressors operate across different timescales, from acute (bleaching events) to chronic (acidification), mirroring our analysis of how gradual versus rapid parameter shifts affect system dynamics.

We added the following discussion to the Results section:

"Parameter h in our model represents coral mortality rate, encompassing the cumulative effects of diverse environmental stressors affecting reefs globally. These include rising sea temperatures that trigger coral bleaching events (significantly increasing h during thermal anomalies), ocean acidification that reduces calcification rates and weakens coral skeletons (gradually elevating h), pollution, sedimentation, and coastal development that impose direct physiological stress, and the increasing frequency and severity of coral diseases worldwide that directly contribute to higher h values. These real-world stressors operate across different temporal scales—from acute (bleaching events) to chronic (acidification)-which aligns with our analysis of how gradual versus rapid parameter shifts influence system dynamics and stability."

D: Ecological Interpretation of Noise Terms

The stochastic components in our model represent natural variability in ecological processes:
- Noise represents coral variability in recruitment success, storm damage, and bleaching intensity
- Noise represents fluctuations in growth rates due to nutrient pulses, seasonal changes, and storm disturbance
- Noise captures variability in colonization success and grazing pressure

While we model these noise terms as uncorrelated for analytical tractability, real environmental disturbances often affect multiple components simultaneously. For instance, storms impact all three variables in correlated ways. Our future work will explore how such correlation structures affect early warning signals.

We added the discussion in the Methods section as
"Environmental disturbances such as temperature fluctuations, storm events, and nutrient pulses simultaneously affect coral, algae, and algal turfs, introducing correlations in the noise structure of natural reef systems. While our potential landscape-flux framework remains theoretically valid for systems with correlated noise, we have chosen to use a diagonal identity matrix for G to maintain analytical tractability. This simplification allows us to focus on the core dynamics while avoiding the substantial increase in mathematical complexity that would result from incorporating non-zero off-diagonal elements to represent correlated noise effects \citep{Wang2015AP}. Future extensions of this model could incorporate these more realistic noise structures to further refine predictions of reef dynamics under stochastic environmental forcing."

Early Warning Signals in Monitoring Data

We added the discussion in the Result section as
"Real-time ecological monitoring data from coral reef ecosystems presents an unprecedented opportunity to bridge theoretical frameworks with empirical validation. By integrating time-series data from reef monitoring stations—capturing coral cover, algal abundance, and environmental parameters—into our landscape-flux methodology, we can operationalize the theoretical results outlined above. In particular, the cross-correlation functions of the coral-reef ecosystem can be estimated directly from observed time

series and hence we may calculate the average difference between forward and backward cross-correlation as an empirical EWS. Our framework thus provides practical early warning tools for policymakers and researchers, bridging the gap between abstract mathematical models and urgent conservation needs in threatened ecosystems."

7. You sometimes refer to transitions in the sense of a bifurcation when continuing in a parameter (mostly g, and then also h at the end), but sometimes you refer to noise-induced transitions. I got confused as to whereas the early-warning signals relate to bifurcations or noise-induced transitions.

Answer:
Thank you for highlighting the need for clarity regarding the types of transitions discussed in our manuscript.

We would like to clarify the distinction between two key transition mechanisms in our work:

Bifurcations with stochastic influences: Our primary analysis examines transitions driven by systematically changing the grazing rate parameter (g) in the presence of environmental fluctuations (noise). As g decreases below a critical threshold, the system undergoes a bifurcation, shifting from a coral-dominated state to an algae-dominated state. The presence of stochastic fluctuations can accelerate these transitions, causing the system to shift between alternative stable states before deterministic thresholds are reached.
Our landscape-flux framework specifically addresses these complex dynamics by quantifying how system stability evolves as parameter g approaches its bifurcation value under stochastic conditions. The framework captures subtle changes in both the potential landscape (representing the stability of alternative states) and probability flux (representing non-equilibrium dynamics).

Regarding parameter h (coral mortality rate), we examined how different fixed values of h modify the system's response to changing grazing pressure (g). Our results demonstrate how the critical threshold of g varies with different values of h, and importantly, how our early-warning indicators consistently detect the approach to these thresholds despite the changing parameter.

This comprehensive approach enables our framework to detect early warning signals in complex ecological systems where both parameter shifts and environmental fluctuations contribute to critical transitions.

8. Perhaps it would help a less technical reader if you'd present an equilibrium analysis of your essentially 2D system. The phase state could be in an appendix, and you could describe the equilibrium dynamics in words. Now, to my feeling, it jumps from the system to all these deduced properties such as the potential.

Answer:
Thank you for the valuable suggestions and we have added a section in appendix A

"Potential landscape and Local Stability Analysis of Equilibrium Systems

In equilibrium systems, the potential function or landscape is an essential tool for describing the stability of system states. For such systems, dynamics are completely determined by the potential landscape, with the system always evolving along the direction of decreasing potential energy until reaching a potential energy minimum. A key characteristic of equilibrium systems is the absence of non-zero probability flux, meaning the system satisfies detailed balance conditions, with zero net flow along any closed path being zero \citep{Wang2015AP,Ge2010PRE,Qian2006JPCB,Prigogine,VanKampen,Yeomans}.

Mathematically, the dynamic equation of an equilibrium system can be represented as a gradient system: $dx/dt = -\nabla U(x)$, where $U(x)$ is the potential function landscape. The system's steady states correspond to extremal points of the potential function, with minima representing stable equilibrium points and maxima representing unstable equilibrium points.

Local stability analysis is a method for studying the behavior of small perturbations near equilibrium points. By linearizing the dynamic equations around an equilibrium point, one obtains the Jacobian matrix characterizing the fluctuations. For equilibrium systems, this matrix is symmetric, and its eigenvalues completely determine the stability of the equilibrium point \citep{Prigogine,VanKampen,Yeomans}:
- All negative eigenvalues: stable node
- Presence of positive eigenvalues: unstable equilibrium point
- Presence of zero eigenvalues: potential bifurcation

The potential landscape of equilibrium systems visually demonstrates the global stability structure of the system, with low potential energy regions corresponding to states where the system is more likely to reside, while the height of potential barriers reflects the difficulty of state transitions. This analytical approach has wide applications in the study of physical, chemical, and biological systems."

9. More detailed comments are in the supplemented PDF.

Answer： We revised the manuscript according the comments in the supplemented PDF in the zip 'Figures and Tables and reply pdf'.

We believe these revisions will substantially improve our manuscript's accessibility while maintaining its scientific rigor. Your thoughtful review has highlighted important areas for enhancement that have genuinely strengthened our work. The revised manuscript now more effectively communicates the significance of our findings to the broader Earth System Dynamics readership while providing the technical details necessary for specialists to evaluate our approach.

We are profoundly grateful for your constructive feedback and the considerable time you have dedicated to reviewing our work. Your expertise and insights have been invaluable in refining both the presentation and substance of our research.

Thank you once again for your thoughtful commentary and guidance throughout this review process.

With sincere appreciation,

Li Xu, Chinese Academy of Sciences
Denis Patterson, Durham University
Simon Asher Levin, Princeton University
Jin Wang, Stony Brook University

Response to Reviewer 2's Comments

Dear Reviewer,

Thank you for your insightful review of our manuscript "Global Stability and Tipping Point Prediction of the Coral Reef Ecosystem." We appreciate your thorough assessment and constructive feedback. Please find below our responses to your comments and suggestions.

1. The paper introduces a method to approximate global stability in non-linear out-of-equilibrium systems, using as an example the case of coral reefs. The authors show that separating the gradient of the potential from the curl force serves as a proxy of changes in the basin of attraction, proposing another early warning for potential tipping points. Interestingly, their proposal seems to outperform other commonly used indicators such as the expected increase in autocorrelation and variance in critical slowing down.

Answer：
We sincerely appreciate your thoughtful evaluation of our manuscript. Your concise summary perfectly captures the essence of our work—separating the gradient of the potential from the curl force to approximate global stability in non-linear out-of-equilibrium systems, with coral reefs as our case study. We are particularly grateful for your recognition that this approach can serve as an effective early warning indicator for potential tipping points.

We are especially encouraged by your observation that our proposed method appears to outperform traditional critical slowing down indicators such as increased autocorrelation and variance. This comparison highlights the potential value of our landscape-flux framework for ecological management and conservation efforts.

2. One of the main contributions of the paper is the possibility of using the cross-correlation, entropy production rate, mean flow, or free energy as early warning given its performance with respect to critical slowing down. There are multiple disadvantages of critical slowing down, one of them is the fact that it only works with very low levels of noise [1]. Do you get equally good performances at higher levels of noise? It seems you're using small fluctuations (D ~ 10^-5). If not, at what signal to noise ratio does the warning disappear? I believe these considerations are important to better understand the applicability of your proposal to real world data.

Answer:
Thank you for raising this crucial point about the noise sensitivity of our early warning indicators, which is indeed central to their real-world applicability. We greatly appreciate your thoughtful consideration of this important limitation of critical slowing down indicators.

We have added the following discussion to our manuscript to address this important consideration:

" While the effectiveness of critical slowing down as early warning indicators is under low noise conditions, a critical question remains regarding their robustness under more realistic, higher noise scenarios. This consideration is particularly important given that traditional critical slowing down indicators are known to perform poorly with increased stochastic fluctuations\citep{hastings2010regime}. We conducted analyses systematically varying the noise magnitude from $D=1 \times 10^{-5}$ to $D=1 \times 10^{-2}$ (Figure \ref{fig4_EPRJD_in_h}A-J). Figure \ref{fig4_EPRJD_in_h} demonstrates how population entropy production rate EPR (A-E) and average flux $Flux_{av}$ (F-J) vary with grazing rate under increasing finite fluctuations. Our findings reveal that both EPR and average flux ($Flux_{av}$) maintain relatively robust performance as early warning signals up to $D=1 \times 10^{-2}$, beyond which signal reliability begins to deteriorate significantly. This represents a substantial improvement over conventional critical slowing down indicators, which typically lose effectiveness at high noise levels. The relative noise robustness of our framework likely stems from the fact that our indicators directly quantify system-wide properties reflecting global stability, rather than local temporal patterns that become increasingly masked by higher noise. " (Figure 4 in Supplement zip)

We have created a new Figure 4 A-J showing the behavior of our indicators across different noise intensities, with panels A-J illustrating how the sensitivity of EPR and $Flux_{av}$ changes with increasing stochastic fluctuations.

“Figure \ref{fig6_DDDD} A and D illustrate the average differences in cross-correlations over time, represented as \(\Delta CCM\) and \(\Delta CCC\), plotted against the grazing rate \(g\). These values provide insight into the dynamics of the coral-algae system, revealing how the interaction strength between states varies as grazing pressure changes. Figure \ref{fig6_DDDD} B and E display the relaxation times, \(\tau_{relaxM}\) and \(\tau_{relaxC}\), in relation to the grazing rate \(g\). The relaxation time quantifies how quickly the system responds to perturbations, serving as a crucial indicator of the stability of the Macroalgae and Coral states under varying conditions. Figure \ref{fig6_DDDD} C and F present the variances \(Var_M\) and \(Var_C\) as functions of the grazing rate \(g\). These variances reflect the degree of fluctuations within each state, highlighting how stability is affected as grazing pressure increases. It is noteworthy that for Figure \ref{fig6_DDDD}, the fluctuation strength is set at \(D=5.0\times 10^{-4}\), while for Figures D-F, the fluctuation strength increases to \(D=1.0\times 10^{-3}\), with a fixed height parameter of \(h=0.44\). This variation in \(D\) is expected to have a significant impact on the observed relationships, further illustrating the delicate balance between grazing intensity and the stability of the coral-algae ecosystem. We observe that while increasing noise can also serve as an indicator for predicting state transitions, its predictive effectiveness diminishes relative to the performance observed at lower noise levels.” (Figure 6 in Supplement zip)

We have created a new Figure 6 (Figures in Supplement zip) showing the behavior of indicators across different noise intensities D=5*10^-4 and D=10^-3, with panels A-F illustrating how the sensitivity of the average differences in cross-correlations over time, the relaxation times and the variances change with higher levels of noise. We observe that while increasing noise can also serve as an indicator for predicting state transitions, its predictive effectiveness diminishes relative to the performance observed at lower noise levels. Specifically, our analysis reveals that elevated noise in certain ranges in the system can trigger warning signals that precede critical transitions between ecological states.

This visual representation clearly demonstrates both the strengths and limitations of our approach under various noise scenarios, providing valuable guidance for potential applications to empirical data.

Thank you again for this insightful suggestion, which has substantially strengthened our manuscript by providing a more nuanced understanding of the practical applicability of our proposed early warning indicators.

Specific comments

3. - Methods: I know the coral reef model used has only two stable states for simplicity. But I think is fair with the reader to point out some of the empirical work that has shown more attractions, up to 6 if I remember correctly: hard corals, turf algae, macro algae, soft corals, coralimorpharians, urchin barrens. See refs 2-3 for examples.

Answer：

Thank you for your insightful comment regarding the complexity of stable states in real coral reef ecosystems. You raise an excellent point that empirical research has demonstrated the existence of multiple alternative stable states beyond the two-state model we employed.

In response to your suggestion, we have substantively revised our Methods section to acknowledge this important ecological reality. We now explicitly discuss that coral reef ecosystems can exhibit up to six distinct stable states as documented in the literature: hard corals, turf algae, macro algae, soft corals, coralimorpharians, and urchin barrens (as noted in references [2] and [3]). This provides readers with a more complete ecological context for interpreting our results.

We have also added text explaining our methodological choice:
"Coral reef ecosystems can exhibit up to six distinct stable states as documented in the literature: hard corals, turf algae, macroalgae, soft corals, coralimorpharians, and urchin barrens \citep{jouffray2015identifying,norstrom2009alternative}. While a more complex model incorporating all six states would better reflect ecological reality, we adopted a simplified two-state approach to facilitate analytical tractability while still capturing the fundamental bistable dynamics characteristic of critical transitions. This simplification enables us to clearly demonstrate the utility of our landscape-flux framework while maintaining mathematical accessibility. Additionally, our approach could potentially be extended to higher-dimensional systems with multiple stable states in future research, acknowledging both the limitations of our current model and opportunities for further development."

These revisions have significantly improved the ecological grounding of our manuscript while maintaining its theoretical focus. We greatly appreciate your recommendation, which has enhanced both the scientific accuracy and broader relevance of our work.

4. - Fig 5. Are the units of the colour bar always as x 10^-3? If so add the scale to all insets. In any case, why si the variation of the scale differs so widely across a, b and c?

Answer:
Thank you for your astute observation regarding the color bar units in Figure 5 (now Figure 3 D,E,F in our revised manuscript) (Figures in Supplement zip). We appreciate your careful examination of these details, which has helped us improve the clarity of our presentation. You are absolutely right that the units should be clearly indicated for all panels.

The scales vary considerably across panels - the scale in Figure 5A (now Figure 3D) is (× 10^-3), while in Figures 5B and 5C (now Figures 3E and 3F), the scale is (× 1). Thus, the color bar for them is correct.

We added the discussion in the Result section as:
"The substantial difference in magnitude of color bar units reflects the fundamentally different metrics being visualized: Figures 3D represents the intrinsic potential landscape derived from the Hamilton-Jacobi equation with zero limit fluctuations, whereas Figures 3E and Figures 3F show the population potential landscape from the Fokker-Planck equation with finite fluctuations. These inherent mathematical differences naturally produce different numerical ranges."

5. ## References
[1] www.doi.org/10.1111/j.1461-0248.2010.01439.x
[2] www.doi.org/10.1098/rstb.2013.0268
[3] www.doi.org/10.3354/meps07815

Answer:
We sincerely appreciate your suggestion and have incorporated the three valuable references you mentioned. These citations significantly enhance our manuscript by providing important context and supporting evidence for our arguments.

Thank you for bringing these relevant works to our attention.

(1) Alan Hastings and Derin B. Wysham, Regime shifts in ecological systems can occur with no warning, Ecology Letters, (2010) 13: 464–472

(2) Jean-Baptiste Jouffray, Magnus Nyström, Albert V. Norström, Ivor D. Williams, Lisa M. Wedding, John N. Kittinger and Gareth J. Williams, Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago, Philosophical Transactions of the Royal Society B, (2015) 370: 20130268

(3) Albert V. Norström, Magnus Nyström, Jerker Lokrantz and Carl Folke, Alternative states on coral reefs: beyond coral–macroalgal phase shifts, Marine Ecology Progress Series, (2009) 376: 295-306

We believe these revisions will substantially improve our manuscript's accessibility while maintaining its scientific rigor. Your thoughtful review has highlighted important areas for enhancement that have genuinely strengthened our work.

Sincerely,

Li Xu, Chinese Academy of Sciences
Denis Patterson, Durham University
Simon Asher Levin, Princeton University
Jin Wang, Stony Brook University