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Review

Beyond the mean: adaptive variability in Amazonian aquatic systems

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Conventional ecological and conservation approaches often rely on average-based strategies, which obscure the complexity of biological systems. This article revisits the concept of the 'Tyranny of the Golden Mean' to argue that variability and plasticity are not sources of disorder, but essential components of ecological robustness, particularly in the Amazon. The Amazon's extraordinary heterogeneity shapes physiological, biochemical and genetic diversity. At genetic, biochemical and physiological levels, Amazonian aquatic species exhibit resilience, enabled by traits like low oxygen tolerance, metabolic flexibility and microanatomical adaptations. Examples span to amphibians, reptiles, aquatic insects and floodplain trees, illustrating that such adaptive strategies are widespread across taxa. These responses are context-specific and often missed by average values. As environmental changes intensify, conservation strategies based on means become insufficient. Recognizing variability is essential, as it underpins resilience to rapid environmental changes. We advocate for adaptive management, in which biological variability is recognized as a source of strength rather than noise. This approach enables the identification of critical thresholds and tipping points, enhancing the capacity to anticipate and respond to disruption. Ultimately, embracing variability improves conservation effectiveness and aligns with the evolutionary and ecological realities of the Amazon.

This article is part of the theme issue 'Embracing variability in comparative physiology: why it matters and what to do with it'.

1. Introduction

Biology relates to variation and variability. Life on the planet assumes its contemporary form through the diversification of strategies at all levels of organization. This diversification has enabled organisms to thrive in diverse environments and may help explain the potential for life on other planets. However, diversity is often described only in terms of means and deviations, oversimplifying the true complexity of organisms and ecosystems. As noted by Hochachka [1], this 'paradox of uniqueness-diversity' highlights how basic biochemical structures are conserved across species, yet evolution has produced remarkable diversity in survival strategies. In the Amazon, this paradox is clearly evident, owing to the remarkable environmental and biological variability that defines the biome.

The Amazon has long been referred to as an 'under-explored biological gold-mine' [2]. The tropical Amazon rainforest is one of the most abundant and highly complex systems worldwide for climate regulation, carbon storage and biodiversity maintenance. It spans about 5.5 million km² over nine nations in South America and shelters nearly 10% of all species known to humans. It also holds one of the largest freshwater reserves globally [3]. Given the depth of ecological and physiological studies available, this manuscript focuses primarily on Amazonian fishes as a model group to illustrate how

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biological variability underpins adaptation and resilience. While other aquatic organisms are also diverse, fishes provide the clearest and most comprehensive evidence for the arguments presented here. Beyond biological diversity, climatic, edaphic and hydrological variations also shape the structure and function of Amazonian ecosystems [4].

Aquatic systems of the Amazon, such as rivers, floodplain lakes and igarapés, are extremely dynamic, influenced by seasonal and regional factors. The annual flood pulse, with high- and low-water periods, shapes aquatic ecology and species distribution, enabling unique physiological adaptations in biotic communities [5,6]. Rising floodwaters cover large forest areas, creating resource-rich habitats that attract fishes and other aquatic organisms. On the other hand, during the dry season, shrinking aquatic habitats bring extreme conditions, hypoxia and altered water composition, demanding rapid metabolic adjustments for aquatic fauna survival [7,8].

Among Amazonian aquatic organisms, fishes represent a particularly informative group for exploring physiological and ecological variability. Their high diversity, widespread distribution across environmental gradients and the availability of comparative physiological data make them a compelling model for illustrating adaptive responses to dynamic environments. While fishes serve as the primary examples, other taxa are also included, where relevant, to broaden the ecological context.

Ecological variability in the Amazon operates across multiple spatial and temporal scales, shaping the distribution and adaptive responses of species in both terrestrial and aquatic environments. For example, soil heterogeneity and moisture gradient influence plant diversity, which in turn conditions faunal composition. In aquatic systems, the extreme seasonality of flood and drought cycles drives the structure and dynamics of aquatic communities [6,9,10]. The annual hydrological cycle is one of the main drivers of variability in Amazonian aquatic systems that regulates habitat connectivity and promotes organism migration in search of resources and areas suitable for reproduction and development [10].

The fishes of the Amazon provide stark evidence of the diversity of evolutionary strategies shaped by environmental variability. Most species show physiological and metabolic adjustments that enable them to survive under extreme hypoxic, thermal and chemical conditions in water [7,8]. Amazonian rivers show a marked contrast in their physicochemical characteristics: whitewater rivers are highly turbid and nutrient-rich, blackwater rivers have low-ionic content and are acidic (pH 3.5–5) and clearwater rivers are highly transparent but nutrient-poor [11]. Such distinctions result in unique patterns of physiological specialization for osmotic and respiratory challenges in aquatic biota, leading to different patterns of species replacement [12].

Hypoxia-tolerant Amazonian fishes such as *Prochilodus nigricans* and *Astronotus ocellatus* show quick adaptive responses by changing blood parameters and ion fluxes to maintain homeostasis in low oxygen waters [7,8]. Thermal fluctuations across the hydrological cycle affect metabolic regulation in fishes. Recent studies have found that acclimation to constant and cycling temperatures elicits different responses, indicating the plasticity of physiological mechanisms required in a highly dynamic environment [13]. Such plasticity is probably underestimated when assessed solely by means values and s.d.

The effect of climate change on Amazonian variability is a major concern. Changes in floods and droughts, with rising temperatures and extreme climate events, threaten the integrity of aquatic ecosystems [14]. Some types of terra-firme stream-inhabiting species are already living very close to their upper thermal limits [15]. Water temperature increases reduce sperm viability and motility in *Colossoma macropomum* [16], as well as larval and juvenile skeletal development [17]. Additionally, events such as El Niño have triggered unprecedented fish mortality, signalling potential ecological collapse [18].

The thesis of the current study is that, given the conditions of Amazonian aquatic ecosystems, recognizing and studying organismal variability in ecological context is essential for developing effective conservation strategies. In other words, without the incorporation of variability into ecological models, species distribution and adaptation issues are likely to be masked, hindering the conservation of Amazonian biodiversity.

For the refinement of predictive models and adaptive management strategies, it is important to understand the interaction between environmental factors and the physiological responses of fishes and other Amazonian organisms. Ecological variability should not be seen as an obstacle to conservation but rather a key aspect that should be integrated into environmental policy directed towards the Amazon to make the approach more effective and apt in that particular context.

This study examines the significance of variability in Amazonian aquatic systems, showing how understanding the diversity of physiological and ecological adaptations can help make environmental policies more effective through robust science and alignment with regional realities.

2. The concept of variability in ecological contexts

Ecological variability is not just a secondary feature of natural systems; it is a fundamental principle that directs and controls biodiversity, the structure of ecosystems and evolutionary processes. Recognizing variability as central to biological systems, ecological theory provides several frameworks to explain how this dynamic element shapes life.

One of the most influential concepts is the 'intermediate disturbance hypothesis' [19], which proposes that species diversity peaks at intermediate disturbance levels: low disturbance allows competitive exclusion to dominate, while high disturbance causes frequent local extinctions. Similarly, ecological resilience theory [20] highlights the ability of an ecosystem to absorb disturbances and return to a stable state without collapsing into a qualitatively different system. This capacity is grounded in physiological and biochemical adjustments that enable survival under fluctuating environmental conditions.

However, traditional ecological approaches have often relied on means and s.d. as primary descriptors of ecosystems. In recent years, this has led to what has been described as the 'Golden Tyranny of the Mean' [21], where assessments obscure meaningful variability, particularly at the extremes of the distribution, where adaptation, failure and innovation occur.

In this context, we identify three primary dimensions of variability relevant to Amazonian systems: (i) environmental variability—spatial and temporal changes in abiotic conditions (e.g. temperature, oxygen, pH); (ii) physiological/biochemical variability—differences in individual responses to environmental fluctuations; and (iii) genetic variability—standing genetic variation that underpins adaptive capacity and evolutionary potential.

In systems such as the Amazon, where factors vary greatly across space and time, variability is not an exception but the rule. Overlooking this complexity may lead to mistakes in understanding the environment and, as a result, misguided efforts in conservation. Therefore, a model has to adopt a paradigm viewing variability as a message, not just noise in the numbers, a message that is increasingly recognized in climate resilience science ([14,22]; figure 1).

(a) Impact on understanding physiological adaptations

The Amazon rainforest harbours a vast diversity of organisms with highly specialized physiological adaptations that enable survival in varied and often extreme habitats. However, analyses that rely on only average values frequently mask the biological complexity and underestimate adaptive potential.

Among aquatic organisms, Amazonian fishes exhibit particularly well-documented physiological strategies to cope with environmental stressors, including increased gill surface area, enhanced haemoglobin–oxygen affinity, altered ventilation patterns and metabolic suppression under hypoxic conditions [5,23]. Additionally, many Amazonian species possess unique adaptations: vascularized swim bladders, cutaneous and gut-based respiration and buccal air use that enable survival in extreme oxygen-depleted waters. Air-breathing fishes such as *Hoplerythrinus unitaeniatus* and *Arapaima giga*s epitomize these anatomical and physiological specializations, allowing them to thrive under hypoxia. These traits are highly plastic, varying not only between species but also within individuals according to developmental stage, habitat and diel or seasonal conditions [8,24]. Such flexibility is masked when only mean trait values are considered, overlooking critical intraspecific and inter-individual flexibility.

Floodplain tree species, similarly, show distinct physiological strategies to withstand seasonal flooding, including development of specialized root systems, hypertrophied stems and anaerobic metabolic capacity [25]. These traits reflect differing tolerance hierarchies and survival strategies across taxa and environments, patterns which are often hidden when variability is collapsed into population-level averages.

(b) Integrating variability into conservation and management

Failure to fully consider physiological acclimation may lead to inaccurate assessments of species' resilience and adaptive capacity. Conservation strategies based on average trait values risk overlooking vulnerable populations and critical adaptive traits that buffer species against environmental change. This is particularly relevant under climate change and anthropogenic pressures, where extremes, rather than averages, are often better predictors of survival or population collapse [14,22].

Recognizing variability as a fundamental feature of ecological systems is essential not only for advancing scientific understanding but also for developing robust, context-sensitive conservation policies. As climatic instability intensifies, ecological models and management frameworks must transition from average-centred paradigms to variability-focused approaches that address multiple levels of biological organization (table 1).

3. Environmental dynamics in the Amazon rainforest

Environmental variability in the Amazon is not a minor feature of its ecosystems. It is a major ecological force that structures and shapes all of ecology and relates to biological adaptation. Such variability occurs at multiple spatial and temporal scales, including marked intra-annual and interannual fluctuations in key environmental parameters such as precipitation, temperature, dissolved oxygen and pH. In aquatic environments, variability is especially pronounced, shaping the ecological challenges species face. For Amazonian fishes and other aquatic organisms, environmental variation is not merely a backdrop for evolution; it is the very context in which specific physiological and biochemical changes are selected and maintained over time ([23,26]; figure 2).

This is most evident in the hydrological cycle that dynamically alternates periods of floods and dryness. These 'pulse dynamics', the predictable seasonal alternation between high-water and low-water periods, reshape habitats by altering oxygen availability, ion concentration, water temperature and the distribution of resources [9,10]. Most ecological studies try to capture system dynamics through such average measurements as mean temperature, mean dissolved oxygen and mean pH; although organisms do not live in average conditions, they exist under extreme conditions and fluctuations. Short-term peaks, troughs and transitions often exert stronger physiological influences than long-term averages, and these extremes are often more closely tied to survival and reproduction than the mean values [14].

In such environments, Amazonian fishes must develop multiple physiological strategies to cope with stressors arising from local conditions, notably low oxygen levels during the dry season, a state most pronounced in some small tributaries and floodplain lakes. For example, hypoxia tolerance may involve increased gill surface area, modulation of haemoglobin–oxygen affinity through changes in red blood cell allosteric effectors and enhanced anaerobic metabolic capacity [5,23,28]. These traits are expressed variably according to the day and season and represent a finely tuned phenotypic plasticity that cannot be understood by a static or average physiological assessment [7].

Changes in temperature also affect metabolic performance. Most Amazonian fish species are found in shallow waters, where daily thermal amplitudes may exceed 6–8°C, especially during the low-water season [15]. Recent studies have found that fishes

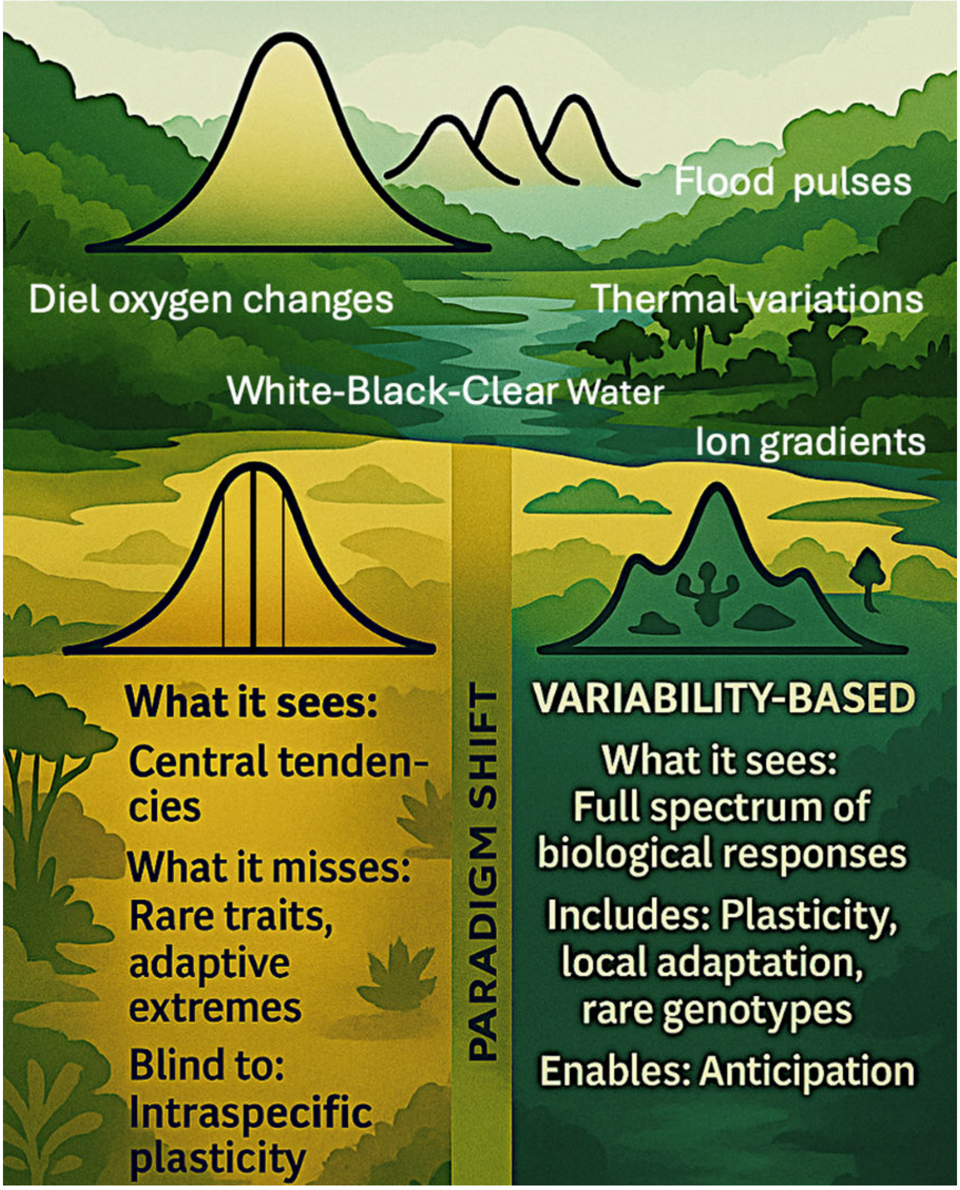

Figure 1. From the mean to the variability—contrasting paradigms in conservation under Amazonian environmental dynamics. Conceptual schematic generated with ChatGPT from author-specified prompts. It contrasts a mean-centred paradigm that prioritizes central tendency with a variability-aware paradigm that treats distributional properties (variance, tails, multimodality) and phenotypic/genetic plasticity as decision-relevant. By emphasizing the full response distribution and standing variation, the variability-aware view enables anticipatory and robustness-oriented conservation under non-stationary hydroclimatic regimes.

exposed to constant and daily changing temperatures use different metabolic pathways. They also show different strategies for energy allocations and mitochondrial efficiency changes [13]. Such thermal adjustments interact with oxygen availability, reflecting the multi-layered and integrated nature of physiological responses to environmental variability across diverse aquatic taxa, not only in fishes.

Fishes favour anaerobic metabolic pathways by increasing the activity of enzymes, such as lactate dehydrogenase and alcohol dehydrogenase, and by modulating ion transport proteins in the gill epithelium in response to hypoxic or acidic conditions, which are common in blackwater environments [7,23]. In such environments, these adjustments occur in response to extreme and variable conditions rather than to mean values, with documented changes including up to approximately 35% variation in haemoglobin P_{50} and measurable shifts in mitochondrial efficiency and enzyme activity [7,8,13]. Some species, including *A. ocellatus*, exhibit these responses within hours, reflecting their exceptional biochemical plasticity under environmental stress [8]. Other species of fish, which inhabit ion-poor and low-pH water (pH 3.5–5), use a combination of an increased density of chloride cells and activities of membrane transporters to maintain osmotic homeostasis despite sharp water chemistry gradients across terra-firme streams, várzea and igapó ecosystems [6,11].

This plasticity is most important in shift zones, like links between blackwater and whitewater systems or stream-floodplain borders, where conditions are more varied and less certain [26,29]. In such zones, many species show unique physiological flexibility shaped by an evolutionary history of adaptation to unstable habitats, often hidden by generalized traits and averages that fail to capture the full range of all levels of biological responses across environmental gradients.

Nutrient and moisture gradients from west to east and northwest to southeast, respectively, impose ecological regimes on fish assemblages [30,31]. Selective pressures on energy metabolism, growth performance and reproductive timing are imposed by these gradients. For instance, the variation in somatic growth and metabolic scaling relationships among populations of

Table 1. Variability-aware conservation indicators across biological levels: definitions, units, relevance and taxon applicability. (Both, animals and plants; Ne, effective population size; GSH : GSSG, reduced glutathione (GSH) : oxidized glutathione (GSSG)—the glutathione redox ratio; TBARS (MDA), thiobarbituric acid–reactive substances commonly reported as malondialdehyde (MDA) equivalents; LDH : CS, lactate dehydrogenase/citrate synthase; HSP70, heat-shock protein 70; CT_{max}, critical thermal maximum; TSM, thermal safety margin; ARR, acclimation response ratio; $T_{max,env}$, maximum environmental/operative temperature; AAS, absolute aerobic scope; $T_{opt,\ AAS}$, optimum temperature for aerobic scope; MMR, maximum metabolic rate; SMR, standard metabolic rate; P_{crit}, critical O_2 tension; F_v/F_m, maximum quantum yield of PSII photochemistry; PSII, photosystem II; $T_{50}(F_v/F_m)$, temperature at 50% loss of F_v/F_m; A_{net}, net CO_2 assimilation rate; g , stomatal conductance (to water vapour); R_d, dark respiration rate; ETR, electron transport rate (through PSII); Ψ_{50}, xylem water potential at 50% loss of hydraulic conductivity.)

biological level	indicator	operational definition	ecological relevance (brief)	taxa
genetic	allelic richness; heterozygosity; Ne	population genetic indices	baseline adaptive capacity; detection of genetic erosion	both
genetic	genetic endemism	% of unique lineages; private alleles	spatial prioritization for conservation units	both
biochemical	GSH : GSSG (glutathione redox ratio)	molar ratio	acute stress buffering; resilience to oxidative peaks	both
biochemical	protein carbonyls; TBARS (MDA)	damage markers	cumulative damage under extremes; functional failure risk	both
biochemical	Na^+/K^+-ATPase activity	enzyme activity	osmoregulatory tolerance (pH/ion gradients)	animals
biochemical	LDH : CS ratio	enzyme ratio	anaerobic versus aerobic bias (hypoxia/temperature response)	animals
biochemical	HSP70 induction temperature (T_{onset})	°C	early warning of thermal stress; plasticity signal	both
physiological	CT_{max} (paired with TSM and ARR)	°C	thermal limit; compare to environment for risk	animals
physiological	thermal safety margin (TSM = $CT_{max} - T_{max,env}$)	°C	proximity to collapse during heat waves	animals
physiological	aerobic scope (AAS) and $T_{opt,\ AAS}$	MMR—SMR; °C	functional performance across temperature	animals
physiological	P_{crit}	mg O_2 L^{-1} (or kPa)	hypoxia tolerance; spatial predictor in low-O_2 habitats	animals
physiological	F_v/F_m (PSII) and $T_{50}(F_v/F_m)$	fraction; °C	photosynthetic integrity and thermal tolerance	plants
physiological	A_{net}, g_s, R_d, ETR	µmol m^{-2} s^{-1}	carbon/water use; thermal and drought stress	plants
physiological	Ψ_{50} (xylem vulnerability)	MPa	hydraulic failure risk; drought tolerance	plants
behavioural and ecological	reproductive success under extremes	rates, viability	demographic consequence of acute events	both
behavioural and ecological	habitat use along gradients	time under hypoxia, microhabitats	microrefugia use; connectivity and exposure	animals

Serrasalmus rhombeus is related to individual physiological variability across spatial contexts [32]. Similarly, such selective pressures may be imposed at the biochemical level by thermal stress, hence impacting reproductive processes and, in this way, impairing sperm motility and viability in *C. macropomum* [16], larval development through skeletal deformities and altered enzymatic activity patterns [17].

As emphasized by Encalada *et al.* [26], the health and resilience of Amazonian freshwater ecosystems rely critically on ecological connectivity and environmental heterogeneity, both of which support physiological and biochemical diversity. When this variability is disrupted by habitat fragmentation, flow regulation or climate-driven homogenization, the adaptive capacity that sustains biodiversity is severely compromised.

(a) Masking biochemical diversity

Besides their morphological and physiological traits, Amazonian organisms develop substantial biochemical adjustments that are strongly influenced by environmental variability. From the production of metabolites to the regulation of enzymes, these biochemical characteristics play a vital role in survival, ecological interactions and adaptive flexibility. Yet they are often expressed in response to extremes and fluctuations, not to average environmental states, and therefore are frequently overlooked in ecological assessments.

Biochemical diversity is a cornerstone of defence strategies in plants. Secondary metabolites such as alkaloids, terpenoids, phenolics and flavonoids form chemical arsenals of increasing complexity against herbivores, pathogens and competitors. These compound varieties are expressed not only in inter-specific dimensions; stark variations manifest within species across environmental gradients, developmental stages and stress exposure. Such variation is driven by local ecological pressures

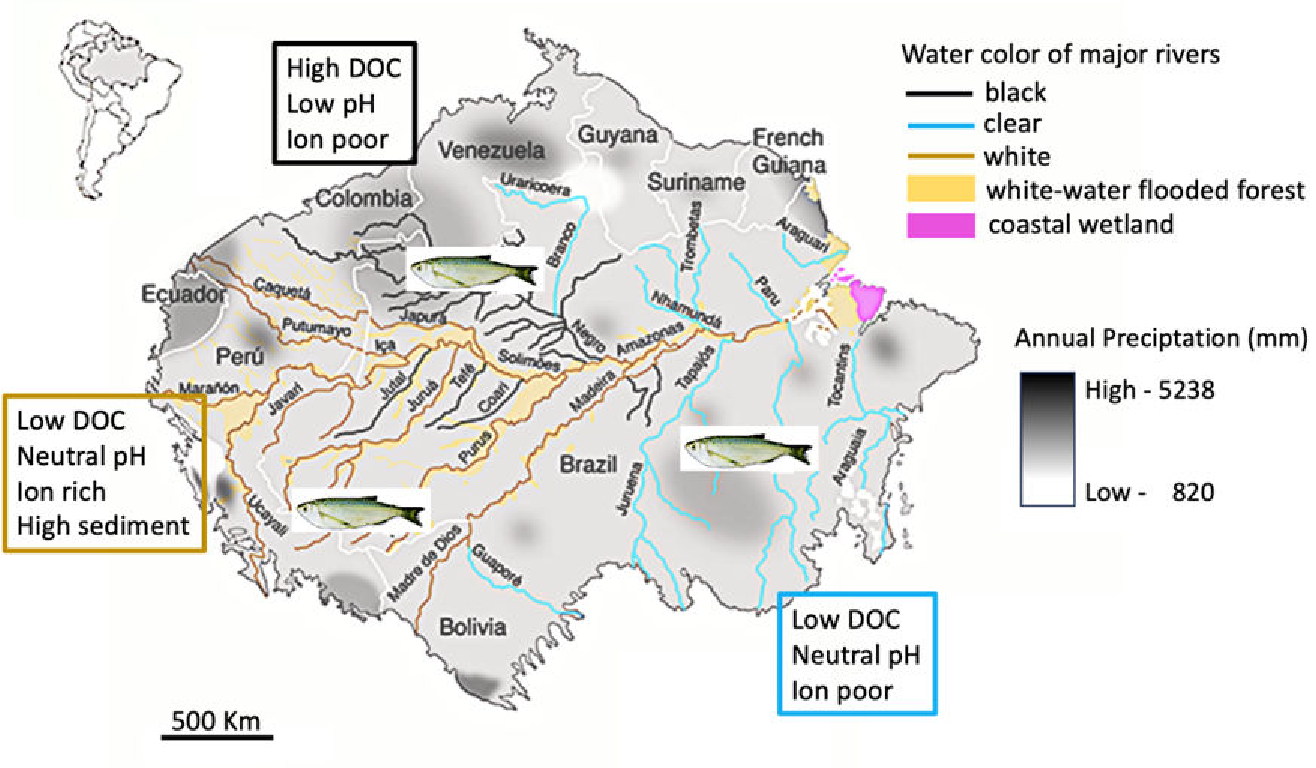

Figure 2. Major river systems of the Amazon Basin categorized by water colour and associated physicochemical properties (modified from Junk *et al.* [27]). Grey shading represents the annual precipitation gradient. The fish species *Triportheus albus* is found across all three water types. Its wide ecological distribution is enabled by differential gene expression, allowing physiological adaptation to distinct water chemistries [24].

and co-evolutionary dynamics and is mostly overlooked by trait-based ecological models that work on average compound concentrations [33,34].

Animals show complex biochemical adaptations as well. Amphibians and reptiles in the Amazon produce unique skin secretions, which can be quite complex, and may have peptides, alkaloids and toxins that are antimicrobial, neurotoxic or even deterrent. These compounds vary enormously between populations and can be influenced by the type of habitat, diet and ecological pressures. In fishes, biochemical adjustments range from modulation of enzymes to detoxification pathways and antioxidant responses that are governed by ambient water chemistry and temperature variability [7,8]. These biochemical traits are key to coping with environmental variability, yet most ecological surveys still rely on structural descriptors and fail to incorporate molecular complexity, which ultimately determines adaptive strategies in Amazonian biota.

(b) Biochemical and physiological variability as a foundation for ecological stability

Oversights of biochemical and physiological variation lead to misrepresentations in ecological models of species' resilience and adaptive capacity. When models rely on trait averages, they risk obscuring the critically important role of locally adapted populations and plastic phenotypes, as well as the transitory nature of their habitats. This reliance would risk homogeneity over heterogeneity, making it imperative to avoid overly simplistic, parameter-based ecosystem protection measures that ignore the very features enabling ecosystems to function.

In a rapidly changing climate, protecting biochemical and physiological diversity is not an academic exercise; it is essential for maintaining ecological processes and evolutionary potential. Functional redundancy, defined as the presence of multiple species performing similar ecological roles, provides adaptive buffering against species loss in variable environments [35], a trait that statistical means tend to conceal. By incorporating physiological and biochemical variability into ecological theory and conservation practice, we can better safeguard not only ecosystem structure but also the dynamic processes that sustain Amazonian biodiversity.

4. Impact on understanding genetic diversity

(a) Limitations in genetic studies

The use of within-population mean genetic values in diversity estimators has increasingly been criticized for hiding the actual extent of genetic variation within real populations. In the Amazon, this simple form of statistical aggregation masks the complex genetic architecture that underlies species' ability to respond to environmental pressures. Methods based on means often do not capture allelic diversity, particularly rare alleles that may be important evolutionary reserves in rapidly changing ecological conditions [36,37]. This is particularly relevant for the highly heterogeneous landscapes in the Amazon, where fine-scale environmental gradients enforce genetic structure even at a fine spatial scale [6,38,39].

Additionally, a focus on mean genetic characteristics may leave out adaptive outliers, that is, individuals or subpopulations bearing genes that give resistance to particular environmental pressures. These uncommon forms are usually on the outside of the genetic grouping but could be crucial to survival during abrupt changes in climate or exposure to pathogen stress [40]. As pointed out by Turner *et al*. [41], not including these genetic peculiarities in models of evolutionary change does not just lower the strength of conservation strategies but also impairs the capacity to forecast ecosystem responses to future scenarios.

The overlooking of within-population diversity has also been associated with a low count of the Amazon's likelihood to reach evolutionary tipping points, critical levels over which evolutionary directions change irreversibly. Just as Nobre *et al*. [42] and Ferrante *et al*. [43] noted, ongoing deforestation plus climatic pressures push Amazonian systems to such thresholds. Thus, genetic diversity will not be able to buffer the collapse of ecosystems. This underlines the need for addressing genetics with urgency, especially when temporal shifts in means become more and more linked with evolutionary dynamics.

(b) Beyond averages: conserving the full spectrum of genetic diversity

These methodological shortcomings have deep implications for conservation biology. Plans based on mean genetic statistics are essentially not suited to protect the complete adaptive potential of species. Conservation groups defined by typical measurements are likely to leave out genetically different subpopulations, which may be essential for the sustainability of the species under such climate insecurities [44,45]. As pointed out by Bellard *et al*. [46], to keep only these genetic middle values weakens the evolutionary capacity required to deal with these new ecological changes.

Also, if conservation planning ignores genetic outliers, it leads to what some authors have called adaptive erosion, the gradual loss of rare yet important alleles from the evolutionary framework [40]. In simple terms, this may indicate the conservation of large populations that look strong by common measures but, in reality, are weak in terms of genes and do not have good abilities to adjust to rapid changes in the environment.

New frameworks guide the integration of phylogenetic and functional trait diversity into conservation planning as proxies for genetic breadth and evolutionary potential [45,47]. These provide a more granular look to assess conservation priorities, especially in megadiverse systems like the Amazon, where ecological functions relate strongly to genetic heterogeneity. Finally, improving genetic conservation in the Amazon calls for a conscious turn from mean-centric models towards strategies that acknowledge and sustain the whole extent of genetic variability, even its rarest and most spatially restricted expressions.

Apart from genetic erosion, rapid changes in the environment, for example, because of climate change, could act as strong evolutionary forces that drive changes to tipping points not only towards collapse but also in the selective shaping of population trajectories. In populations wherein genetic traits are normally distributed, the impact of selective environmental pressure could be disproportionately borne by extreme classes of traits, hence selecting against rare or previously neutral genotypes. Such selection does not result in a general decline but acts to promote an adaptive redirection, driving the increase in frequency of certain genetic variants and the opening up of new evolutionary pathways [40,41]. Such a process would enhance the short-term resilience of the population but would also erode the genetic base, thus increasing vulnerability in the long term to further disturbances. In Amazonian ecosystems, where local adaptation is shaped by fine-scale environmental gradients, it is possible that these dynamics will further induce divergence among the populations, consequently bringing in their wake new evolutionary lineages or changed adaptive baselines [48,49]. The recognition of this dual potential, both as a threat and as a driver of evolutionary transformation, is key to the anticipation of biodiversity responses in the Anthropocene.

5. Implications for conservation strategies

The Rio Negro constitutes a critical reference site for Amazonian conservation, where ecological modelling should shift towards dynamic approaches that account for environmental heterogeneity and its biological consequences. Current conservation-relevant models, including species distribution models, trait-based assessments and phylogenetic diversity frameworks, typically aggregate population-level traits or use mean environmental conditions as inputs, approaches that risk obscuring locally adapted phenotypes and physiological extremes critical for survival. Traditional static models, often based on population averages, fail to capture the fine-scale variability that defines species' physiological and ecological responses. Although mean-based analyses offer statistical simplicity, they obscure the true scope of biochemical, physiological and behavioural plasticity that underlies ecosystem resilience. In highly variable tropical systems, such as the Rio Negro basin, it is the range and plasticity of responses, not central tendencies, that determine adaptive capacity and persistence.

For example, unexpected fish die-offs during the 2023 Amazon drought occurred when hydrological and thermal thresholds were exceeded, conditions not predicted by average-based models, which failed to capture localized extremes. Field observations conducted during a recent expedition to Lago do Prato, in the Anavilhanas Archipelago, shortly after a delayed rainy season, revealed a markedly depauperate aquatic system, probably resulting from preceding drought and lag-phase hydrological conditions. Although initial assessments indicated high species richness, overall abundance was substantially reduced. Subsequent surveys, performed under normalized hydrological conditions, documented a striking recovery in both species richness and population density. These findings underscore the often-overlooked latent resilience embedded within aquatic communities, emphasizing the importance of incorporating variability and dynamic environmental feedback into conservation models and policies and the need to integrate physiological thresholds (e.g. $\mathrm{CT}_{\mathrm{max}}$, oxygen affinity, metabolic scope) as early warning indicators in spatially explicit planning frameworks.

(a) Oversimplification of ecosystem complexity

Use of average-based ecological indicators may not present a proper picture of the actual individual experiences. For instance, regional average deforestation might reflect apparent stabilization, but actual specific sectors within these regions continue to experience strong ecological stress. Such localized stress often arises when environmental thresholds are exceeded, events that average-based indicators fail to predict, leading to unexpected mortality or reproductive failure. This stress, in turn, reflects site-specific physiological acclimatization, for example, fish populations experiencing thermal stress increasing their metabolic rates, or seasonal hypoxia enhancing anaerobic pathways.

Species such as *P. nigricans* and *A. ocellatus*, among Amazonian fishes, show quick upregulation of haemoglobin–oxygen affinity and ion regulatory proteins in hypoxia [7,8], as mentioned above. Such use of average oxygen levels in a watershed is the weak link when it comes to assessing conservation status. This is because microenvironmental stressors cannot be captured by this average parameter, nor by their induced biochemical responses, highlighting the need to incorporate physiological and biochemical variability metrics into conservation modelling.

This is true for plant communities as well. Their species-specific physiological tolerance for factors like inundation, soil acidity or nutrient limitation most often remains unobserved beneath some ecosystem-level average. For example, alkaloids and phenolics, ecologically important biochemical defence mechanisms, exhibit great variability along gradients but, for the most part, are not incorporated into conservation planning models.

(b) Inadequate protection measures

Conservation policies based on generalized trait data often overlook the failure of populations that rely on specialized biochemical capacities, which are critical for delayed or lagged adaptation under extreme environmental conditions. These failures are particularly evident when environmental fluctuations exceed physiological thresholds, such as those related to temperature, oxygen availability or ionic composition, conditions under which populations without sufficient biochemical plasticity are unable to persist. This particularly affects populations characterized by elevated antioxidant defences or high metabolic flexibility, traits that are essential in habitats where thermal amplitude, pH or ion concentrations fluctuate beyond typical physiological thresholds.

For example, in acidic and low-ionic blackwater systems, fish species exhibit compensatory biochemical responses to support osmoregulation, such as increased chloride cell density and elevated ATPase activity [11]. Without the identification and prioritization of these physiologically specialized populations within conservation units, critical reservoirs of adaptive plasticity might be excluded from management strategies, undermining the species' capacity to persist in increasingly degraded habitats (figure 3).

Evidence from recent studies demonstrates that incorporating biochemical and physiological metrics into conservation planning, such as mitochondrial efficiency, enzymatic activity (e.g. lactate dehydrogenase) and reproductive tolerance to thermal stress, provides early warning indicators of vulnerability that are invisible to average-based approaches [16,28]. Research conducted at the Laboratory of Ecophysiology and Molecular Evolution (LEEM/INPA) has demonstrated that physiological diversity at the biochemical level, encompassing shifts in mitochondrial efficiency, activation of lactate dehydrogenase and sperm thermal tolerance, is strongly associated with environmental gradients. Such variation cannot be inferred from ecological averages alone ([15,16]; figure 3).

(c) Ineffective policy development

Policies based on aggregated data are likely to overlook spatially explicit biochemical hotspots. For instance, while average deforestation rates may appear stable, fish assemblages are already experiencing localized vulnerabilities in reproductive potential, particularly at habitat edges where temperatures are elevated. Such site-specific vulnerabilities highlight a mismatch between coarse-scale conservation indicators and the physiological thresholds that actually determine species persistence. Evidence indicates that exposure to high temperatures affects *C. macropomum*, leading to impaired sperm motility and altered larval morphology, manifestations of biochemical disruption at both cellular and developmental levels [16,17].

Furthermore, extreme events, such as the 2023 Amazonian drought, have demonstrated that mortality patterns are not uniform but are shaped by site-specific biochemical thresholds. Species lacking the capacity to activate compensatory mechanisms, such as heat-shock protein synthesis, metabolic suppression or alternative respiratory pathways, succumb more rapidly under these extreme conditions. These observations underscore the urgency of regionally tailored conservation strategies that account for species-specific physiological limits and biochemical tipping points [18].

To address these gaps, conservation strategies must integrate biochemical and physiological metrics into spatially explicit ecological models, recognizing that these dimensions provide early indicators of ecosystem instability and declining resilience. Explicitly contrasting mean-trait-based conservation planning with variability-aware frameworks, which incorporate tipping points, edge-case phenotypes and local adaptation, strengthens the predictive and preventive power of management policies. A conservation framework grounded in molecular and organismal biology, rather than relying solely on statistical abstractions,

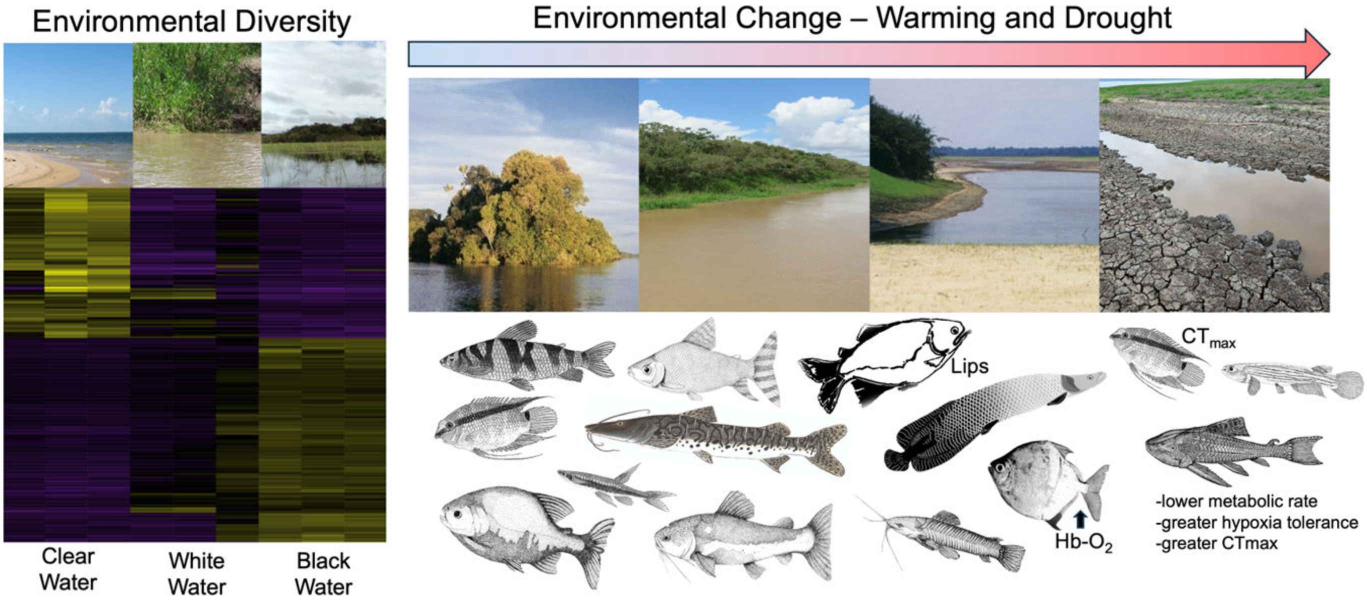

Figure 3. Environmental diversity and adaptive responses of Amazonian fishes. The left panel illustrates environmental heterogeneity across Amazonian aquatic systems: clearwater, whitewater and blackwater, visualized through habitat-specific gene expression profiles in *Triportheus albus*. The heatmap, adapted from Araújo *et al*. [24], shows distinct gene expression patterns, with colour-coded bars indicating expression levels: black (low), purple (downregulated) and yellow (upregulated). These patterns highlight the molecular plasticity of *T. albus*, a species broadly distributed across contrasting environments, and its capacity for context-specific physiological responses to ecological variation. The right panel presents a conceptual model illustrating how warming and increasingly extreme hydrological shifts, such as intensified droughts and floods, challenge the resilience of Amazonian fishes. As aquatic habitats dry, shrink or heat more frequently, fishes rely more heavily on physiological adaptations. Illustrations highlight traits linked to resilience or vulnerability, including air-breathing capacity, lips expansion, oxygen transport efficiency ($Hb–O_2$), pH regulation and thermal tolerance (CT_{max}). The average obscures a rich mosaic of ecological and molecular information embedded in environmental complexity and genomic plasticity. It is precisely this hidden variability, often masked by mean responses, that Amazonian fishes rely upon to cope with accelerating global change.

is better equipped to predict ecological tipping points and safeguard the functional diversity that is critical for the resilience of Amazonian ecosystems in the face of climate change.

6. Moving beyond the 'Tyranny of the Golden Mean'

Moving beyond the limitations of mean-based approaches requires more than methodological refinement; it demands a shift in epistemological perspective. Variability should not be treated merely as statistical noise or secondary complexity, but rather as the fundamental expression of biological complexity and evolutionary potential. The ecological and physiological heterogeneity observed in Amazonian systems is not peripheral; it is central to their resilience. Conservation science must, therefore, move away from frameworks that prioritize generality and instead embrace those grounded in differentiation, specificity and nuance. This shift should be informed by integrative conservation frameworks that explicitly incorporate biochemical, physiological and genetic dimensions of variability into both monitoring programmes and decision-making processes. Ultimately, the strength of Amazonian ecosystems lies not simply in their diversity, but in the adaptive capacity that such diversity enables: the ability to absorb deviation, buffer disruption and reorganize in the face of environmental change.

(a) Embrace variability

Biological variability is an essential and active component of living systems. It is not merely statistical dispersion, but the foundation upon which natural selection operates and through which ecosystems respond to perturbations. Consequently, conservation approaches must shift from modelling the 'average' individual to recognizing the ecological and evolutionary significance of deviations at both individual and population levels. For instance, studies on Amazonian fishes have revealed substantial physiological variation in heat and hypoxia tolerance [7,15]. Individuals at the extremes of these distributions often hold the key to population persistence under extreme environmental stress.

Biological diversity reflects higher levels of ecological organization, where emergent properties cannot be captured through simple additive models of individual traits. For example, fluctuations in enzyme expression or metabolic fluxes are not merely organismal adjustments; they represent deeply embedded regulatory architectures shaped by evolutionary pressures across environmental gradients. By defining and tracking such physiological and biochemical signatures, including plasticity indices, thermal margins and metabolic thresholds, conservation assessments can move beyond descriptive trait averages towards functional diagnostics of resilience. Physiological and biochemical traits should not be treated as universal proxies, but rather integrated into conservation models according to ecological context and management objectives.

(b) Adopt comprehensive approaches

Single-layer conservation diagnostics, whether genetic, ecological or population-based, are insufficient to address the complexity of environmental change acting across multiple biological scales. Instead, conservation science must adopt integrative methodologies that encompass the full spectrum of biological organization, from allelic diversity and gene expression to protein profiles, biochemical traits and ultimately traits expressed through ecological interactions. Such a multi-layered approach is essential to capture the mechanisms underlying resilience and adaptive capacity in dynamic ecosystems.

In practice, this means developing diagnostic models capable of integrating information across genotypic, phenotypic and environmental datasets, linking physiological thresholds (e.g. CT_{max}, enzymatic tipping points) with ecological performance under real-world variability. A truly holistic conservation strategy must go beyond merely assembling biological layers; it must account for the interconnections and feedbacks that define adaptive systems. This requires diagnostic models capable of integrating information across multiple levels, from genotypic plasticity and biochemical resilience to ecological function. For instance, recent research on *Hypostomus* spp. from ecologically distinct Amazonian basins has shown that differential expression of ion transporters, along with locally adapted variants in osmoregulatory genes, is associated with population survival across environments ranging from acidic ion-poor blackwaters to ion-rich whitewaters [50]. Similarly, fine-scale morphological analyses of Amazonian stingrays, *Potamotrygon* spp., have revealed that specialized gill adaptations, such as Na^+/K^+-ATPase-rich mitochondria-rich cells and extensive mucous secretions, enhance osmoregulatory performance under low-ionic conditions, highlighting the diagnostic value of microanatomical and biochemical traits in conservation planning [51].

(c) Localized conservation efforts

Effective conservation in the Amazon must integrate spatially explicit strategies that are ecologically contextualized. The region’s vast hydrographic and geomorphological complexity gives rise to distinct environmental niches, which play a critical role in shaping adaptive landscapes at the local scale. Consequently, the design of conservation units cannot ignore site-specific physiological and ecological conditions. Homogenized protection strategies risk overlooking and excluding key reservoirs of adaptive diversity, thereby compromising long-term ecosystem resilience.

Recent findings reinforce that such site-specific adaptive diversity is often invisible to traditional genetic or distributional surveys but can be revealed by physiological and biochemical diagnostics. The limitations of broad-scale conservation approaches have recently been highlighted by studies demonstrating the profound influence of localized environmental pressures on population structure and adaptive traits. Evidence suggests that evolutionary divergence in Amazonian fish populations is shaped less by broad ecological speciation mechanisms and more by site-specific selection within highly heterogeneous habitats [52]. This underscores the need for conservation models that are sensitive to microhabitat variation. For example, one study found that the composition of gut microbial communities in Amazonian fishes is strongly structured by spatial factors and environmental variables, particularly water chemistry [53]. These findings indicate that phenotypic plasticity extends beyond the host organism to include microbiota-mediated adaptive responses, reinforcing the importance of incorporating multiple biological dimensions into conservation frameworks.

Complementary insights from Almeida-Val *et al.* [6,54] have long demonstrated that fish species inhabiting contrasting hydrological systems exhibit distinct biochemical and physiological responses, shaped by fine-scale variations in pH, oxygen availability, ion concentrations and temperature regimes. These responses are not peripheral characteristics but fundamental components of organismal fitness and population persistence under environmental stress [6,54]. Physiological markers, such as osmoregulatory enzyme activity and oxidative stress indicators, offer a more precise delineation of functional population units than traditional taxonomic or distribution-based criteria, providing critical information for adaptive conservation planning.

Thus, conservation frameworks must move beyond biogeographic generalizations and incorporate site-specific physiological diagnostics as primary criteria for area selection and management prioritization. Integrating such localized data will enhance the ecological relevance of conservation measures by aligning them more closely with actual environmental pressures. Moreover, it will enable the proactive identification of populations with high evolutionary potential, populations that may remain undetected through genetic markers or species occurrence data alone.

(d) Adaptive management

Adaptive management should be regarded not merely as a reactive tool, but as a central pillar of proactive conservation in the dynamic ecosystems of the Amazon. Given that environmental change, particularly under the influence of climate change, is largely nonlinear and difficult to predict, conservation practices must themselves become dynamic. This requires integrating real-time monitoring, early warning physiological indicators and predictive modelling into adaptive management plans that can be rapidly adjusted in response to observed environmental and biological feedback.

The use of physiological early warning indicators, such as shifts in metabolic rate, incidence of larval deformities, enzymatic activity and transcriptomic responses, offers a powerful tool for detecting ecological stress before it manifests at the population level [18,49]. These indicators can guide proactive interventions and support flexible, evidence-based decision-making frameworks. As mentioned above, recent observations during LEEM expeditions to Lago do Prato in the Anavilhanas archipelago documented rapid ecological recovery following extreme stress events, provided that resilience mechanisms were robust and actively engaged. Identifying and reinforcing such mechanisms must be central to adaptive management strategies and cannot be achieved through reliance on population averages alone.

7. Conclusion

The conservation of Amazonian biodiversity requires moving beyond mean-based ecological frameworks and embracing the full spectrum of variability that defines biological and ecological systems. Recognizing variability as the primary driver of resilience is not merely theoretical, but a principle grounded in ecological and evolutionary processes, and a strategic imperative for sustaining species and ecosystems in the context of rapid environmental change. This calls for conservation models that integrate genetic, biochemical, physiological and ecological dimensions, explicitly linking individual variation to population-level resilience, ecosystem stability and evolutionary potential.

Averages, while providing broad overviews, often mask extremes, outliers and local adaptations that determine survival under stress. The Tyranny of the Golden Mean has too often produced conservation policies that overlook rare alleles, specialized biochemical capacities and physiological extremes—critical elements of a species' adaptive toolkit. Embedding variability-aware approaches into conservation planning enables anticipation of tipping points, early detection of ecological decline and the design of targeted, timely interventions.

Implementing multi-layered diagnostics that integrate high-resolution environmental data with functional biological indicators—from metabolic enzyme profiles to osmoregulatory and reproductive thresholds—can provide a comprehensive and predictive view of ecosystem resilience. Such approaches not only strengthen conservation outcomes in the Amazon but also offer a model for biodiversity management under global climate change, habitat degradation and emerging stressors.

Preserving the Amazon's biological variability is both a scientific and an ethical imperative. Safeguarding species means protecting the mechanisms that enable life to persist, reorganize and generate complexity in the face of disturbance. The challenge is substantial, but so is the opportunity: to redefine conservation science in a way that values heterogeneity and uses adaptive potential at every level of biological organization. By doing so, we safeguard the evolutionary resilience that will determine the future of the Amazon and global biodiversity.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. Artificial intelligence (AI) was employed in the preparation of this manuscript to enhance language clarity and readability. Specifically, ChatGPT (OpenAI, GPT-4 model) was used to assist in improving grammar, syntax and flow of the text. Additionally, AI assistance was used in the conceptual generation and visual design of figure 1, based on scientific content and direction provided by the authors. All scientific interpretations, intellectual contributions and final approvals are the sole responsibility of the authors.

Authors' contributions. A.L.V.: conceptualization, data curation, funding acquisition, writing—original draft, writing—review and editing; V.M.F A.-V: conceptualization, formal analysis, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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