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REVIEW

Climate-driven trophic interactions and their impact on the phenotypic plasticity of coral and the keystone urchin *Diadema antillarum* in shaping Caribbean reef resilience

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ABSTRACT: Caribbean coral reefs face unprecedented degradation from climate change and anthropogenic stressors, yet critical knowledge gaps remain regarding how organismal plasticity and trophic dynamics interdependently determine ecosystem trajectories. This review synthesizes emerging evidence demonstrating that plasticity in reef-building corals and a keystone herbivore, the long-spined sea urchin *Diadema antillarum*, operates interdependently, with functional significance contingent upon ecological context. We examined how epigenetic mechanisms, particularly DNA methylation, facilitate coral acclimatization and transgenerational resilience, while behavioral and physiological adjustments in *D. antillarum* maintain grazing functions under stress. Critically, even thermally acclimated corals cannot persist without functional herbivory to suppress macroalgal competition, revealing that plasticity and trophic structure are inseparable determinants of reef resilience. By integrating molecular, physiological, and ecological perspectives, we identify thresholds beyond which plastic responses prove insufficient to prevent phase shifts toward macroalgal dominance. This synthesis provides mechanistic insights essential for designing evidence-based conservation strategies that simultaneously enhance organismal adaptive capacity and restore functional trophic relationships in degraded reef ecosystems.

KEY WORDS: Phenotypic plasticity · Trophic dynamics · Coral–macroalgal interactions · *Diadema antillarum* · Caribbean reefs · Climate change · Epigenetic mechanisms

1. INTRODUCTION

Coral reef ecosystems are among the most biodiverse and productive marine habitats (Mumby et al. 2008, Hughes et al. 2017). Unfortunately, they are undergoing unprecedented degradation from multiple anthropogenic stressors including ocean warming, acidification, eutrophication, habitat destruction, and overfishing (Hughes et al. 2017, 2023, Hoegh-Guldberg et al. 2019). These environmental changes have significant implications for ecosystem stability, as coral reefs support extensive marine biodiversity and provide critical services including coastal protection and fisheries sustainability (Knowlton et al. 2021). Yet ~50% of reefs worldwide have experienced significant decline over the past 3 decades (Fabricius et al. 2024), creating an urgent need to understand the mechanisms underlying reef resilience.

Phenotypic plasticity — the capacity of organisms to modify physiology, morphology, and behavior in response to environmental change without genetic alteration (West-Eberhard 2003, Pigliucci et al. 2006) — is a key mechanism allowing organisms to persist in fluctuating environmental conditions (Ken-

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kel & Wright 2022). In corals, phenotypic plasticity manifests through morphological adjustments, metabolic reconfiguration, and immune responses (Bruno & Edmunds 1997, Drury et al. 2017, Kenkel & Matz 2017, Drury & Lirman 2021). Critical to this capacity is the endosymbiotic relationship with dinoflagellate algae (family Symbiodiniaceae), which inhabit coral tissues and provide photosynthetic nutrients (Baker et al. 2008, Silverstein et al. 2015, Hume et al. 2016). These symbiotic partnerships are also a means of acclimatization through dynamic community restructuring, metabolic adjustments, and shifts in gene expression (Silverstein et al. 2015, Putnam 2021, Anthony et al. 2024). Epigenetic mechanisms, including DNA methylation and histone modifications (Fig. 1a), are implicated in facilitating these plastic responses

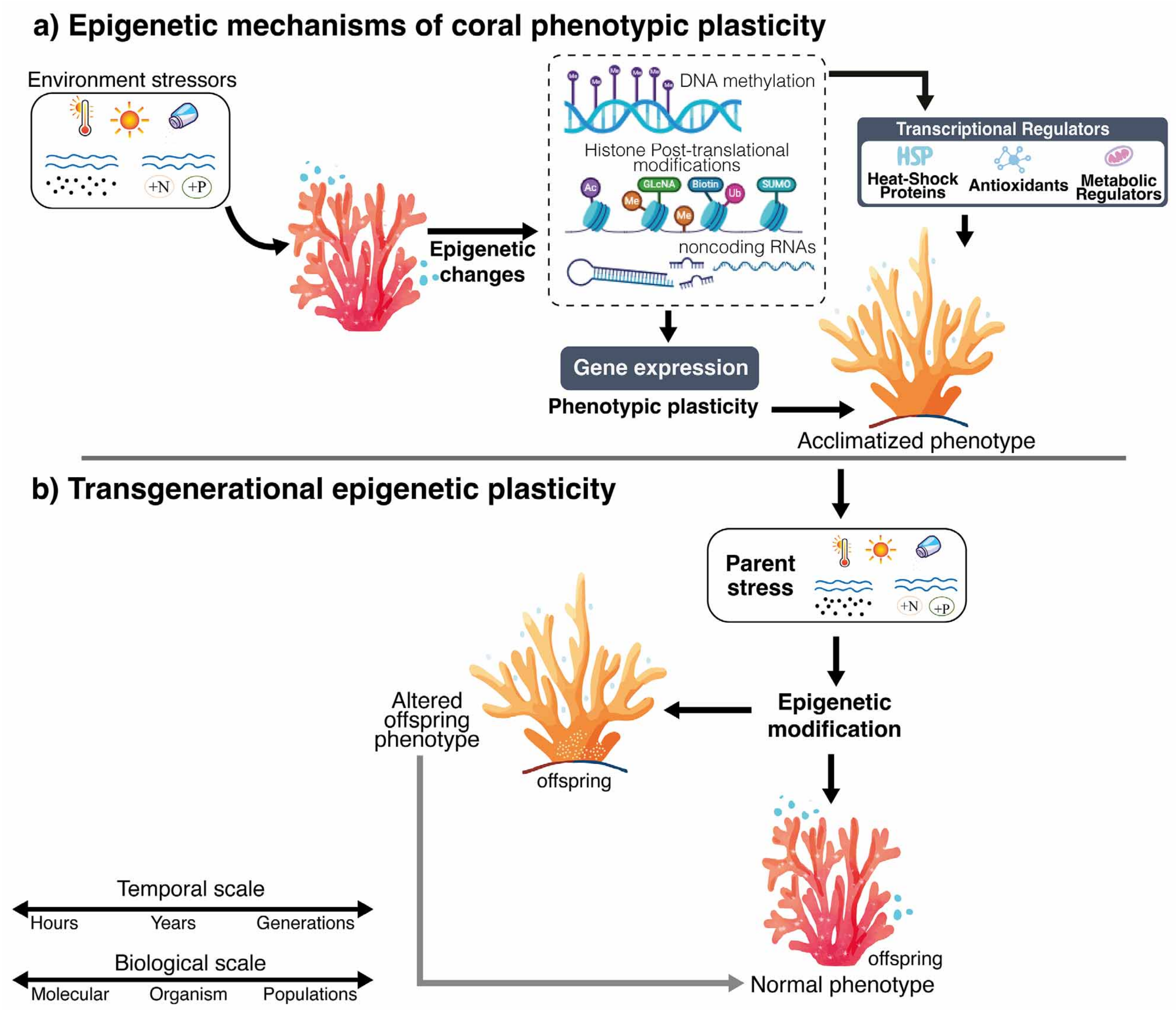

Fig. 1. Epigenetic regulation of coral phenotypic and transgenerational plasticity. (a) Environmental stressors, e.g. thermal anomalies, salinity fluctuations, nutrient enrichment, and sedimentation, trigger epigenetic modifications including DNA methylation, histone modifications, and non-coding RNAs, modulating gene expression in response to environmental cues. These molecular processes interact with canonical stress-response pathways (e.g. heat-shock proteins, antioxidant enzymes) to facilitate physiological adjustments underpinning phenotypic plasticity. (b) Gene-expression changes drive physiological responses (e.g. altered symbiont density, antioxidant capacity, shifts in autotrophy—heterotrophy balance). Stress-induced epigenetic modifications can be maintained through gametogenesis and transmitted to subsequent generations, constituting transgenerational epigenetic inheritance potentially conferring enhanced stress tolerance independent of genetic sequence variation. Grey arrows denote phenotypic reversion of the altered offspring phenotype back toward the baseline ('normal') state in the F_2 generation, reflecting partial epigenetic resetting or environmental-dependent reversion of inherited marks. The temporal and biological scales frame epigenetic plasticity as a mechanism bridging proximate molecular responses with ultimate evolutionary consequences, potentially accelerating adaptive trajectories in rapidly changing marine environments

to environmental challenges (Torda et al. 2017, Liew et al. 2018, Rodríguez-Casariego et al. 2020).

Reef ecosystem dynamics are strongly influenced by the interactions between corals, macroalgae, and herbivores. Among the latter, the long-spined sea urchin *Diadema antillarum* is a keystone herbivore in Caribbean reefs, exerting top-down control on macroalgal growth (Fig. 2a) and facilitating coral settlement and growth (Mumby et al. 2016, Latijnhouwers et al. 2024). While herbivorous fishes (particularly parrotfishes and surgeon fishes) and fish predators of sea urchins (including triggerfishes and some wrasses) also contribute to reef trophic structure (Mumby et al. 2006a, Adam et al. 2015), this review focuses specifically on the direct top-down control exerted by *D. antillarum* herbivory on macroalgae. Historically crucial to coral-dominated reefs, a *D. antillarum* mass die-off in the early 1980s led to ecosystem phase shifts toward macroalgal dominance (Lessios 2016), and populations have remained suppressed due to disease outbreaks, recruitment failure, and habitat degradation (Rodríguez-Barreras et al. 2023b). A second mass mortality event beginning in 2022 has further threatened recovery (Sharp et al. 2023, Hylkema et al. 2023, Levitan et al. 2023), yet the extent of phenotypic plasticity in this species — particularly its capacity for morphological, physiological, and behavioral adaptation — remains an open question with significant ecological implications.

Macroalgal proliferation affects coral health through competition for space, allelopathic interactions (chemical interference competition mediated by bioactive metabolites), shifts in microbial communities, and biogeochemical alterations (López-Jiménez et al. 2020, Adam et al. 2022). Both corals and sea urchins can respond to macroalgal abundances via plastic responses (e.g. altered foraging, shifts in symbionts or physiological allocation), although severe macroalgal competition may also impose strong selective mortality, with cascading ecological consequences (Barott et al. 2012, Shearer et al. 2014). Corals demonstrate plasticity through modifications of skeletal density, polyp size, symbiont densities, and energy allocation (Grottoli et al. 2006, Doherty et al. 2024, Wang et al. 2024), and upregulate stress defenses including antioxidants and lipid storage (Baumann et al. 2021, Marangoni et al. 2021). Sea urchins display behavioral changes in foraging and diet patterns (Hernández & Russell 2010, Kriegisch et al. 2019, Sun et al. 2019), morphological modifications in spine density and test architecture (Ebert 1996, Hughes et al. 2012, Bodmer et al. 2017), and physiological adjustments in digestion and metabolism (Russell 1998, Cui et al. 2024). These responses shape coral—macroalgal competitive dynamics and broader resilience trajectories (Hughes et al. 2007, Barott et al. 2012, Adam et al. 2022).

The differential capacity for phenotypic plasticity among reef organisms may determine which species can persist under challenging environmental conditions, representing a critical yet poorly understood aspect of reef resilience. This review operates from a central premise: phenotypic plasticity in reef organisms and trophic dynamics function as interdependent, context-dependent determinants of reef resilience. We examine 3 interconnected mechanisms: (1) molecular and physiological plasticity enabling individual acclimatization, (2) trophic mediation of competitive outcomes, and (3) threshold dynamics where plastic capacity intersects with ecological context to determine ecosystem trajectories. Specifically, this review (1) examines how variations in macroalgal abundance drive phenotypic plasticity in corals and *D. antillarum*, and its impact on their resilience, (2) explores how environmental changes modulate the trophic dynamics among corals, macroalgae, and *D. antillarum*, and (3) identifies key knowledge gaps and future research directions. To support the scope and synthesis of this review, we used a structured literature-search strategy focused on studies addressing phenotypic plasticity, epigenetic regulation, macroalgal competition, and trophic interactions involving coral reefs and *D. antillarum*. Details of the search strategy and screening criteria are provided in Text S1, and the studies retained for synthesis are summarized in Table S1, both available in the Supplement at https://www.int-res.com/articles/suppl/meps15139_supp.pdf.

2. MOLECULAR AND PHYSIOLOGICAL MECHANISMS OF PLASTICITY

2.1. Epigenetic mechanisms underlying coral plasticity

Reef-building corals exhibit remarkable phenotypic plasticity across multiple biological scales, including morphological or structural changes in skeletal traits (Todd 2008), symbiont community dynamics affecting bleaching susceptibility (Baker et al. 2008, Drury & Lirman 2021), physiological diversity in thermal tolerance (Hume et al. 2016), and cellular adjustments in energy allocation (Roth 2014, Gibbin et al. 2018). The mechanistic basis underlying this plasticity is mediated by highly dynamic epigenetic machin-

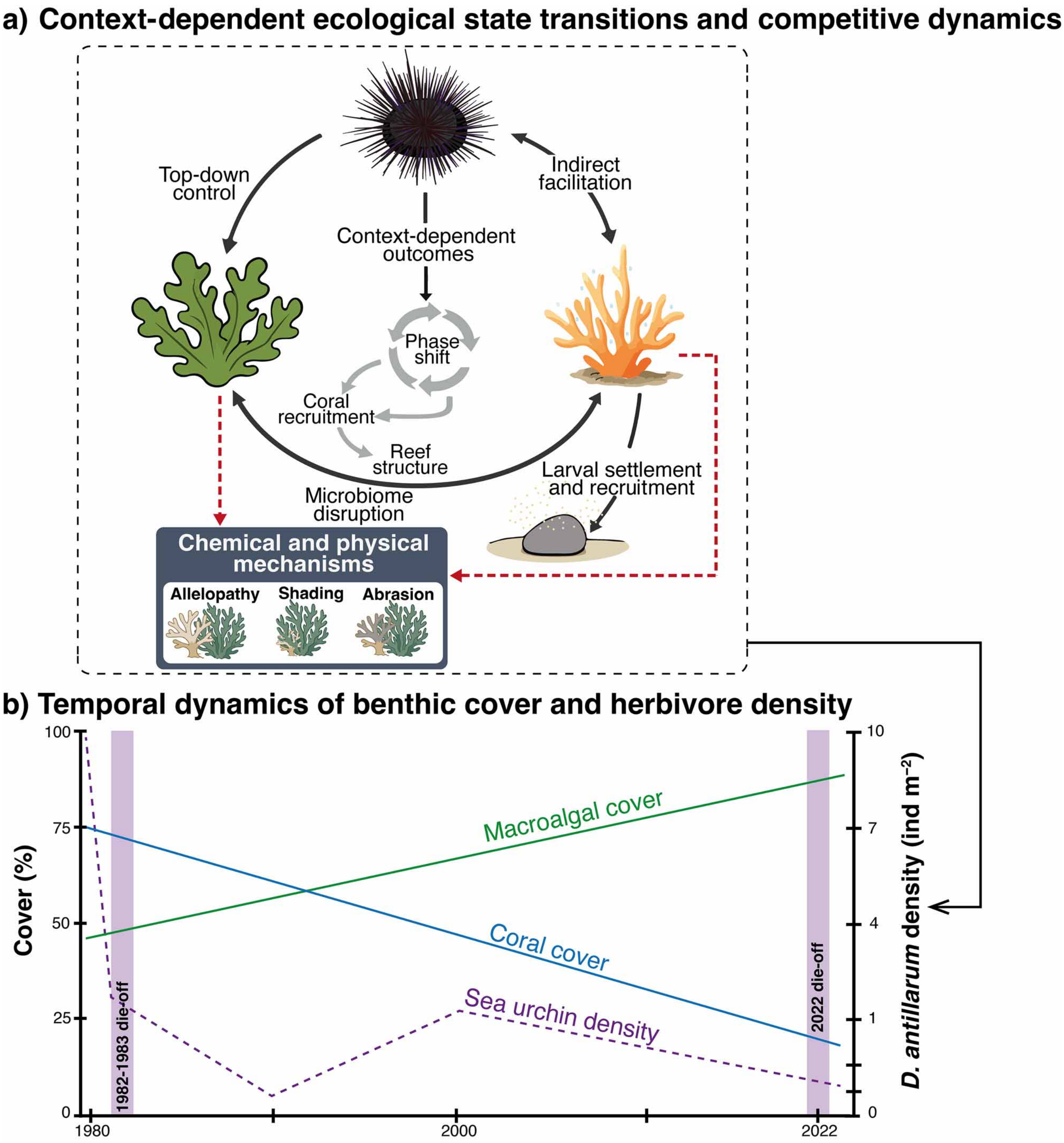

Fig. 2. Trophic control of coral—macroalgae interactions by *Diadema antillarum*. (a) *D. antillarum* exerts critical top-down control through direct macroalgal consumption and indirect facilitation of coral recruitment processes. The conceptual model integrates multiple regulatory pathways: allelopathic interference competition, microbial community dysbiosis, physical settlement inhibition, and larval recruitment dynamics. The strength of these top-down controls varies with urchin density and ambient environmental conditions. Black arrows represent empirically quantified ecological fluxes; grey arrows indicate theoretically supported pathways requiring additional validation; dashed red arrows denote context-dependent stress responses and conditional regulatory mechanisms. (b) Conceptual/hypothetical relationship, showing the temporal dynamics and the inverse relationships between benthic cover states and herbivore density across a 40 yr monitoring period (1980—2022), illustrating the quantitative manifestation of trophic cascade effects and ecosystem state transitions described in the mechanistic framework. This figure was built based on data from Levitan (1988b, 1989), Bruno et al. (2009), Mumby & Harborne (2010), Lessios (2016), Haas et al. (2016), Tebbett et al. (2023), Hylkema et al. (2023), and Levitan et al. (2023)

ery comprising DNA methylation, histone modifications, chromatin remodeling complexes, and non-coding RNAs, which modulate gene expression without altering the DNA sequence (Eirin-Lopez & Putnam 2019). Notably, in corals, DNA methylation has a dual regulatory mechanism — promoter hypermethylation silences gene transcription, while gene-body methylation influences alternative splicing and modulates expression levels — providing precise spatiotemporal control of gene expression that enables coordinated phenotypic plasticity in responses to environmental challenges (Liew et al. 2018, Gomez-Campo et al. 2024) (Fig. 1). These modifications target genes encoding stress-response proteins, metabolic enzymes, and cellular regulatory pathways.

Empirical evidence demonstrates correlations between DNA methylation patterns and trait plasticity in corals (Dimond & Roberts 2016, Putnam et al. 2016, Dimond et al. 2017, Liew et al. 2018, Durante et al. 2019, Rodríguez-Casariego et al. 2020, Hackerott et al. 2023). Notable findings include differential DNA methylation profiles in *Acropora* spp. associated with thermotolerance (Dimond & Roberts 2020, Rodriguez-Casariego et al. 2022, Peterson et al. 2024) and modified DNA methylation in *Pocillopora damicornis* under ocean acidification conditions (Putnam et al. 2016, Jiang et al. 2024). Correlational evidence suggests these epigenetic modifications may facilitate integrated signaling networks comprising heat-shock proteins, antioxidant enzymes (e.g. superoxide dismutase, catalase), and metabolic regulators that coordinate cellular stress responses (Cziesielski et al. 2019, A. Williams et al. 2021). This environmental—epigenomic interface suggests that these epigenetic modifications may facilitate morphological, metabolic, and reproductive adjustments, representing a critical mechanism for coral resilience (Fig. 1).

2.2. Coral adaptation and acclimatization in changing environments

Adaptation and acclimatization represent distinct but complementary processes through which organisms respond to environmental change. Acclimatization — the phenotypic adjustment to environmental change occurring within an individual's lifetime — represents one form of phenotypic plasticity. In contrast, adaptation refers to genetic changes arising through natural selection across generations. Plasticity can facilitate genetic adaptation by sustaining populations through environmental shifts (genetic assimilation), revealing cryptic genetic variation to selection, and by itself being a target of selection (Fox et al. 2019, 2021, Burgess et al. 2021). Plastic mechanisms operate across scales: immediate acclimatization boosts short-term survival, while persistent mechanisms (e.g. epigenetic or transgenerational effects) alter offspring phenotypes and the selective landscape (Putnam et al. 2016, Torda et al. 2017, Eirin-Lopez & Putnam 2019, Liew et al. 2020). Thus, plasticity can functionally bridge proximate acclimatization and ultimate adaptation without conflation.

Multiple studies demonstrate adaptive responses of corals to climate change, revealing a complex interplay of mechanisms that enhance resilience across different temporal and spatial scales. Accordingly, *Acropora hyacinthus* populations from warmer environments exhibit enhanced thermal tolerance, which is maintained under common garden conditions, thus suggesting genetic adaptation (Oliver & Palumbi 2011). Selective breeding experiments with *A. millepora* yield rapid adaptation to elevated temperatures on shorter timescales, with parent—offspring phenotyping revealing significant heritability of thermal tolerance traits (Dixon et al. 2015, Humanes et al. 2024). Long-term ecological observations have shown increased resistance to elevated temperatures over a 50 yr period (Grottoli et al. 2018), while an emergent increase in coral thermal tolerance (~0.1°C decade^{-1}) has been documented, mitigating bleaching impacts and suggesting progressive population-level acclimation or selective processes (Lachs et al. 2023).

Epigenetic modifications may interact with natural selection in complex ways: transgenerational epigenetic inheritance — defined as the transmission of environmentally induced epigenetic modifications from parent to offspring through mechanisms that bypass traditional genetic inheritance pathways (Fig. 1) — can potentially enhance resilience by preparing offspring for similar stressors (Putnam & Gates 2015, Liew et al. 2018, 2020 Peterson et al. 2024). While such inheritance can buffer offspring from environmental stress, potentially reducing selection intensity in the short term, it may also facilitate adaptation by allowing populations to persist through environmental transitions during which genetic adaptation can occur. Offspring from thermally conditioned parents display enhanced thermotolerance with distinct DNA methylation patterns (Fig. 1) (Liberman et al. 2022), and *Montipora capitata* progeny from heat-exposed parents exhibit significantly enhanced survival under thermal stress (Drury et al. 2022a). These findings suggest that phenotypic plasticity via epigenetic mechanisms may facilitate faster responses to climate change than traditional genetic adaptation alone (Torda et al. 2017, Eirin-Lopez & Putnam 2019), though the persistence, reversibility, and functional significance of these modifications require further investigation.

2.3. Plasticity mechanisms in *Diadema antillarum*

Parallel to the molecular plasticity observed in corals, *D. antillarum* demonstrates multiple forms of phenotypic flexibility that maintain herbivorous function under variable environmental conditions. While the epigenetic foundations of urchin plasticity remain less well characterized than those of corals, behavioral, morphological, and physiological evidence collectively indicates substantial adaptive capacity in this keystone species.

D. antillarum shows plasticity in multiple traits relevant to its herbivorous function and survival. Behavioral plasticity manifests in predator avoidance during nocturnal grazing (Sherman 2015, Bodmer et al. 2021) and adjustments in consumption rates responding to macroalgal community composition (Williams 2022). Foraging plasticity allows individuals to modify grazing patterns, foraging radius, and habitat utilization in response to macroalgal density gradients (Rodríguez-Barreras et al. 2023a).

Morphological adaptations manifest in the phenotype–environment matching: individuals develop white spines in low-light environments while preferring shaded crevices, whereas individuals in exposed areas develop black spines while grazing open reef flats (Bodmer et al. 2017). Under predation pressure, sea urchins allocate metabolic resources toward spine reinforcement (Bodmer et al. 2021), while in nutrient-limited environments, resources prioritize gonadal development over somatic growth (Levitan 1989, Cabanillas-Terán et al. 2019, Hassan et al. 2022). Physiologically, *D. antillarum* exhibits moderate tolerance to sedimentation stress, though chronic exposure can reduce feeding efficiency and growth rates (Kobelt et al. 2020). Populations across environmental gradients display varied physiological tolerances, but the genetic versus plastic basis of this variation remains poorly characterized. Thermal tolerance experiments reveal seasonal acclimatization with fluctuating upper thermal limits (Sherman 2015), and flexible acid–base regulation, which may partially mitigate the effects of ocean acidification, although these adaptations incur energetic trade-offs that can compromise other physiological functions or development processes (Bielmyer et al. 2005, Ganeshan et al. 2019, Hashemi et al. 2024).

Despite these indicators of adaptive capacity, plasticity mechanisms in *D. antillarum* remain underexplored relative to corals, particularly regarding responses to multiple simultaneous stressors. Population declines have limited comparative studies across environmental gradients, and the epigenetic basis of plasticity represents a critical knowledge gap (DeBiasse & Kelly 2016, Byrne et al. 2020). Understanding the mechanistic basis, limits, and ecological consequences of *D. antillarum* plasticity remains essential for predicting how restored populations will function under future climate scenarios.

3. ORGANISMAL RESPONSES AND ECOLOGICAL FUNCTIONS

The parallel examination of plasticity mechanisms in corals and *Diadema antillarum* in Section 2 establishes that both organisms possess molecular and physiological capacity for environmental responsiveness. However, the ecological significance of this capacity depends on its translation into phenotypic adjustments that operate within the trophic context of reef ecosystems. This section therefore bridges molecular mechanisms and ecosystem-level function by examining how corals and *D. antillarum* express plastic potential in ways that influence competitive interactions and trophic structure. We find that, although both organisms exhibit substantial plasticity at the molecular level, the ecological consequences of these responses depend critically on their magnitude, energetic costs, and interactions with other reef organisms.

3.1. Coral responses to macroalgal competition

Interactions with macroalgae fundamentally shape how coral plasticity manifests in reef environments, revealing the context-dependent nature of adaptive responses. Macroalgal competition for resources, space, along with release of allelopathic compounds — lipophilic secondary metabolites including terpenoids, phenolics, and halogenated compounds that chemically inhibit coral physiological processes (Rasher et al. 2011, Vieira et al. 2016) — can suppress coral growth (Fig. 3), causing tissue necrosis, shifts in microbial communities, and metabolic stress (Rasher et al. 2011, Brown et al. 2018, Clements et al. 2020), while suppressing key stress response pathways (Fu et al. 2023). Overgrowing macroalgae also abrade surfaces, block larval settlement, introduce pathogens, and alter water chemistry (Rasher et al. 2011, Greff et

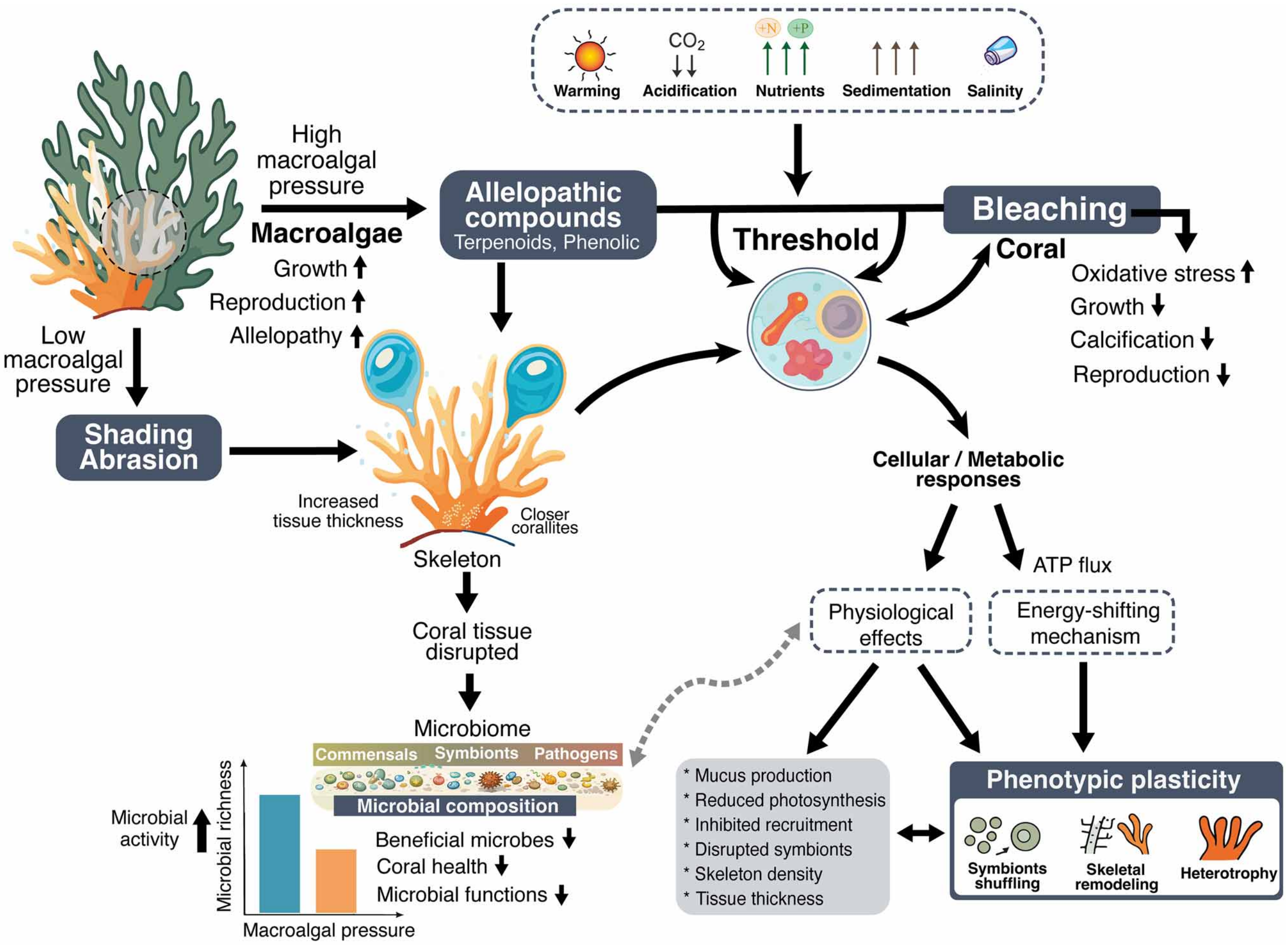

Fig. 3. Context-dependent feedback linking multiple environmental stressors, macroalgal pressure, and coral plasticity under coral—macroalgae competition. This mechanistic model illustrates the multi-scale adaptive responses exhibited by corals when subjected to macroalgal overgrowth and associated chemical stressors resulting from anthropogenic stressors. Macroalgal competitive pressure initiates cascading physiological disruptions through dual pathways: direct allelopathic compounds (terpenoids, phenolic compounds) compromise coral tissue integrity and symbiont photosynthetic efficiency, and indirect stress amplification through microbial dysbiosis and reduced photosynthetic efficiency of symbionts. Coral compensatory responses encompass morphological plasticity (modified corallite architecture, altered skeletal density), energy-shifting (ATP flux shifting toward maintenance processes), and behavioral adaptations (enhanced heterotrophic feeding, increased mucus production). Microbiome dysbiosis, symbiont shuffling, and skeletal remodeling collectively represent integrated stress response strategies. Solid arrows indicate direct or empirically validated mechanistic pathways; dashed grey arrow denotes stress-mediated regulatory cascades and secondary physiological effects. The small bar chart indicates microbial richness responses to macroalgal pressure (blue = relative increase; orange = relative decrease). Boxed items summarize major phenotypic plasticity outcomes and key physiological impairments

al. 2017). Such complex, multi-stressor contexts highlight the need to study coral plasticity under ecologically realistic conditions.

In direct response to macroalgal contact and allelopathic exposure, corals exhibit structural plasticity including adjustments to skeletal density, corallite spacing, and tissue thickness (Box & Mumby 2007, Todd 2008), alongside physiological responses such as altered energy allocation patterns and enhanced immune function (Barott et al. 2012, Morrow et al. 2017). Some species enhance oxidative stress responses and mucus production (Morrow et al. 2017), while others reduce skeletal density but increase tissue biomass to maximize feeding capacity (Todd 2008). These morphological and physiological adjustments represent compensatory mechanisms that can partially maintain growth and reproductive functions during competition (Fig. 3) (Barott et al. 2012, Shearer et al. 2014). Corals can reallocate metabolic resources and increase heterotrophic feeding to compensate for photosynthetic limitations imposed by macroalgae (Grottoli et al. 2006, Ferrier-Pagès et al. 2010), suggesting partial acclimatization capacity to macroalgal pressures.

However, the energetic costs associated with maintaining defensive responses against macroalgal competition can compromise other vital functions, including reproduction, growth, and immune responses (Fig. 2). When macroalgal cover reaches sufficiently high levels, the cumulative energetic costs of defensive responses — including enhanced heterotrophy, mucus production, and immune function — can exceed coral energy budgets, resulting in tissue necrosis, reduced calcification, and elevated mortality despite plastic compensatory mechanisms (Rasher et al. 2011, Barott et al. 2012). These threshold dynamics reveal a fundamental limitation: coral plasticity can buffer against moderate competition but cannot indefinitely sustain function under severe macroalgal pressure. This constraint underscores the critical importance of trophic controls that prevent macroalgae from reaching competitive dominance — controls primarily mediated by herbivores such as *D. antillarum*.

3.2. Ecological role, population declines, and ecosystem consequences of *D. antillarum*

The long-spined sea urchin *D. antillarum* is a keystone herbivore whose ecological significance extends far beyond its individual biomass contribution to Caribbean reef ecosystems (Mumby et al. 2016, Latijnhouwers et al. 2024). While *D. antillarum* represents the dominant herbivorous echinoid in shallow Caribbean reefs (<30 m), other sea urchin species — including *Echinometra viridis, E. lucunter,* and *Lytechinus variegatus* — contribute to herbivory in specific habitats and depth zones (Carpenter 1988, Lessios 1988). However, none exhibit the ecological impact or functional role comparable to *D. antillarum* in maintaining the unique ecological importance due to its high population densities, nocturnal grazing behavior, and capacity to access cryptic reef areas inaccessible to other herbivores (Muthiga & McClanahan 2007, Precht & Precht preprint https://doi.org/10.7287/peerj.preprints.1565v1).

At densities of 4–8 ind. m^{-2} in Caribbean reefs, *D. antillarum* effectively controls macroalgal growth, with grazing rates removing substantial proportions of daily algal production (Levitan 1988a, 1989). However, effective grazing capacity varies with urchin test diameter, macroalgal community composition, and resource availability (Olmeda-Saldaña et al. 2021, Pilnick et al. 2023). At densities exceeding 1–2 ind. m^{-2} with test diameters >5 cm, *D. antillarum* can significantly reduce macroalgal biomass and enhance coral recruitment on degraded reefs (Idjadi et al. 2010, Pilnick et al. 2023). Their grazing generates complex mosaic macroalgal successional stages that enhance benthic biodiversity and facilitate nutrient cycling (Kriegisch et al. 2019, Ladd et al. 2021, Hylkema et al. 2022), supporting diverse reef organisms, including juvenile corals and crustose coralline algae, and contributing to reef accretion processes and overall ecosystem stability (Burkepile & Hay 2010).

The catastrophic collapse of *D. antillarum* populations in 1983–1984 due to a waterborne pathogen (Lessios 1988, Hewson et al. 2023), reduced populations by over 95% (Levitan et al. 2023) and fundamentally transformed Caribbean reef dynamics. This die-off triggered rapid phase shifts from coral- to macroalgae-dominated states: macroalgal cover rose 5% to 40–70% across numerous reefs (Hughes 1994, Carpenter & Edmunds 2006, Jackson et al. 2014). Macroalgal proliferation then created self-reinforcing feedbacks (Bodmer et al. 2015, Steneck et al. 2019) — via shading, allelopathy, and microbial shifts — that inhibited coral recruitment and calcification (Mumby et al. 2007, Ritson-Williams et al. 2020), reducing reef structural complexity (Jackson et al. 2014). Despite localized recoveries, *D. antillarum* densities remain far below pre-1983 levels (Rodríguez-Barreras et al. 2015, Hylkema et al. 2022, Levitan et al. 2023), rarely exceeding approximately 1–1.5 ind. m^{-2} (Rodríguez-Barreras et al. 2015). Concerningly, a second mass mortality event beginning in 2022 has devastated recovering populations across multiple Caribbean locations, with mortality patterns mirroring the 1983–1984 die-off and involving the same scuticociliate pathogen (*Philaster* sp.) (Hylkema et al. 2023, Levitan et al. 2023). This recent event underscores the persistent vulnerability of *D. antillarum* populations and the continued threat to Caribbean reef resilience.

Genetic analyses suggest reduced genetic diversity following the mass mortalities, potentially limiting adaptive capacity (Peralta-Serrano et al. 2024), and Allee effects along with low larval recruitment continue to impede population recovery (Levitan et al. 2014). Nevertheless, recent restoration initiatives underscore the urchin's ecological importance: reefs with recovering *D. antillarum* populations showed significant coral recruitment — 78–125% higher coral recruitment than urchin-depleted sites (Idjadi et al. 2010, Latijnhouwers et al. 2024) — although complete transitions to coral dominance remain incompletely documented.

The contrast between coral compensatory responses (Section 3.1) and urchin population dynamics reveals a critical asymmetry: coral plasticity operates at the individual level and can buffer against moderate stress but cannot overcome competitive exclusion when herbivory fails. The ecosystem-level function of *D. antillarum* creates the trophic conditions under which individual coral plasticity can translate into population persistence. This interdependence between organismal response capacity and trophic structure establishes the foundation for understanding context-dependent reef resilience.

4. TROPHIC INTERACTIONS AND CONTEXT-DEPENDENT OUTCOMES

Having established the molecular mechanisms underlying plasticity (Section 2) and the organismal responses that emerge from these mechanisms (Section 3), we now examine how these individual-level capacities interact within the complex trophic network linking corals, macroalgae, and *Diadema antillarum*. This section demonstrates that phenotypic plasticity functions not in isolation but as a mediator of competitive and facilitative interactions whose outcomes depend critically on ecological context. The integration of plasticity mechanisms with trophic dynamics reveals threshold relationships that determine whether reefs maintain coral dominance or transition to alternative macroalgal-dominated states.

4.1. Competitive mechanisms in the coral—macroalgae—*D. antillarum* system

Macroalgae compete aggressively with corals through multiple mechanisms including substrate monopolization, biogeochemical cycle alteration (e.g. nitrogen fixation, phosphorus retention), and release of allelopathic compounds that inhibit coral recruitment and growth (Barott & Rohwer 2012, Morrow et al. 2017, Mumby & Steneck 2018). Dense macroalgal stands physically shade or abrade corals (Box & Mumby 2007), and their lipophilic allelochemicals (e.g. terpenoids, phenolics) disrupt coral physiology (Vieira et al. 2016, Morrow et al. 2017, Fong et al. 2023). When intensified by anthropogenic stress, these interactions create threshold conditions favoring macroalgal dominance (Fig. 3). Metabolomic analyses reveal that macroalgae can disrupt coral microbiomes, impair symbiont photosynthesis, and inhibit larval settlement (Morrow et al. 2017, A. Williams et al. 2021, Pozas-Schacre et al. 2025). These effects intensify in degraded reef systems with reduced herbivory. The synergistic impacts of ocean warming, acidification, sedimentation increase, and nutrient loading can amplify coral cellular damage under macroalgal allelopathy, leading to positive feedback loops that further compromise coral health and competitive ability (Fig. 3).

The resurgence of *D. antillarum* since the 1980s die-off is critical for reef recovery (Miller et al. 2003, Hylkema et al. 2023). Exclusion experiments demonstrate that reefs with restored urchin populations have reduced macroalgal biomass and higher coral recruitment (Davis et al. 2023), particularly significant on overfished reefs (Idjadi et al. 2010, Bodmer et al. 2021). The effectiveness of herbivory depends on macroalgal composition, nutrient availability, and urchin density (Steneck et al. 2018), with excessive urchin densities potentially causing bioerosion (Carreiro-Silva & McClanahan 2001). Together, these interactions form a dynamic balance: unchecked macroalgae impose shading, allelopathy, and altered nutrients that can overwhelm corals, whereas sufficient grazing by *D. antillarum* (and other herbivores) relieves algal pressure and aids coral recovery. These trophic interactions between *D. antillarum*, corals, and macroalgae are highly context dependent, with outcomes determined by the relative magnitudes of competitive, facilitative, and antagonistic processes.

4.2. Plasticity as a mediator of ecological interactions

Phenotypic plasticity enables corals and *D. antillarum* to respond adaptively to environmental pressures, mediating their ecological interactions. The plastic responses documented at molecular and organismal levels (Sections 2 and 3) gain ecological meaning only through their effects on species interactions and community structure. This mediation operates bidirectionally: plasticity modulates how organisms experience competitive interactions, while competitive context determines whether plastic responses enhance fitness or merely delay competitive exclusion.

The *D. antillarum*—coral interaction demonstrates contextual dependency based on macroalgal abundance. Urchin grazing benefits corals under high macroalgal density but may damage coral recruits when macroalgal cover is low (Edmunds et al. 2024, Lachnit et al. 2025). Urchins also indirectly influence coral phenotype by altering substrate microbial communities and biofilm composition, enhancing larval settlement cues and post-settlement survival, particularly for brooding corals (Castillo et al. 2024). When *D. antillarum* effectively controls macroalgae, coral plastic adjustments can sustain growth despite sublethal stress. However, when macroalgal cover exceeds critical thresholds (~40–50% benthic cover), the cumulative energetic costs of defensive responses — including enhanced heterotrophy, mucus production, and immune function — can exceed coral energy budgets, resulting in tissue necrosis, reduced calcification, and mortality despite plastic compensatory mechanisms (Rasher et al. 2011, Barott et al. 2012).

Therefore, an herbivory threshold often exists above which macroalgal proliferation can be suppressed, creating conditions conducive to coral recruitment and survival (Holbrook et al. 2016). Reefs with recovering *D. antillarum* populations demonstrate increased coral recruitment rates, juvenile survival, and reduced macroalgal biomass (Carpenter & Edmunds 2006, Idjadi et al. 2010), although trajectories toward coral dominance depend on multiple factors including coral propagule supply, water quality, and the severity of prior degradation (Edmunds & Carpenter 2001). These bidirectional relationships highlight phenotypic plasticity as a mediating factor in coral–macroalgae–urchin interactions and a potential resilience mechanism for Caribbean reefs (Edmunds & Putnam 2020). The interdependence of coral and urchin plasticity with trophic context underscores that organismal acclimatization capacity alone cannot determine ecosystem outcomes — trophic structure fundamentally shapes whether plastic responses translate into ecological resilience. This principle establishes the conceptual foundation for understanding how climate-driven alterations to both organismal physiology and trophic relationships jointly determine reef trajectories under environmental change.

5. CLIMATE-DRIVEN TROPHIC ALTERATIONS

The coupled molecular–organismal–trophic framework developed in Sections 2–4 shows that reef resilience emerges from the integration of plastic capacity and functional trophic structure. This section examines how anthropogenic climate change disrupts both components simultaneously, creating synergistic pressures that can drive ecosystem transitions beyond reversible thresholds. By analyzing multistressor interactions and their effects on the coral–macroalgae–*Diadema antillarum* system, we identify critical junctures where management interventions might maintain reef function versus conditions where alternative stable states become inevitable.

5.1. Impacts of climate change on reef trophic dynamics

Climate change destabilizes coral reefs through cascading effects on trophic dynamics and community structure (Hughes et al. 2023, Klein et al. 2024). Multiple stressors, including thermal stress, acidification, altered nutrient regimes, and overfishing, compromise reef resilience by undermining critical herbivore–coral interactions, particularly those mediated by keystone species such as *D. antillarum* (Vega Thurber & Hay 2023). Climate-induced coral mortality reduces structural complexity, while simultaneously constraining herbivore physiological performance, as *D. antillarum* exhibits narrow thermal safety margins (3–5°C) that limit adaptive capacity under extreme warming scenarios (Sherman 2015). This dual pressure mechanism significantly lowers the grazing threshold required to prevent coral–macroalgal phase shifts, accelerating ecosystem transitions to macroalgal dominance (Anthony et al. 2011).

Thermal stress disrupts the coral–*Symbiodinium* relationship, causing bleaching and mortality (Baker et al. 2008, Hughes et al. 2017, Cornwall et al. 2024), and ocean acidification reduces calcium carbonate availability (Cornwall et al. 2024), hindering skeletal formation (Fabricius et al. 2011, B. Williams et al. 2021). These stressors extend beyond corals to disrupt critical trophic interactions, favoring macroalgal growth (McCook 2001, Adam et al. 2022). Historically, *D. antillarum* regulated macroalgal cover until the 1983–1984 die-off, which rapidly shifted reefs toward macroalgal dominance (Adam et al. 2015, Sherman 2015). Reefs where *D. antillarum* are present often show increased coral recruitment and cover rebound (Carpenter & Edmunds 2006, Idjadi et al. 2010, Levitan et al. 2014). However, ocean acidification also alters urchin physiology by reducing test calcification, spicule formation, and skeletal integrity (Hazan et al. 2014), potentially diminishing their grazing role (Mumby et al. 2007, Sherman 2015).

Climate change and anthropogenic stressors create synergistic pressures that compromise coral–herbivore–macroalgae dynamics. Warming-induced coral bleaching diminishes substrate availability while ocean acidification (>450–500 ppm CO_2) impairs recovery, potentially driving phase shifts toward macroalgal dominance even under functional herbivory (Anthony et al. 2011). Nutrient enrichment from agricultural runoff, urbanization, and wastewater — frequently exceeding critical thresholds (~1 µM dissolved inorganic nitrogen) — stimulates macroalgal proliferation that directly competes with corals (Lapointe 1997, McCook 2001, Fabricius et al. 2024). Sedimentation further complicates these dynamics by smothering corals, reducing light penetration, and increasing nutrient availability (Hughes 1994, Wooldridge 2009, Wenger et al. 2016).

Climate-intensified precipitation and storm frequency (Kundzewicz 2008, Tabari 2020, Ehtasham et al. 2024) exacerbate nutrient loading and sedimentation, which smothers corals and alters bottom-up trophic controls (Kwiatkowski et al. 2019, Becker & Silbiger 2020). These conditions sometimes can overwhelm even healthy *D. antillarum* grazing capacity (Ramseyer et al. 2021, Godard et al. 2024) while simultaneously reducing urchin growth, reproduction, and survival (Kobelt et al. 2020, Wijers et al. 2024, Godard et al. 2024). This multi-stressor environment challenges the physiological tolerances of both organisms, representing a significant vulnerability point for reef ecosystems globally (Bruno et al. 2009, Becker & Silbiger 2020, Hill & Hoogenboom 2022) (Fig. 4).

5.2. Threshold dynamics and implications for reef resilience and management

The interplay between phenotypic plasticity and trophic dynamics critically shapes the adaptive capacity of reef organisms (Bellwood et al. 2024). Models incorporating natural adaptation (acclimatization, genetic adaptation) suggest coral persistence under moderate warming, whereas models ignoring adaptation predict collapse (Drury et al. 2022b, Lachs et al. 2023). The integration of biophysical thresholds with biological plasticity provides a framework for understanding how reefs navigate between coral- and macroalgae-dominated states under multiple stressors (Fig. 4).

Recent studies document significant plastic responses in both corals and *D. antillarum* that may enhance resilience. Corals demonstrate thermal plasticity through symbiont modification, enhancing bleaching survival (Baker et al. 2008, Drury et al. 2022b). Transgenerational plasticity mechanisms function as potential resilience factors: offspring of heat-

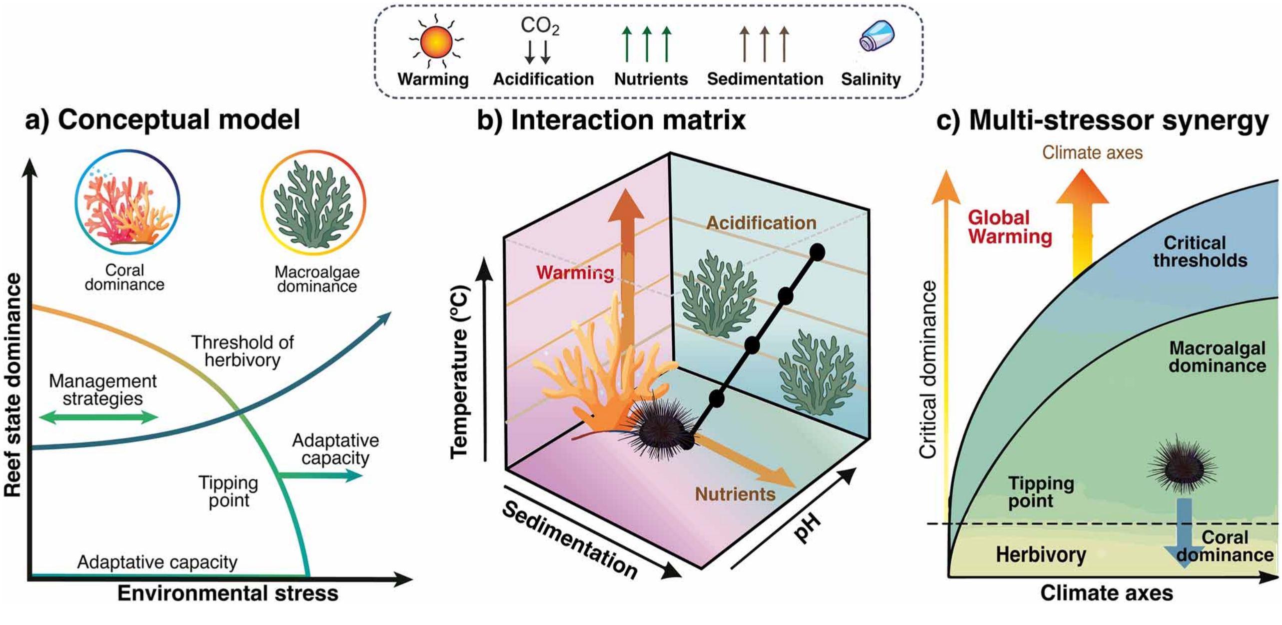

Fig. 4. Multi-stressor interactions and climate-driven regime shifts in coral reef resilience. (a) Conceptual trajectory model illustrating the non-linear transition pathways between coral-dominated and macroalgal-dominated ecosystem states, depicting how cumulative stress exposure erodes coral competitive advantage through impaired calcification, compromised symbiont function, and altered metabolic capacity. Blue line: projected trajectory under current management, color gradients in circles: degree of ecosystem stability/variability, gradient in threshold herbivory line: uncertainty range in tipping point location. (b) Three-dimensional interaction matrix quantifying the combinatorial effects of multiple stressors, identifying synergistic thresholds where interactive effects exceed additive predictions, indicating non-linear system responses. (c) Interactions between global (thermal stress, acidification) and local (eutrophication, sedimentation) stressors contributing to ecological bottlenecks compromising reef resilience. Herbivory-mediated top-down control acts as a critical buffer mechanism that can moderate competitive outcomes under moderate stress conditions. This quantitative approach facilitates prediction of ecological tipping points and provides empirical foundations for adaptive management strategies targeting cross-scale stressor interactions in coral reef conservation

stressed corals have enhanced thermal tolerance via DNA methylation changes (Putnam & Gates 2015) and modified gene expression profiles (Liew et al. 2020, Peterson et al. 2024), and *D. antillarum* larvae from stressed parents display altered physiological responses (Sherman 2015).

However, plasticity alone is insufficient for maintaining ecosystem function under combined thermal and local stressors (i.e. ocean warming and acidification, nutrient enrichment, increased sedimentation, and overfishing or disease-induced loss of key herbivores); trophic context is crucial to determine community outcomes. Even heat-acclimated corals struggle when overgrown by macroalgae. Caribbean reefs with functional *D. antillarum* populations have demonstrated greater resistance to macroalgal overgrowth despite warming, whereas those without effective grazers shifted to macroalgal dominance (Carpenter & Edmunds 2006, Idjadi et al. 2010, Levitan et al. 2014, Precht & Precht preprint https://doi.org/10.7287/peerj.preprints.1565v1). Thus, reef resilience depends on feedback between coral resistance and herbivore function. Moreover, adaptive plasticity may not keep pace with rapid climate change (Holbrook et al. 2016, Nash et al. 2016). Trade-offs between thermal tolerance and competitive ability in corals suggest acclimatization to one stressor may increase vulnerability to others (Matsuda et al. 2023, Scharfenstein et al. 2023, Roik et al. 2024). Models indicate that reefs with robust *D. antillarum* populations may persist under moderate warming (+1.5°C) but could potentially collapse under severe scenarios (Edmunds & Carpenter 2001, Bodmer et al. 2017, Bodmer 2019, Williams 2022), highlighting the importance of preserving functional herbivore populations as a resilience-building strategy.

Building on the multi-stressor evidence, modeling and empirical studies indicate that beyond ~450 ppm CO_2 — where acidification and CO_2-driven physiological stress impair calcification and reduce herbivore efficacy — local management becomes decisive for maintaining coral dominance (Anthony et al. 2011). Reducing nutrient inputs, sediment loads, and fishing pressure can enhance reef resilience (Hughes et al. 2023) but must be coupled with global climate mitigation efforts (Hoegh-Guldberg et al. 2023a,b). Ultimately, resilience requires aligning coral adaptive capacity with functional ecosystem structure: even adaptive corals require effective herbivory to prevent macroalgal overgrowth. Understanding this interplay between physiological plasticity and trophic dynamics is essential for predicting whether reefs will persist in coral-dominated states or shift to alternative ecological regimes under continuing climate change (Fig. 4).

6. CONCLUSIONS

The complex interplay between phenotypic plasticity and trophic dynamics represents a key determinant of reef trajectories under accelerating environmental change. Both corals and *Diadema antillarum* exhibit plasticity through epigenetics, metabolic shifts, and behavioral adjustments. However, the benefit of these responses depends on trophic context. Herbivory by *D. antillarum* mediates macroalgal competitive pressure and sustains reef resilience (Mumby et al. 2006b, Bodmer et al. 2021), illustrating the interdependence of physiological and ecological processes. Climate stressors and anthropogenic pressures increasingly risk exceeding both plastic and adaptive capacities while disrupting critical trophic relationships (Hughes et al. 2023, Vega Thurber & Hay 2023).

Restoring *D. antillarum* populations through hatchery-based propagation and restocking, translocation, and substrate enhancement to facilitate natural recruitment (Hassan et al. 2022, Hylkema et al. 2022) represents a promising management strategy for shifting macroalgal-dominated reefs toward increased coral dominance (Arnold & Steneck 2011, de Breuyn et al. 2023). Emerging restoration approaches integrating *D. antillarum* with coral nursery systems demonstrate synergistic benefits, including reducing fouling macroalgal growth and enhancing coral survival rates, and may facilitate microbiome conditioning that improves post-outplanting performance (Craggs et al. 2019, Lachnit et al. 2025). However, achieving grazing densities sufficient to suppress macroalgal proliferation remains challenging (Holbrook et al. 2016), particularly following the 2022 mortality event.

Despite growing recognition of the role of plasticity in resilience, several gaps persist regarding the mechanistic integration of plasticity and trophic dynamics. The persistence, reversibility, and functional significance of stress-induced epigenetic modifications remain unresolved (Hackerott et al. 2023), while the synergistic roles of host genotype, symbionts, and microbiomes in holobiont plasticity require deeper mechanistic understanding (Torda et al. 2017, Drury 2020, Shaver et al. 2022). Most studies remain short-term and lack integration across biological scales (Parkinson et al. 2020). Empirical data linking coral plasticity to herbivore-mediated outcomes are scarce. Advancing reef conservation requires multifactorial field experiments manipulating abiotic stressors (temperature, pH, nutrients, sedimentation) and biotic factors (urchin density, macroalgae), alongside advanced genomic approaches to disentangle mechanisms and guide evidence-based conservation strategies.

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