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A boom-or-bust approach—The ‘Glass Cannon’ hypothesis in host microbiomes

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Abstract

In Focus: Dunphy, CM, Vollmer, SV, Gouhier, TC. (2021) Host-microbial systems as glass cannons: Explaining microbiome stability in corals exposed to extrinsic perturbations. *Journal of Animal Ecology*, 90, 1044–1057. The importance of symbiotic microbial communities for the functioning of animal hosts is now well-documented; however, the interactions between host microbiomes and stress are less well-understood. Dunphy et al. used a common garden experiment to show that host-microbiomes vary in their resilience across different coral species. The authors then used mathematical modelling to provide novel evidence that species with microbiomes that are regulated by host processes are robust to perturbation from stressors, but that robustness comes at a higher cost to the host. Conversely, species with microbiomes that are regulated by microbial processes are generally much more resilient and cheaper to support, but when disrupted by external stressors, the communities break down entirely—these latter species are termed ‘glass cannons’. This novel hypothesis has important implications for how host microbiomes function in a rapidly changing world that exposes animal hosts to multiple biotic and abiotic perturbations.

KEYWORDS

biological control, coral immunity, host-microbial interactions, microbiome, resistance, stability

Symbiotic microbial communities provide an expansive range of functions for their hosts, influencing digestion and nutrient absorption, immunity and disease resistance, and even behaviour and fecundity (Antwis et al., 2020). The last decade or so has seen considerable and valuable ‘cataloguing’ of host-microbial communities, the biological and environmental factors that influence them, and the implications of this for host functioning (Antwis et al., 2020). However, we still have a relatively poor understanding of how microbial communities respond to change or stress, and how host processes and the microbiome interact to regulate this response. This is important because host microbiomes may provide a vital barrier or buffer to environmental change for their hosts, through their diverse functional repertoire and their ability to rapidly respond to environmental

change. For example, corals of the Persian–Arabian Gulf can withstand remarkably high salinities and temperatures exceeding 35°C through their association with *Symbiodinium thermophilum*, which may have been naturally selected by extreme temperatures during the Holocene (D’Angelo et al., 2015; Hume et al., 2016).

Recently, researchers have started to look more closely at this relationship between host microbiomes and stability. Much of this work has been linked to the ‘Anna Karenina’ principle—first applied to host microbiomes by Giongo et al. (2011) and later succinctly reviewed by Zaneveld et al. (2017), propelling it into the foreground of current microbiome research. It derives from the opening line of Tolstoy’s famous novel of the same name, which says, ‘All happy families look alike; each unhappy family is unhappy in its own way’

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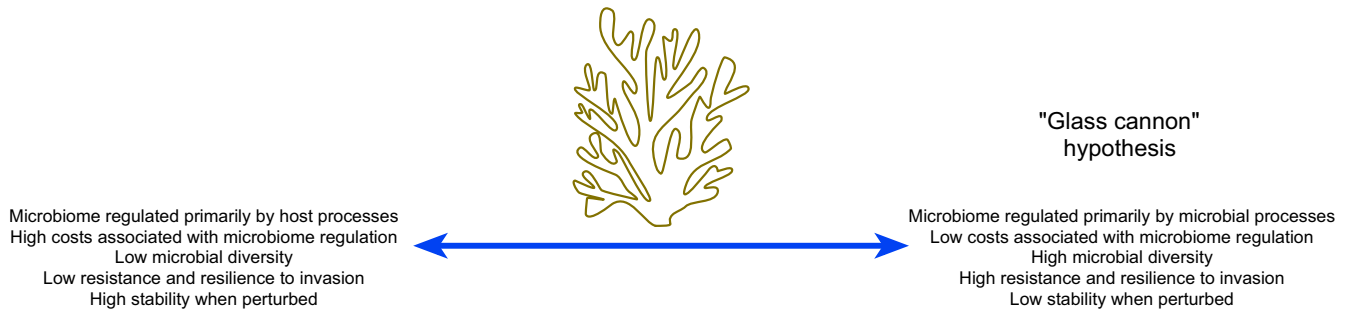


FIGURE 1 A schematic of the 'glass cannon' hypothesis, representing the two extremes of microbiome regulation in hosts, the costs and implications of this for host resilience to disturbance, and the outcomes when perturbed. Hosts that regulate their own microbiome do so at high cost, but with the benefit of high stability when perturbed. This is important because these types of microbiomes are also more susceptible to disturbance due to their low diversity. Conversely, hosts that have self-regulating microbiomes have lower associated costs overall, but these microbiomes are more diverse and more resistant to disturbance. However, if the microbiome is perturbed, the whole community breaks down and the host is incredibly vulnerable—like a glass cannon

(Tolstoy, 1877). The Anna Karenina principle proposes that individuals with stable microbiomes will show low variability with one another and over time (i.e. 'happy' microbiomes are similar to one another), whereas unstable or dysbiotic microbiomes will be highly variable (i.e. 'unhappy' microbiomes are different to one another). Although other work has demonstrated that this isn't necessarily the case in all study systems and under all types of disturbance (e.g. Lavrinienko et al., 2020; Sweet et al., 2019), the literature around microbiome stability is now growing in an already busy field of microbiome research (Figure 1).

The recent paper by Dunphy et al. (2021), published in the *Journal of Animal Ecology*, takes this one step further, looking at interspecific variation in microbiome stability, and how this links to the mechanism by which an organism obtains its symbiotic community. Using a common garden experiment with three species of coral, the researchers dosed half their study organisms with antibiotics and kept the other half as a control, before transplanting them all back into the field, and monitoring their bacterial microbiomes over 6 months. They found that perturbed individuals of one of the coral species—the mustard hill coral *Porites astreoides*—had an unstable microbiome when transplanted into the field, whereas the control individuals had a stable microbiome. This suggests that organisms with normally 'happy' microbiomes that are resilient to change can become 'unhappy' when challenged with an additional stressor. The authors then used mathematical modelling to show that when microbiomes are regulated by host processes (such as host-derived antimicrobials), they are robust to perturbation from stressors, but that robustness comes at a higher cost to the host. Conversely, species with microbiomes that are regulated by microbial processes (such as microbially derived antimicrobials) are much cheaper for hosts to support but are also much more susceptible to disruption from external stressors. Interestingly, the microbiomes associated with species that fit into this latter category also show greater resilience to change—the problem arises when an external stressor knocks out key microbes responsible for regulating the total microbiome (e.g. keystone species Banerjee et al., 2018). Dunphy et al. (2021) neatly term these species as 'glass cannons' as they support highly effective microbiomes until a disturbance causes

the communities to shatter, leaving the hosts vulnerable to problems with infectious diseases and microbiome-derived physiological processes. Generally speaking, this suggests that host-level regulation is akin to an innate immune response that can deal reasonably well with most types of threats and provide reasonable levels of stability in general. However, microbial regulation is akin to a more targeted adaptive immune response that responds acutely to some threats but completely fails to protect against others.

These findings have important implications for hosts in our rapidly changing world, as they suggest that, for some species, the buffer provided by their microbiomes against external stressors may be fragile and particularly susceptible to multiple synergistic stressors. The results also suggest the potential for 'surprises' when it comes to predicting which coral species will be resilient to perturbation, since those operating as glass cannons might appear extremely resilient today but fold up like a cheap tent in response to future, targeted threats. We still know relatively little about the host and community processes that drive microbiome assembly, and what this means for host resilience to change. This will be a particularly important area for research in the next few years and we seek to understand the full potential for host microbiomes to mitigate the range of threats facing species on our planet.

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