

Emergent hotspots of biotic disturbances and their consequences for forest resilience

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Over the past several decades, forests worldwide have experienced increases in biotic disturbances caused by insects and plant pathogens – a trend that is expected to continue with climate warming. Whereas the causes and effects of individual biotic disturbances are well studied, spatiotemporal interactions among multiple biotic disturbances are less so, despite their importance to ecosystem function and resilience. Here, we highlight an emerging phenomenon of "hotspots" of biotic disturbances (that is, two or more biotic disturbances that overlap in space and time), documenting trends in recent decades in temperate conifer forests of the western US. We also explore potential mechanisms behind and effects of biotic disturbance hotspots, with particular focus on how altered post-disturbance recovery (successional pathways) can have profound consequences for ecosystem resilience and bio-diversity conservation. Finally, we propose research directions that can elucidate drivers of biotic disturbance hotspots and their ecological effects at various spatial scales, and provide insight into this new knowledge frontier.

Front Ecol Environ 2023; 21(8): 388-396, doi:10.1002/fee.2659

E cosystems worldwide are changing rapidly as a result of the individual and combined effects of climate warming and associated disturbances (Seidl *et al.* 2017). Understanding the mechanisms that underpin ecosystem resilience – the capacity to tolerate disturbance without permanently

In a nutshell:

- Hotspots of biotic disturbances areas where two or more distinct biotic disturbances overlap in space and time, such as simultaneous outbreaks of insects and plant pathogens at a given location – are widespread in western US forests
- Overlapping biotic disturbances can have profound effects on ecosystem resilience but are poorly characterized and understood
- Biotic disturbance hotspots can be the result of linked disturbance interactions or coincident overlap from strong broad-scale climate drivers
- Compounded effects from biotic disturbance hotspots may erode important resilience mechanisms, such as disturbance legacies and compensatory responses
- We present a framework for understanding the causes and consequences of biotic disturbance hotspots that can inform conservation and ecosystem management

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Temperate conifer forests in the northern hemisphere are experiencing unprecedented increases in biotic (eg insect and/or plant pathogen) disturbances (Raffa et al. 2008; Millar and Stephenson 2015). Between 2003 and 2012, biotic disturbances collectively affected more temperate forested area annually than any other disturbance type, including fire (van Lierop et al. 2015) – although trends vary across forest biomes (eg in boreal forests, fire and logging have affected a larger area than biotic disturbances; Zhang et al. 2022). Even with recent increases in forested area burned to levels that exceed biotic disturbances globally (Zhang et al. 2020; Jones et al. 2022), biotic disturbances remain a key driver of forest dynamics and ecosystem change. Since the early 2000s, biotic disturbances have reduced live carbon pools by nearly twice as much as wildfire over the entire western US, with trends variable among ecoregions (Berner et al. 2017). To date, most research examining biotic disturbances has focused on individual biotic disturbance agents affecting specific host tree species (eg Chapman et al. 2012), and forest responses to single biotic disturbances over a limited spatial extent (eg Veblen et al. 1991). Far less is known about how multiple biotic disturbances interact across space and time (Burton et al. 2020), or how these dynamics vary across scales (Raffa et al. 2008).



Figure 1. (a) Forest disturbance by a single biotic disturbance agent, in which mountain pine beetle (*Dendroctonus ponderosae*) killed the host (lodgepole pine [*Pinus contorta*]) but the non-host (subalpine fir [*Abies lasiocarpa*]) survived, versus (b) a biotic disturbance hotspot, where – in overlapping outbreaks – spruce beetle (*Dendroctonus rufipennis*) killed Engelmann spruce (*Picea engelmannii*), and western balsam bark beetle (*Dryocoetes confusus*) and *Armillaria* root rot killed subalpine fir. Image credits for (a) and (b): BJ Harvey. Complementary datasets illustrate the extent and trends over time in biotic disturbance hotspots, observed in (c) <0.5-ha US Forest Service (USFS) Forest Inventory and Analysis (FIA) plots from the 11 western conterminous US states (r = 0.32, P = 0.16) and (d) aerial detection surveys covering USFS Regions 1–6, which comprise the western conterminous US states, aggregated to 25-ha grid cells. In (c), the red circles and black line represent individual data points (years) and the linear regression, respectively, whereas the shaded area denotes the 95% confidence interval for the linear regression slope.

We present a framework for addressing an emerging phenomenon with important consequences for forest resilience: hotspots where two or more distinct biotic disturbances overlap in space and time. First, we present recent trends of such overlapping biotic disturbances and review relevant ecological literature on disturbance interactions and their consequences. Second, we propose a framework for testing mechanisms of biotic disturbance interactions across spatial and temporal scales. We close by exploring key frontiers for understanding the causes and effects of biotic disturbance hotspots and propose several important and related research questions oriented toward generating insights that can help guide environmental management.

Biotic disturbance hotspots: empirical trends across the western US

In the 21st century so far, biotic disturbance activity has been particularly severe in western North America. Since the late 1990s, 5–10 million ha of forests within the western

conterminous US and Canada have experienced widespread and severe tree mortality from bark beetles, defoliators, and fungal pathogens across tree taxa (Raffa et al. 2008; Meddens et al. 2012), converting approximately 15 teragrams of carbon from live to dead biomass annually (Berner et al. 2017). Disturbances caused by individual biotic agents, such as the mountain pine beetle (Dendroctonus ponderosae), have been well studied (eg Kurz et al. 2008). Although individual biotic agents can cause high (>50%) host tree mortality within a stand, specificity between insects or pathogens and their host trees often leads to strong compensatory responses of surviving non-host trees (eg subalpine fir [Abies lasiocarpa] after an outbreak; Figure 1a). Consequently, the loss in live biomass for the primary host tree species of the disturbance agent leads to gains in live biomass for surviving individuals of both host and non-host tree species. However, much less explored are locations where disturbances caused by two or more biotic agents overlap, and instead of experiencing compensatory growth from the loss of their neighbors, species that survive disturbance from one biotic agent are

killed by another (eg a spruce beetle [*Dendroctonus rufipennis*] outbreak killed Engelmann spruce [*Picea engelmannii*] while a simultaneous and combined outbreak of western balsam bark beetle [*Dryocoetes confusus*] and Armillaria root rot [*Armillaria* spp] killed subalpine fir; Figure 1b). The spatial and temporal overlap among multiple biotic disturbance agents compromises forest capacity to resist and recover post-disturbance, with unknown impacts on forest resilience.

Here, we present extensive data on the emergent phenomenon of biotic disturbance hotspots. Such hotspots can occur when two or more distinct biotic disturbances affect the same location in the same year (Figure 1, b–d), or, when lagged in time, may indicate potential mechanistic links (Figure 2). Using two complementary datasets – one containing fine-scale data collected from permanent plot locations and the other containing broad-scale data collected from aerial forest health surveys – we show that, from 1997 through 2019, biotic disturbance hotspots have occurred in approximately 50,000 km² of forests throughout the western US,

accounting for approximately 7% of total area affected by all biotic disturbances. Analysis of data from a broad network of <0.5-ha field plots included in the US Forest Service (USFS) Forest Inventory and Analysis (FIA) program suggests that, annually, 12–16% of forests affected by biotic disturbances are biotic disturbance hotspots (Figure 1c). At slightly coarser scales, USFS Aerial Detection Survey (ADS) data from fixed-wing aircraft, aggregated to 25-ha grid cells, similarly indicate that approximately 5% of forests affected by biotic disturbances each year are hotspots, with a sharp rise to a peak of 18% in 2016 and a subsequent decline (Figure 1d).

Expectations of biotic disturbance interactions

As forest disturbance activity has increased worldwide in recent decades, so too have concepts and hypotheses around disturbance interactions (see Burton *et al.* [2020] for a review). For example, interacting disturbances can be mechanistically linked in that the occurrence or magnitude of one disturbance affects the likelihood or magnitude of another (Simard *et al.* 2011). Successive outbreaks of the same biotic agent, such as a bark beetle species, are generally characterized by negative (or inhibitory) links – because the initial outbreak removes the key ingredients (eg susceptible host trees) necessary for subsequent outbreaks (Hart *et al.* 2015; Burton *et al.* 2020). For disturbances involving different species of biotic agents, interactions may be positive, negative, or nonexistent, depending on the



Figure 2. Different potential dynamics of biotic disturbance interactions in forests. The solid orange line and dashed blue line represent the area affected by two different species of biotic agents on the same or different host tree species, within the same location (eg forest stand).

drivers of each disturbance. Despite the severity and extent of recent biotic disturbances in western North American forests (Meddens *et al.* 2012), interactions among distinct biotic agents of disturbance and their combined effects on different co-occurring host trees have received scant attention.

Several types of interactions among disturbances caused by different species of biotic agents might be expected based on findings reported in the ecological literature and current mechanistic understanding (Figure 2). First, given a fixed total area of forest in western North America (over contemporary timescales), increases in the area affected by individual biotic agents will inevitably result in overlap of affected areas. Such overlap could be a result of spatially correlated inciting factors like drought (eg the Moran effect; Moran 1953), as that which recently occurred in California's Sierra Nevada mountains (Young et al. 2017). When this occurs, synchronous pulses of tree mortality caused by different biotic agents may overlap in space but are responding to a common broad-scale driver as opposed to any mechanistic link with one another (Figure 2a). Second, two disturbances caused by different biotic disturbance agents can be linked through positive feedback mechanisms, such as when defoliating insects reduce tree vigor, leaving trees more susceptible to bark beetle attacks (Hadley and Veblen 1993). In this case, an expected lag (eg 3-7 years) would occur between outbreaks of the two positively linked biotic agents occurring in the same place, as time is required for the first

agent to affect host susceptibility for a second agent (Figure 2b). Third, the occurrence of one insect outbreak can decrease the likelihood or severity of a subsequent insect outbreak (negative links; Figure 2c), as susceptible host trees are removed and non-host trees respond to additional resource availability with strong compensatory growth and increased vigor. Such outcomes are common, leading to conspicuous non-overlap of current bark beetle outbreaks with past outbreaks of the same species (Veblen et al. 1991; Hart et al. 2015), or rapid growth response of tree species that are non-hosts for the first biotic agent (Diskin et al. 2011). Finally, and potentially the most important interaction with respect to the emerging phenomenon of biotic disturbance hotspots, is the case when either two disturbances unexpectedly overlap or a potential positive link unexpectedly materializes in place of an expected negative link (Figure 2d). These links could occur when a bark beetle outbreak (by beetle species A) in one host tree species (host tree species X) is followed closely in time and space by a second bark beetle outbreak (by beetle species B) in a co-occurring but different host tree species (host tree species Y) (Andrus et al. 2020a; Harvey et al. 2021). Such links would presumably be unexpected, as host tree species Y, which was not attacked by the first biotic agent (beetle species A), would be expected to benefit in terms of compensatory growth and increased vigor following the loss of a competitor (host tree species X) and would consequently be more resistant to attack by the second biotic agent (beetle species B) (Veblen *et al.* 1991). After adequate time has passed, mechanistic links between biotic disturbances will fade into more typical ecosystem dynamics, as compensatory responses of different host trees can lead to growth into tree size classes that are more susceptible to biotic agents (Buonanduci *et al.* 2020).

In addition to aggregate trends (Figure 1, c and d), individual pairwise combinations of overlapping biotic disturbance agents that compose hotspots can provide insight into potential mechanisms underpinning interactions (Figure 3). Such pairwise combinations could be further separated into those that correspond to different typologies of linked interactions among disturbances caused by biotic agents in different feeding guilds and host tree species (Figure 2). For example, defoliators such as western spruce budworm (*Choristoneura freemani*) are expected to precede outbreaks



Figure 3. Detections from pairwise combinations between two distinct biotic disturbance agents across the western conterminous US states (1997–2019) when both agents were (a) spatially and temporally overlapping and (b) spatially overlapping but lagged in time (3–7 years). Data are the same as in Figure 1d (USFS Aerial Detection Surveys). Because detections are counted per cell and per year, a given cell may be counted multiple times toward total detections. Pinyon pine mortality, five needle pine decline, and subalpine fir mortality complex are mapped as mortality complexes for the host trees where a single mortality agent is not identified; ips engraver beetles include multiple species of beetles in the genus *lps*.

of Douglas-fir beetle (Dendroctonus pseudotsugae) (Figure 3b, lower left) through positive links (Hadley and Veblen 1993; Cole et al. 2022). However, Douglas-fir beetle outbreaks preceding western spruce budworm outbreaks are unexpected positive links that have occurred in the past two decades (Figure 3b, upper right). Unlinked overlap of multiple host-specific bark beetle outbreaks may be expected to occur if triggered by a common driver (eg drought), and may be synchronous (Figure 3a) or characterized by short lags due to differences in temperature-dependent developmental rates among the life stages of different biotic agents. Such overlap is widespread (eg Figure 3b, overlapping mountain pine beetle, spruce beetle, and subalpine fir mortality complex all occurring in combination with one another and in varying sequential order), and these biotic disturbance hotspots are concerning because they could indicate that the compensatory responses of non-host trees that survive one outbreak are eroding, leaving those trees susceptible to subsequent biotic disturbances.

Biological legacies, compensatory responses, and ecosystem resilience

Biotic disturbance hotspots likely have profound impacts on resilience mechanisms, potentially leaving forests more 409309, 2023

vulnerable to state change. When occurring in relatively short succession or synchronously, two disturbances can produce synergistic compounded disturbance effects (Paine *et al.* 1998). For instance, compounded effects from multiple severe fires in short succession can send forests on qualitatively different post-fire trajectories as compared to individual effects from single fires (Turner *et al.* 2019). However, the potential compounded effects of overlapping biotic disturbance agents have received little attention (but see Andrus *et al.* [2020a] for an example). Two related dimensions of ecosystem resilience that can be eroded in biotic disturbance hotspots are biological legacies and compensatory responses (Figure 4).

Biological legacies – the organic material (both living and dead) that persists after a disturbance (Franklin *et al.* 2000) – are critical to supporting resilience of ecosystem structure and function to disturbance (Johnstone *et al.* 2016). For example, as bark beetle outbreaks are often host specific, many post-outbreak forests are characterized by abundant live non-host trees (eg Diskin *et al.* 2011) and relative stability in total woody carbon pools because slow decay of snags and logs is offset by live tree growth (eg Hansen 2014) (Figure 4, single biotic disturbance pathway). However, compounded effects from multiple biotic agents killing different host tree species and age classes thereof could sharply reduce live tree



Figure 4. Conceptualized outcomes of how disturbance dynamics (biotic disturbance hotspots versus single biotic disturbances) and their consequences can produce a range of compensatory responses and biological legacies along gradients of environmental stress (eg drought) to affect forest resilience.



Figure 5. Contrasting patterns of tree regeneration following early 21stcentury Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreaks in the northern US Rocky Mountains, in which (a) mesic sites exhibited strong compensatory responses and abundant live biological legacies while (b) dry sites exhibited weak compensatory responses and few living biological legacies. Image credits for (a) and (b): DC Donato.

legacies, shifting the balance of woody carbon toward more dead than live biomass (Figure 4, hotspots pathway). For instance, in bark beetle outbreaks, tree mortality is often highest among older large-diameter overstory host tree species; whereas in defoliator outbreaks, mortality is highest among younger understory seedlings and saplings; and in fungal pathogen outbreaks, mortality is widespread across size/age classes of susceptible species. The nature of dead wood legacies left by different biotic disturbance agents can therefore differ substantially (eg differences among tree species and tree sizes in wood chemistry and density), potentially altering the residence time of dead woody carbon pools in biotic disturbance hotspots as compared to legacies generated by single biotic disturbance agents.

If biotic disturbance hotspots result in high levels of tree mortality, the importance of seeds as biological legacies

contributing to regeneration and forest persistence becomes elevated. However, hotspots may also produce compounded effects on available seed banks. For example, most outbreaks of bark beetles cause mortality of the largest and oldest trees, which disproportionately produce the most cones and seeds (Andrus et al. 2020b). Smaller trees that survive bark beetle outbreaks can respond by producing more cones per tree when they are released from competition with neighbors (Andrus et al. 2020b), but this effect may be negated by additional overlapping disturbances. For example, outbreaks of defoliators (eg Choristoneura spp) produce disproportionately higher mortality of smaller understory trees (Hadley and Veblen 1993) and reduce cone production to near zero when defoliation is severe (Chrisman 1980; Simard and Payette 2005). In such cases, overlapping biotic disturbances can result in compounded effects on post-disturbance reproductive capacity and potentially shift successional trajectories toward non-forest systems. Understanding how biotic disturbance hotspots affect both living and dead biological legacies, and in turn resilience, is an important frontier.

Compensatory responses - when the loss or decline of one ecological component is offset by the growth or increase of another (Gonzalez and Loreau 2009) - are particularly important in the face of biotic disturbances because effects are often unevenly distributed across age, size, and species of tree. For instance, post-outbreak growth releases from surviving trees can be rapid and long lasting (Veblen et al. 1991), providing stability and fostering resilience (Lloret et al. 2012). However, compensatory responses can vary at broad scales across environmental gradients (Redmond and Kelsey 2018), and if environmental conditions are particularly stressful or unsuited to surviving individuals, compensatory responses may be dampened (Figure 4, low compensation pathways for both hotspots and single biotic disturbances). Following Douglas-fir beetle outbreaks in the Rocky Mountains of the northern US, for instance, tree regeneration was qualitatively slower in dry and marginal sites than in mesic sites (Figure 5). In such cases, a gradient of stress could drive divergence in responses, ranging from trajectories toward recovery to pre-outbreak levels (in locations under low levels of stress) to a loss of forest cover and conversion to non-forest ecosystems (in locations under high levels of stress). Little is known about how compensation varies across spatiotemporal scales and levels of biological organization (Gonzalez and Loreau 2009), or how ecosystems compensate in the face of multiple disturbances (Lindenmayer et al. 2016) - underscoring the need for additional research on the overlap of biotic disturbances along gradients of environmental stress (Figure 4).

An improved understanding of how biotic disturbance hotspots are affecting forest resilience can inform ecosystem management in a warming and more disturbance-prone world (Millar and Stephenson 2015), and support societal decisions regarding altered delivery of ecosystem services (Lindenmayer *et al.* 2016). Where severe and spatially extensive, biotic disturbance hotspots could be thought of as counterparts to disturbance refugia (Krawchuk et al. 2020), which are locations where ecosystem structure is relatively unchanged by multiple disturbances and where resilience remains high. Instead, biotic disturbance hotspots are sites of potentially severe cumulative disturbance effects and may differ from other disturbance interactions in important ways. For example, as the effects of biotic disturbance hotspots are concentrated on trees (versus a broader array of plant functional types), impacts on functional diversity may differ from overlapping disturbances that directly affect a wider range of taxa (eg fires). Understanding the severity and scale at which biotic disturbance hotspots can catalyze shifts from forest to non-forest is an important priority. Increased focus on biotic disturbance hotspots can provide indications of how resilience mechanisms are unraveling, and highlight where management intervention to resist, adapt, or direct ecosystem change may be warranted (Schuurman et al. 2022).

Understanding biotic disturbance hotspots and their consequences

One key priority for understanding biotic disturbance hotspots is testing whether the extent of spatiotemporal interactions among biotic disturbance agents is changing as the climate warms and, if so, through what mechanisms. For example, are increases in the occurrence and spatial extent of biotic disturbance hotspots greater than expected from random chance as biotic disturbance activity increases? Testing patterns of observed spatiotemporal overlap against null models of expected overlap due to random chance could provide answers to this important question (Hart et al. 2015; Cole et al. 2022), with departures from random overlap suggesting mechanisms supporting positive or negative links (Figures 1–3). In addition, recent outbreaks in North America were characterized by broad-scale synchrony among pathogens and feeding guilds of insects (Raffa et al. 2008), but whether spatial synchrony in outbreak dynamics has increased over longer time periods is less understood. Generally, spatial cross-synchrony between biotic disturbance agents has received limited attention, as tests thereof are challenging without spatially extensive and long-term datasets and computational power. However, where such datasets extend beyond the periodicity of outbreak cycles (ie several decades), tests of spatial cross-synchrony could yield insights into the mechanisms that facilitate the development of biotic disturbance hotspots. Finally, can the occurrence of biotic disturbance hotspots be predicted from factors across different scales (eg broad-scale climate and local-scale forest structure and topographic setting) that are known to affect each biotic disturbance agent individually? Are biotic disturbance hotspots more common near the core or near the edges of the respective ranges of host trees, insects, and pathogens? Although modeling efforts for individual biotic disturbances show promise (eg Chapman et al. 2012),

expanding these efforts to encompass spatiotemporal modeling of multiple biotic disturbances simultaneously could provide insights into the unique and shared drivers of different biotic disturbances.

A second key priority for understanding biotic disturbance hotspots is testing how the nature of biological legacies left by and compensatory responses following - hotspots differs from disturbances caused by single biotic agents. For example, if biotic disturbance hotspots are characterized by greater cumulative severity (eg higher tree mortality across more individuals and species), fewer remaining live legacies could slow compensatory responses. Conversely, if biotic disturbance hotspots occur where tree species diversity exceeds the number of host-specific disturbances, diverse stands should be more resistant to highseverity disturbance (Jactel and Brockerhoff 2007), leaving more diverse live legacies behind. Greater diversity of legacies increases the array of potential compensatory responses (Gonzalez and Loreau 2009) - providing response diversity that is critical to ecosystem resilience in the face of stressors (Elmqvist et al. 2003; Mori et al. 2013). Addressing these research needs at broad scales could be approached with remote sensing (to quantify disturbance severity of multiple biotic agents) (Rodman et al. 2021) and geospatial datasets of vegetation conditions (to compare patterns with pre-disturbance structural and compositional diversity). Complementary analyses could be conducted at fine scales using long-term and spatially explicit forest measurements where key demographic parameters are tracked (Andrus et al. 2021).

As increasing disturbance activity drives the coincident and mechanistically linked overlap of multiple biotic disturbance agents, the need to understand the causes and effects of biotic disturbance hotspots will become increasingly important. The effect of biotic disturbance agents in forest ecosystems has long been associated with strong compensatory responses in unaffected areas or host trees. However, as the climate continues to warm, increased disturbance severity from multiple biotic disturbance agents may diminish the capacity for compensatory responses. Efforts to increase our understanding of biotic disturbance hotspots can inform climate-adaptive forest management that can be responsive to emergent and dynamic novel disturbance regimes.

Acknowledgements

Support for this research was provided by the US National Science Foundation (award 1853520) and the McIntire-Stennis Cooperative Forestry Research Program (grant #NI17MSCFR XXXG003/project accession #1012773) from the US Department of Agriculture National Institute of Food and Agriculture. Special thanks to A Orrego for initial GIS data acquisition and processing. PCT acknowledges support from the David RM Scott Endowed Professorship in Forest Resources. BJH acknowledges support from the Jack Corkery and George Corkery Jr Endowed Professorship in Forest Sciences.

Data Availability Statement

Data used in this study are already published and publicly available from the USFS Aerial Detection Survey Program (https://www.fs.usda.gov/foresthealth/applied-sciences/aviat ion/aviation-aerial-survey.shtml) and the USFS Forest Inventory and Analysis Program (https://www.fia.fs.usda.gov).

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Discovery of solar sea slugs in the Falkland Islands

Lysia patagonica – a small (~70 mm) sea slug – is known to occur along coasts of mainland South America (*J Mollus Stud* 2021; doi.org/10.1093/mollus/eyab003). In 2020, *E patagonica* or a close relative (pictured here) was first sighted in the Falkland Islands. However, specimens have not been formally described. Considering the distance and oceanic currents between the Falklands and South America, which can disrupt population connectivity, the individuals found in the Falklands could either belong to a distinct founder population or possibly represent a new species.

The members of the genus *Elysia* are known as "solar sea slugs" because they absorb photosynthetic plastids from the plants they consume and they bask in the sunshine, turning their bodies bright green. This mechanism of gaining energy through photosynthesis is analogous to corals and their symbiotic algal cells (zooxanthellae). In some parts of the world, solar sea slugs are increasingly difficult to find (eg *Elysia cholorotica* in California), are too rare to study (*National Geographic* 2018; https://on.natgeo.com/3WgSp1K), and are sensitive to climate change (*J Mollus Stud* 2021; doi.org/10.1093/mollus/eyab003).

More specimens were observed by the authors in 2022 at other locations, including Rookery Bay, Yorke Bay, Cape Pembroke, and Elephant Beach. Most of these sites are close to the capital (Stanley), and new discoveries in shallow-water environments will likely increase as scientists (professionals and amateurs alike) continue to explore local rock pools. However, the process of describing biodiversity is time-consuming and requires expert taxonomic skillsets. Collected specimens have been sent for formal identification; however, the length of time between discovery and description is extensive (*Antarct Sci* 2021; doi.org/10.1017/S0954102020000462). In the interim, locals are peeking into new tidal environments, and who knows what else they might find?



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