# Shared Insights across the Ecology of Coral Reefs and African Savannas: Are Parrotfish Wet Wildebeest?

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*Comparison across terrestrial and aquatic ecosystems facilitates a broader understanding of ecological patterns. Although meta-analyses are important for quantitative synthesis across ecosystems, detailed comparisons of natural history and species interactions also illuminate convergence among systems. We compare the ecology of superficially dissimilar African savannas and coral reefs via shared characteristics including: (1) hyperdiverse guilds of large vertebrate herbivores and predators, (2) similar mechanisms driving positive feedback loops between herbivory and primary production, (3) similar roles of disturbance and herbivory in mediating ecosystem state, and (4) numerous smaller vertebrate and invertebrate species that underpin diversity and ecosystem processes. Our goal in comparing the natural history and ecology of these ecosystems is to facilitate others in finding their own comparative systems. We encourage scientists, especially early-career scientists, to explore ecosystems other than their primary focus. Whatever your ecosystem of study, examining the ecology of its analog in another environment may enliven your career.*

*Keywords: ecosystem function, grazing ecosystem, herbivory, synthesis, trophic cascade*

> *“Of all fishes the so-called Scarus, or parrot, is the only one known to chew the cud like a quadruped.”*
>
> —Aristotle (350 BCE)

**Comparing commonalities and differences across** ecosystems allows for a broader understanding of ecological patterns and a deeper understanding both within and across systems (Webb 2012). For example, meta-analyses have identified broad similarities in how herbivores affect production and diversity in primary producer communities across marine, freshwater, and terrestrial communities (Cyr and Pace 1993, Gruner et al. 2008). Although these quantitative syntheses are important for understanding common patterns in ecological processes across ecosystems, their generality can overlook similarities and differences in the mechanisms that regulate these processes. Digging into the commonalities of natural history and species interactions also can be informative for generating synthesis in different ways (Paine 2005), pointing to similarities in how disparate ecosystems operate, and highlighting what kind of species interactions are important. This comparative natural history has deep roots that go at least as far back as Aristotle (350 BCE).

Specific comparisons across aquatic and terrestrial systems can serve as a valuable direction for the field of ecology (Borer et al. 2005, Shurin et al. 2006). Of course, there are many fundamental differences between aquatic and terrestrial ecosystems. For example, water limitation is key for controlling primary production in many terrestrial systems (Nemani et al. 2003), but is likely less important in aquatic systems. In aquatic systems, especially marine ones, species often have highly mobile larvae that results in wider ranges of dispersal than their terrestrial counterparts (Carr et al. 2003). Terrestrial systems have primary producers with longer generation times than aquatic systems and have nutrients that are more stationary in soils compared to those in fluid aquatic systems (Burkepile 2013). But, these concrete differences among ecosystems should not impede the search for generality in ecological processes across seemingly incongruent ecosystem types (Webb 2012).

In the present article, we compare the similarities in the ecology of African savannas and coral reefs with a particular focus on functional identity, species interactions, and ecological processes. African savannas typically have a continuous grass layer with scattered shrubs and trees (figure 1a; *sensu* Ratnam et al. 2011). Coral reefs typically exist as a matrix of reef building corals, other sessile invertebrates, and

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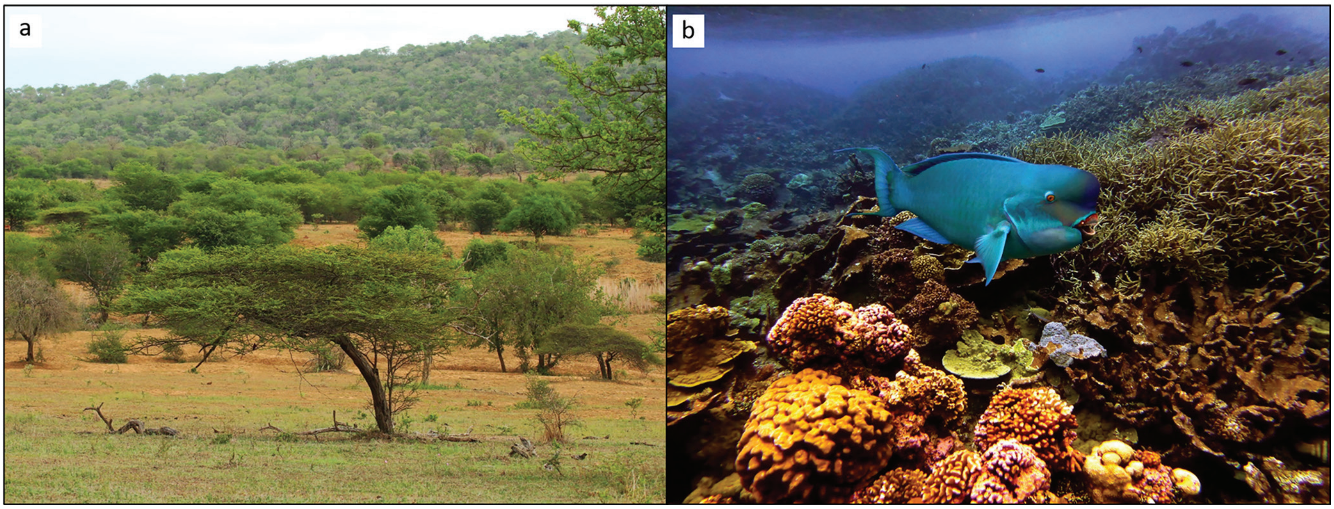


*Figure 1. Both (a) African savannas and (b) coral reefs have high structural heterogeneity created by woody vegetation and corals, respectively. Woody plants and grasses in savannas and corals and algae in reef systems support high levels of primary production that supports a high diversity and abundance of herbivorous and carnivorous species. Photographs: (a) Keenan Stears, (b) Katie Davis Koehn.*

filamentous algae (figure 1b; Knowlton and Jackson 2001). Although seemingly very different on the surface, we chose these two ecosystems for several important similarities. First, in both ecosystems, a diverse guild of vertebrate herbivores that varies orders of magnitude in body size drives herbivory. This herbivory is a dominant process that, together with other disturbances, drives community dynamics, facilitates spatial heterogeneity, and promotes nutrient cycling. Second, a suite of diverse vertebrate predators creates nested, size-structured food webs, affecting herbivore population dynamics and shaping herbivore behavior. Third, both ecosystems are higher in species diversity and animal biomass than many of their terrestrial or marine counterparts. Fourth, this diversity and abundance leads to a host of species interactions that underpin community dynamics and ecosystem function. Finally, we have personal experience working in both coral reefs and African savannas, equally annoyed by fire corals and *Acacia* thorns, which facilitates comparisons of their ecology via time spent scratching in the dirt and swimming in the waves.

Our objective is not to deliver a detailed, quantitative review of the literature for any one idea or system. Instead, we hope to provide insightful comparison in the ecology of very different ecosystems in order to stimulate researchers' interest in searching for generality by finding their own comparative ecosystems. Lawton (1999) sought to determine whether there were general laws in ecology, however, he concluded that in community ecology, generality is contingent on a myriad of local factors, making it difficult to identify laws at the community level. However, our across-ecosystem comparison approach allows us to smooth out the overwhelming contingencies within each system, thereby, revealing the generalities that are common to both ecosystems. The late Robert T. Paine captured our main premise over a decade ago when writing about how to increase communication among marine and terrestrial ecologists writing, "If cross-environment communication is to be increased and barriers are to be reduced, I believe it will best be achieved from the bottom up, that is by building on the accumulated wisdom about individual species and the consequences of their interactions." (Paine 2005). The primary goal of our piece is to encourage scientists, especially younger scientists, to look past their ecosystem or species of choice and dig into the natural history and ecology of a comparative ecosystem, preferably a dry ecosystem if you study a wet one and vice versa.

## Herbivore functional groups: Grazing grasses and browsing seaweeds

One of the striking similarities between coral reefs and African savannas is the abundance and diversity of herbivores that can be classified into analogous functional groups (or guilds) on the basis of their diet, digestive morphology, and physiology (e.g., Choat and Clements 1998). With respect to their diets, herbivores are often classified as grazers that consume grasses in terrestrial systems or fast-growing filamentous algae in their marine counterparts (also called *scrapers* or *croppers* in reef systems), browsers that consume forbs and woody species on land or larger upright macroalgae in the sea, or mixed feeders that both graze and browse (Kartzinel et al. 2015, Burkepile et al. 2018). Although these main functional groups often focus on large ungulates in savanna systems and fishes in reef systems, there are a host of other smaller herbivores in both African savannas (e.g., termites, grasshoppers, rodents) and coral reefs (e.g., urchins, snails, amphipods) that are too numerous to detail here.

Common grazers in African savannas are wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), and white rhinoceros (*Ceratotherium simum*), whereas in coral reef systems, species of parrotfishes (many species within the Scarini tribe) and surgeonfishes (many species within family Acanthuridae) target filamentous algae (figure 2). Common browsers in African savannas include black rhinoceros (*Diceros bicornis*), giraffe (*Giraffa* spp.), and kudu (*Tragelaphus strepsiceros*), whereas in coral reefs, unicornfishes (*Naso* spp.), rabbitfishes (*Siganus* spp.), and chubs (*Kyphosus* spp.) fill similar niches. Finally, mixed feeders in savannas include African elephants (*Loxodonta africana*) and impala (*Aepyceros melampus*) that eat both grasses and woody plants. On coral reefs, some species of both parrotfishes and surgeonfishes feed on filamentous algae and large macroalgae (Burkepile et al. 2018). This grazer–browser continuum likely promotes the coexistence of a diverse guild of herbivores through resource partitioning (Kartzinel et al. 2015).

There is also finer scale niche partitioning within these larger functional feeding groups. In African savannas, different browsing species such as giraffe, kudu, and steenbok (*Raphicerus campestris*), minimize competition by browsing trees, such as *Vachellia* and *Senegalia* (previously *Acacia*) spp., at different heights. Giraffe exploit leaves highest in the tree canopy that are inaccessible to the smaller species (Cameron and du Toit 2007). Similarly, many browsing fishes in coral reef systems partition their niche by exploiting different parts of the same macroalgal species. When browsing large species of brown macroalgae, such as *Sargassum* spp., rabbitfishes tend to eat the leaves, whereas chubs and unicornfishes tend to eat the stalks (Streit et al. 2015).

Grazers show a similar level of niche partitioning based on the height or length of their food. Grazing parrotfishes on Caribbean coral reefs partition their feeding on the basis of the height of filamentous algal turfs, with some species focusing on short filaments and others preferring longer filaments (Adam et al. 2018). Comparably, grazing ungulates in savanna systems often partition grass resources on the basis of the height of the grass. For example, species such as wildebeest, white rhino, and hippopotamus (*Hippopotamus amphibius*) focus on short grasses, whereas other species such as zebra and African buffalo (*Syncerus caffer*) prefer to feed on taller grasses (e.g., Kleynhans et al. 2011). Body size, digestive physiology, and mouth morphology appear to drive this niche partitioning in African savannas (Bell 1971, Arsenault and Owen-Smith 2008), with similar differences likely driving niche partitioning in reef systems (Hoey and Bonaldo 2018).

In both ecosystems, herbivores represent a huge range in body size with dramatically different impacts across the body size spectrum (box 1). In African savannas, herbivores range from small antelope, such as the 10 kilogram (kg) steenbok to the 4000 kg elephant, the largest land animal. In coral reefs, herbivores range from approximately 100-gram surgeonfishes up to 45 kg for the largest parrotfishes on coral reefs. Therefore, both systems have over a two order of magnitude range in body size. For savanna herbivores, body size is a unifying principle determining foraging behavior and food quality, the well-known Jarman–Bell principle (Bell 1971, Jarman 1974). Given that smaller species of herbivore (e.g., impala, warthog) have higher mass-specific metabolic rates than larger species of herbivore (e.g., rhinoceros, elephant), the smaller species require higher-quality diets, whereas larger species can subsist on abundant, low-quality forage (Owen-Smith 1988, Codron et al. 2007). It is unclear how well this principle may apply to coral reef herbivores. Many species of herbivorous fish change diet through ontogeny with smaller individuals often feeding on higher quality food (Horn 1989). However, there is no identified trend for similar interspecific patterns between food quality and body size (Clements et al. 2009).

In savannas, the largest herbivores or megaherbivores (more than 1000 kg), including elephant, white rhinoceros, and hippopotamus, are important ecosystem engineers. These species, through their foraging, wallowing, and dung inputs, provide important ecosystem services by creating spatial and temporal heterogeneity that provides habitat and resources for a range of other species (box 1; Waldram et al. 2008, Stears et al. 2018). Large, bioeroding parrotfishes on reefs have similar ecosystem engineering abilities, specifically their ability to prey on live and dead corals, physically change habitats, and create marine sand via the digestion of coral prey. This bioerosion from the largest parrotfishes, such as the 45 kg humphead parrotfish (*Bolbometopon muricatum*), can generate up to 85% of the new sand on some coral reefs (Perry et al. 2015), literally building islands via sand production. These largest herbivores often have unique roles in ecosystems that are irreplaceable by smaller species (Owen-Smith 1988), and their removal from savanna and coral reefs has strong cascading effects throughout ecosystems (Bellwood et al. 2011, Young et al. 2013).

The combination of herbivore functional diversity and body size results in the most species diverse assemblages of vertebrate herbivores on the planet, with dozens of different herbivore species present in the most diverse savannas and reefs (Olff et al. 2002, Bellwood et al. 2004). In both ecosystems, the intense herbivory by these diverse assemblages has created a complex coevolutionary dance between plants and herbivores. Herbivores have selected for convergent sets of traits in primary producers of both ecosystems such as sets of species that tolerate herbivory via rapid growth rates, basal meristems, and vegetative spreading, such as fast growing grasses in savannas and filamentous algae on reefs (McNaughton 1984, Steneck and Dethier 1994). Other primary producers have adopted a more defensive strategy that relies on chemical or physical defenses to repel herbivores rather than tolerate them, resulting in an evolutionary arms race between herbivores and vegetation, whereby plants continue to evolve new antiherbivore defenses that influence spatial and temporal patterns in herbivory (Hay 2009, Charles-Dominique et al. 2016). In both ecosystems, the producer species that have adopted the strategy to defend themselves are often most successful when they use both chemical and physical defenses to ward off the diverse suite

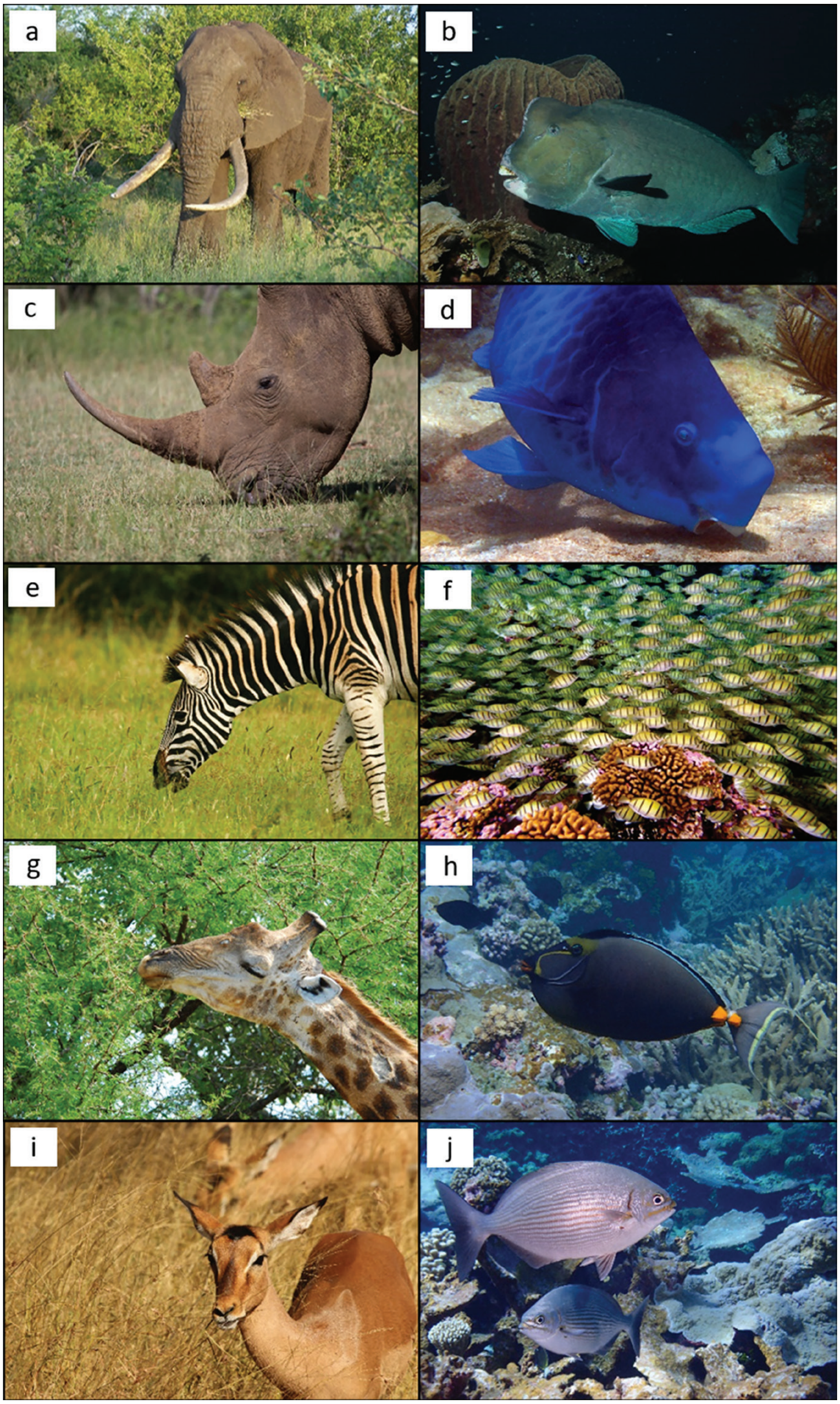
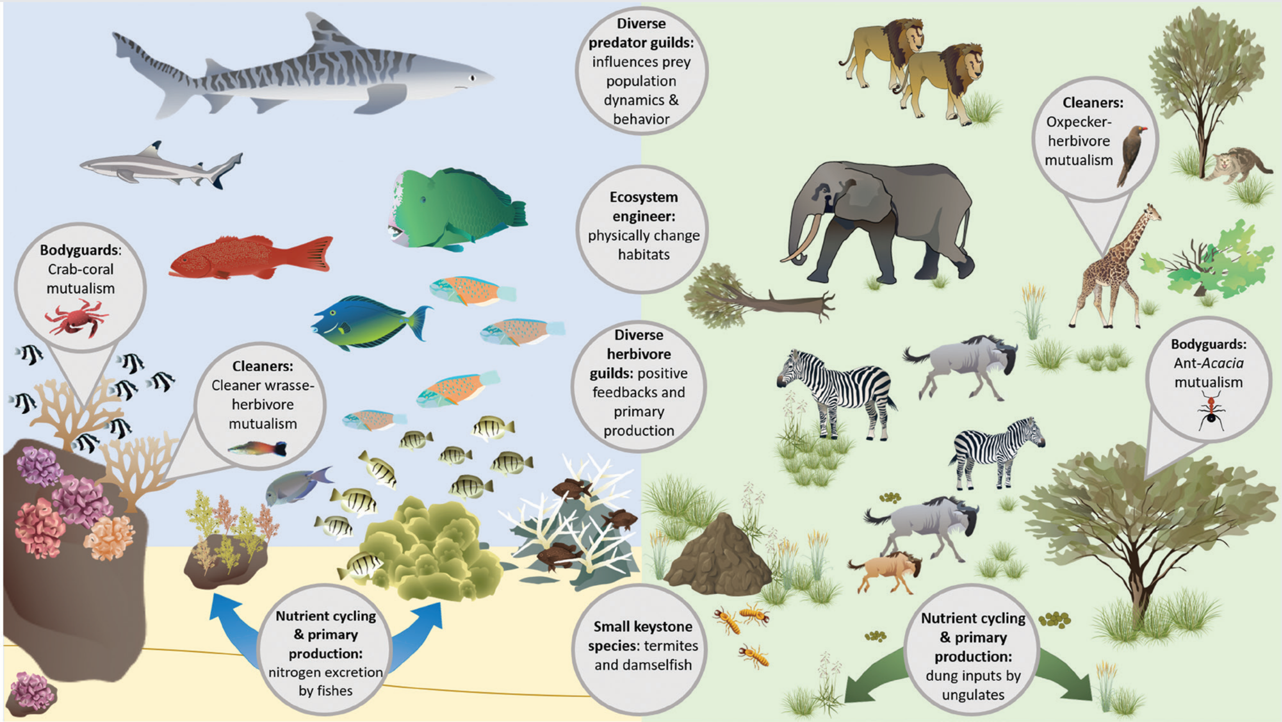


*Figure 2. A diverse herbivore guild drives many aspects of community dynamics and ecosystem functions in both African savannas and coral reefs. Examples of key herbivores from African savannas: (a) African savanna elephant (*Loxodonta africana*), a key mixed feeder and ecosystem engineer; (c) white rhinoceros (*Ceratotherium simum*), a megaherbivore grass grazer; (e) zebra (*Equus burchelli*), an important herd-forming grazer; (g) giraffe (*Giraffa camelopardalis*), a browser of trees and shrubs; (i) impala (*Aepyceros melampus*), a small, abundant grazer and browser. Examples of key herbivores from coral reefs: (b) humphead parrotfish (*Bolbometopon muricatum*), a key grazer, bioeroder, and ecosystem engineer; (d) blue parrotfish (*Scarus coeruleus*), an important large grazer of filamentous algae; (f) convict surgeonfish (*Acanthurus triostegus*), a schooling grazer; (h) orangespine unicornfish (*Naso lituratus*), an important macroalgal browser; and (j) chub (*Kyphosus vaigiensis*), a schooling macroalgal browser. Photographs: (a, c, g) Deron Burkepile, (b) Michael Mehta Webster, (d) Thomas Adam, (e) Keenan Stears, (f, h, j) Katie Davis Koehn, (i) Melissa Schmitt.*

## Box 1. Comparative ecology of coral reefs and African savannas.

On the surface, these two systems are seemingly disparate. However, by scratching through the grass, or submerging yourself underwater, commonalities between these systems become apparent. Seeking to understand these similarities provides an opportunity to broaden our interpretation of ecological processes and patterns. Below, we highlight the similarities between African savannas and coral reefs with a particular focus on generality in functional identity, species interactions, and ecological processes.



### Diverse predator guilds

Both ecosystems have a diverse group of predators with a range of body sizes, hunting strategies (e.g., roving or cursorial, ambush), home ranges, and different prey bases, which is often a function of body size of both predator and prey. These predators often affect the population dynamics and behavior of smaller prey, whereas larger prey are often immune to predation risk.

### Diverse herbivore guilds

A diverse guild of herbivores exists in both systems, encompassing a huge range of body size (over two orders of magnitude) and similar functional groups (e.g., grazers, browsers, mixed-feeders). These herbivores affect plant community dynamics and influence state shifts (i.e., grass-to-woody dominance, coral-to-algae dominance), with differential impacts of the different functional groups.

### Ecosystem engineers

The largest herbivores (e.g., elephants, large parrotfish) have outsized influence on these systems, often physically changing habitats by knocking down trees or bioeroding reef substrate. Their loss via human exploitation removes unique functions from these ecosystems.

### Nutrient cycling and primary production

Abundant herbivores efficiently recycle nutrients to primary producers in both systems, facilitating primary production and creating a positive feedback between herbivores and producers.

### Small keystone species

Small, abundant species such as termites in savannas and damselfish in reefs create hotspots of nutrient-enriched primary producer communities that act as key resource areas for larger herbivores.

### Bodyguards

Foundation species often have bodyguards, ants in trees and crabs or shrimp in corals that protect their hosts from damage by larger animals in exchange for nutrient rewards provided by the foundation species.

### Cleaners

Abundant ungulates and fishes have selected for a group of mutualistic cleaning species, such as oxpeckers and cleaner wrasse, respectively, which remove their parasites and facilitate the health and diversity of large animal communities.

So, are parrotfish wet wildebeest? By emphasizing the similar mechanisms that drive ecosystem processes in both savanna and coral reef systems, we encourage researchers to seek their own analogous study system and benefit from the cross-fertilization of ideas that can only improve our understanding of how ecosystems function.

of herbivores that exist in these ecosystems (Cooper and Owen-Smith 1985, Schupp and Paul 1994).

### Herbivores, disturbance, and ecosystem transitions: Are fires terrestrial tempests?

Coral reefs and savannas are often used as examples of systems with abrupt shifts between ecosystem states (Scheffer and Carpenter 2003). Reefs can transition from coral to algal dominance (Mumby et al. 2007), whereas savannas can transition from grass to tree dominance (Bond 2019). In both ecosystems, herbivores play important roles in mediating these ecosystem transitions, especially in concert with disturbances, and different groups of herbivores are more or less important for preventing or reversing the transition from one state to another.

On coral reefs, abundant herbivorous fishes prevent establishment of large macroalgae, facilitating the recruitment, growth, and survivorship of corals (Williams et al. 2019). The loss of herbivores, and resulting increase in macroalgae, often does not result in widespread coral mortality. However, after large coral-killing disturbances, such as cyclones or coral bleaching events, herbivores can influence the trajectory of coral recovery. On reefs with abundant herbivores, corals often recover relatively rapidly after disturbances, whereas reefs with fewer herbivores can transition to a macroalgae-dominated state (Graham et al. 2015). Importantly, once macroalgae become dominant, the amount of herbivory needed to reverse that state may be significantly higher than the herbivory needed to prevent the initial state transition, suggesting important negative feedback loops that reinforce these state changes (Schmitt et al. 2019). Browsing fishes are key for removing large, adult macroalgae once they become abundant (Burkepile and Hay 2011), whereas grazing or scraping fishes are key for preventing the establishment of macroalgae (Adam et al. 2011). Therefore, the herbivores that prevent the establishment of a macroalgae-dominated state differ from those that may reverse this state change.

Herbivores have similar sway over the transition between open, grass-dominated savannas with few trees and savannas with a high density of woody vegetation. Although fire is an important driver of the abundance of woody vegetation in savannas (Sankaran et al. 2005), the impacts of grazing and browsing often shape the impact of fire on woody vegetation, helping to influence the presence of the open savanna state (van Langeveld et al. 2003). However, herbivores have species-specific effects depending on the life stage of the woody vegetation. Smaller herbivores, such as impala, may serve as a strong population bottleneck for trees at the seedling stage by causing direct mortality and by keeping woody species small, making them more likely to be killed by fire (Staver and Bond 2014). However, there are few herbivores other than an elephant that can knock down and kill large trees or severely damage tall shrub canopies, potentially converting dense stands of woody vegetation to open savanna (Dublin et al. 1990, Augustine and McNaughton 2004). However, fire may be the primary driver of the transition from wood-dominated to grass-dominated systems (Bond 2019), with herbivores reinforcing grass dominance once the transition occurs by suppressing woody vegetation. Therefore, similar to reefs, different species of herbivores are important for either preventing or reversing ecosystem state changes in savanna systems.

### Herbivore facilitation of primary production: Everyone eats, poops, and pees

The term *grazing ecosystem* was first used to describe the savanna of the Serengeti in East Africa where large herds of ungulates migrate across the landscape, tracking available forage and nutrients, and removing the majority of primary production (Bell 1971). However, *grazing ecosystem* has also been used to describe a host of different ecosystems, both terrestrial and aquatic, where herbivores have outsized impacts on ecosystem processes (Frank et al. 1998, Burkepile 2013). In both African savannas and coral reefs, abundant herbivores result in upward of 50% of primary production passing up the food chain, with dramatic impacts to the dynamics of primary producer communities (McNaughton 1985, Carpenter 1986). Furthermore, the diversity in feeding style and body size, described previously, may facilitate herbivory via complementary feeding and efficient removal of primary producer biomass (McNaughton 1985, Rasher et al. 2013). Abundant herbivores and their intense herbivory also create several positive feedback loops that facilitate primary production and enhance vegetation quality.

Some of the best-studied examples of positive feedback loops of herbivores on plants in savanna ecosystems are the creation of grazing lawns where intense grazing stimulates primary production (Hempson et al. 2015). Several factors function to create this positive feedback cycle (box 1). First, the constant grazing–regrowth–regrazing keeps grass shoots in a physiologically active stage (Anderson et al. 2013), which promotes nutrient uptake from the soil via roots. Second, grazers increase nutrient availability to plants via inputs of their dung and urine (Augustine et al. 2003). Third, high grazing and increased nutrient availability promotes plants with increased nutrient concentrations (Hempson et al. 2015). Fourth, heavy grazing reduces competition for light by keeping grass short (Hempson et al. 2015). These productive grazing lawns with increased nutrient concentrations attract increased densities of grazers that reinforce these positive feedback loops. Importantly, primary productivity in grazing lawns remains remarkably high even under high grazing intensities (Hempson et al. 2015). The concept of grazing lawns may also extend to browsing lawns, where intense browsing from giraffe and kudu can facilitate high foliage regrowth rates in trees such as *Acacia nigrescens* (Fornara and du Toit 2007), initiating a similar set of positive feedback loops to grazing lawns.

This feedback cycle between herbivory and primary production is also likely important on reefs, although less well studied. As in grass-dominated systems, intense herbivory keeps algae in short, fast-growing growth forms where there

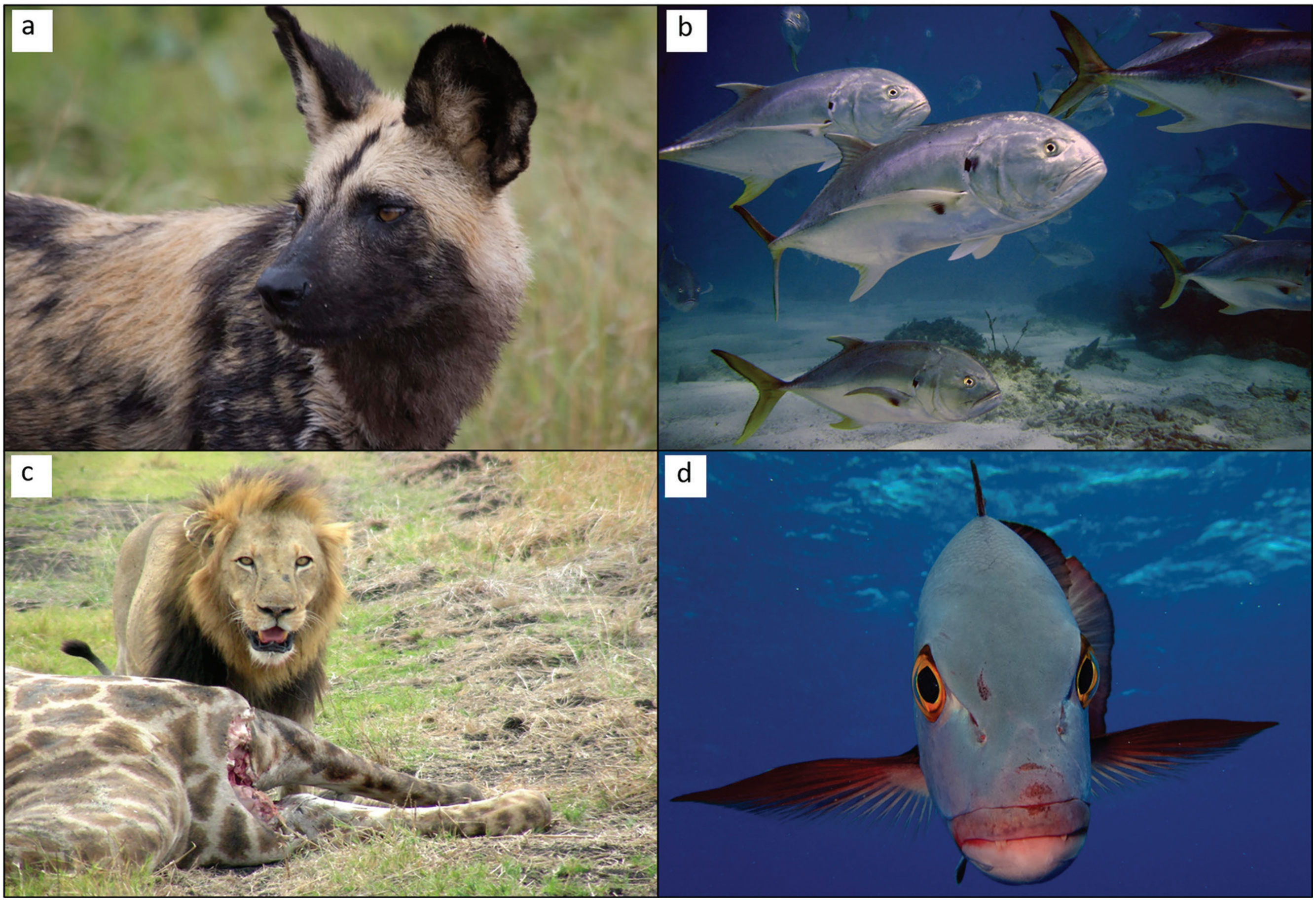


*Figure 3. A diverse predator guild affects both the population dynamics and behavior of the diverse suite of herbivores. These predators differ in hunting modes such as cursorial or roving predators like (a) wild dogs (*Lycaon pictus*) in African savannas and (b) yellow jacks (*Caranx bartholomaei*) on coral reefs, or ambush predators such as (c) lions (*Panthera leo*) in African savannas and (d) two-spot red snappers (*Lutjanus bohar*) on coral reefs. Photographs: (a, b, c) Deron Burkepile, (d) Katie Davis Koehn.*

is minimal self-shading or competition for light (Carpenter 1986). Furthermore, grazing likely facilitates the flux of nutrients to algae and relieves nutrient limitation by decreasing algal height and density, which increases water flow within and nutrient delivery to the algal community (Carpenter and Williams 2007). Like with terrestrial herbivores, aggregations of herbivores in coral reefs is linked to increases in nutrient availability and higher nutrient content of algae (Williams and Carpenter 1988, Burkepile et al. 2013), which can, in turn, increase herbivory on nutrient rich algae (Shantz et al. 2015). Therefore, in both systems, the large aggregations of herbivores that congregate on high-quality vegetation facilitate positive feedback loops on primary production and forage quality.

### Predators, trophic cascades, and fear dynamics: Who's afraid of the big bad barracuda (or lion)?

Charismatic predators such as wild dogs (*Lycaon pictus*) and lions (*Panthera leo*) in savannas and sharks (many species in family Carcharhinidae) and grouper (such as *Mycteroperca* and *Epinephelus* spp.) on coral reefs influence the population dynamics, foraging behavior, and the ecosystem-level impact of herbivores (figure 3, box 1). The diverse herbivore community with a wide range of body sizes means that the populations of different species can be either sensitive or insensitive to predation. For savanna ecosystems, predators often account for 100% of mortalities in smaller herbivores such as gazelle or impala while minimally affecting the largest herbivores such as elephant and rhinoceros, which are typically limited by resources or poaching (Sinclair et al. 2003). Similarly, in coral reef systems, larger predators can suppress the populations of smaller herbivorous fishes with minimal impact on the populations of larger herbivores (Mumby et al. 2006). Indeed, the biggest herbivores in reef systems are often limited by habitat or overharvest rather than predation (Bellwood et al. 2011).

Even though predators may significantly affect the populations of the smaller herbivore species, it is not clear that this effect has an indirect effect on primary producer communities (i.e., a trophic cascade). Many examples of trophic cascades in marine and terrestrial ecosystems come

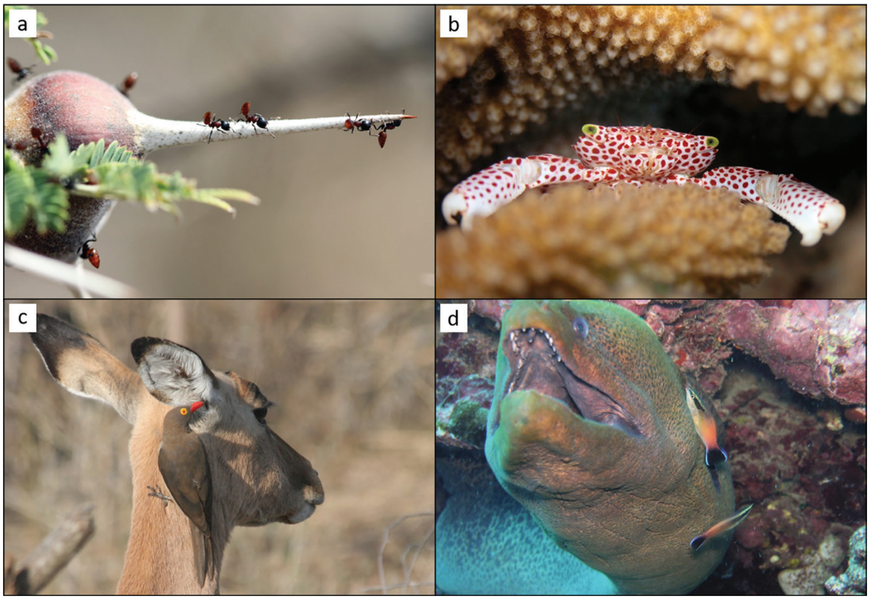


***Figure 4. Because of high species diversities in both African savannas and coral reefs, there are a number of mutualisms that fill similar roles in both systems. For example, (a) acacia ants (*****Crematogaster mimosa*****) and (b) crabs (*****Trapeziid*** ***spp.) defend their hosts, trees and corals respectively, from predation events, whereas (c) oxpeckers (*****Buphagus erythrorhynchus*****) and (d) cleaner wrasse (*****Labroides rubrolabiatus*****) both remove parasites from ungulates and fishes, respectively. Photographs: (a) Todd Palmer, (b, d) Melissa Schmitt, (c) Russell Schmitt.***

from relatively simple, linear food chains (Borer et al. 2005). However, the high species diversity of both predators and herbivores creates potential functional redundancies in predator–prey interactions, possibly resulting in the lack of cascading effects of predators being observed on primary producer communities (Bascompte et al. 2005). Indeed, it has been challenging to link fluctuations in the biomass of large predators in African savannas and coral reefs to changes in the biomass of primary producers (Terborgh and Estes 2010). Even though predators in these species rich ecosystems may have little effect on primary producers by affecting the abundance of herbivores, predators appear to affect producer communities via their impact on herbivore behavior by creating landscapes or reefscapes of fear that change the impact of herbivory across the landscape or reefscape (Brown and Kotler 2004, Catano et al. 2016).

Herbivores must balance the needs of getting food to survive and reproduce while avoiding being eaten. These tradeoffs often shape the temporal and spatial use of habitat by herbivores in order to minimize the risk of predation (Brown and Kotler 2004). In African savannas and coral reefs, increasing evidence suggests that the threat of predation strongly influences foraging behavior, thereby altering habitat selection, foraging budgets, and changing group dynamics in areas with increased predation risk (Schmitt et al. 2014, 2016, Catano et al. 2016).

Emerging research shows that these effects of predation risk can have important effects on primary producer communities. For example, in a Kenyan savanna, areas of chronically low risk (low use by leopard (*Panthera pardus*) and wild dog) were hotspots of use for the mixed-feeding impala (Ford et al. 2014). In these low risk areas, browsing by impala led to increases in physically well-defended (i.e., thorny) tree species. Conversely, impala avoided areas frequently used by predators (high risk areas), which resulted in a spatial refuge for poorly defended tree species. Therefore, predation risk altered plant species distribution across the landscape by altering herbivore behavior. Similarly, on a Fijian coral reef, the extent of the tide determines the distribution of sharks, creating a distinct reefscape of predator abundance at high versus low tide (Rasher et al. 2017). At high tide, when sharks can roam freely across the lagoon, herbivory by surgeonfishes and parrotfishes decreased as compared to during low tide when sharks were excluded from the lagoon. As a result, the riskiest areas that were the most consistently accessible to sharks had higher abundance of algae than areas of lower risk. Together, these data suggest that the impact of fear from predators on herbivore behavior may have an outsized impact on producer communities in both reefs and savannas.

## Smaller herbivores as facilitators of diversity: Are termites dry damselfishes?

When experiencing a coral reef or African savanna, it is easy to be overwhelmed by the abundance of large herbivores. Elephants and large parrotfishes are mobile, charismatic and easily capture the imagination. Their impacts on the landscape are often immediately apparent from the trees they knock down or the big bites of reef they consume. However, to overlook the smallest denizens of savanna and reef ecosystems would be to ignore crucial herbivores whose behavior can influence ecosystem function.

In African savannas, termites are some of the most abundant but possibly most overlooked members of the herbivore community. Many termite species create large termitaria, or mounds, where they incubate foraged vegetation to grow the fungi that is their dominant food source. Termite mounds create microenvironments that are enriched with nitrogen and phosphorus when compared to adjacent soils (box 1; Brody et al. 2010). These termitaria create spatial heterogeneity across the landscape by creating biogeochemical hotspots, altering plant species diversity and nutritional quality, and generating nodes of important food resources for mammalian herbivores (Davies et al. 2016). In addition, through their nitrogen enrichment, termites can facilitate trees, which are important foundation species, by enhancing nitrogen fixation by the trees and their bacterial symbionts (Fox-Dobbs et al. 2010). For example, *Acacia drepanolobium* trees found at the edge of termite mounds had a higher probability of reproducing compared to trees growing off termite mounds (Brody et al. 2010), likely driven by termite-mediated nitrogen inputs.

Similar to termites, damselfishes on coral reefs maintain territories that they use to create gardens of filamentous algae that they exploit (box 1). Some species of damselfishes are actually algal gardeners that actively weed out undesirable species of algae while facilitating species that they prefer (Hata and Kato 2006). The end result is often a damselfish territory whose algal composition is vastly different than that of the rest of the coral reef (Ceccarelli et al. 2001). These algae may also be higher in nutrient content, much like the grasses on termite mounds, likely because of the consistent local nutrient excretion of the damselfishes on their garden (Blanchette et al. 2019). Because damselfishes tend to cultivate palatable algae in their gardens, their territories are prime feeding targets for larger herbivorous fishes such as surgeonfishes and parrotfishes. These larger herbivores often forage in schools in order to overwhelm damselfish defenses and gain access to their gardens (Robertson et al. 1976). Territorial damselfishes also repel corallivorous fishes, making damselfish territories a refuge for some reef-building coral species to escape predation (Pruitt et al. 2018). Furthermore, the nutrients from these aggregating damselfishes likely also facilitate the growth and health of corals (Holbrook et al. 2008). Although damselfishes actively defend their territories against large intruders (and the lead author in the present article has the scars to prove it) but termites do not, these taxa still have similar impacts on the ecosystem. Both termites and damselfishes can facilitate foundation species (trees or corals), increase primary producer diversity, and generate key hotspots of resources for larger herbivores.

## Bodyguards facilitate foundation species: Are crabs aquatic ants?

Trees in savannas and stony corals on reefs are both foundation species that provide food and structure and facilitate overall species diversity in these ecosystems (Ellison et al. 2005). In both systems, top-down pressure from consumers can determine the abundance and distribution of these foundation species. In savannas, browsers such as elephant, giraffe, and kudu affect the success and distribution of trees (Greve et al. 2012), whereas in reefs, butterflyfishes, pufferfishes, urchins, and sea stars affect the abundance and diversity of corals (Cole et al. 2008). In both systems, the impacts of these consumers have selected for smaller, mutualistic species that defend their foundation species hosts.

In African savannas, many *Acacia* tree species host mutualistic ants that defend their trees against herbivorous insects and mammalian browsers (figure 4a, box 1; Goheen and Palmer 2010). In return for the defense, *Acacia* trees often have domatia that provide a refuge for the ants as well as extrafloral nectaries that provide carbohydrate-rich nectar as a food source for their bodyguards (Hocking 1970). One of the most studied ant–*Acacia* relationships comes from East Africa where symbiotic ants (e.g., *Crematogaster* and *Tetraponera* spp.) defend their host trees *Acacia drepanolobium* against destructive browsers (Goheen and Palmer 2010). When ants detect feeding activity by browsing mammals, they swarm the branches being consumed and bite the vulnerable parts of the large herbivore (e.g., lips, nose, trunk), driving them away. This defense is key to the survival of ant-hosting trees. When these ants are experimentally removed from *A. drepanolobium,* the likelihood of the tree being eaten by elephants increased dramatically (Goheen and Palmer 2010). As a result, these ant-hosting trees often escape major herbivore damage even when large browsers such as elephants are abundant.

This host–bodyguard mutualism is also key for corals. Many coral species host several taxa of gobies (e.g., *Gobiodon* and *Paragobiodon* spp.), snapping shrimp (*Alpheus* spp.), and crabs (e.g., *Trapezia* and *Tetralia* spp.) that protect their coral hosts against corallivores (figure 4b, box 1; Pratchett 2001). When challenged by the crown-of-thorns sea star (*Acanthaster planci*), one of the most voracious coral predators, mutualist crabs attack the thorns and tube feet of the sea star, driving it off the host colony (Pratchett 2001). In return for this defense, corals produce lipid bodies that the crabs use as a food resource (Stimson 1990), although it is unclear how widespread this reward is among coral taxa. The specific species of coral bodyguard often determines the strength of defense against corallivores, with the presence of the most effective defenders resulting in the hosting coral species being low preference for corallivores (Pratchett 2001). In corals, multiple bodyguard species living within a coral can mount a more efficient defense against predators than can single species alone (McKeon et al. 2012). In contrast, ant-hosting trees typically host a single species of ant in an individual tree, with different species competing with each other for space on the host (Palmer 2003).

## Cleaning mutualisms: Are cleaner wrasse oceanic oxpeckers?

One of the defining characteristics that African savannas and coral reefs have in common is their large standing biomass of animals that drive important ecosystem processes. The presence of these abundant animals has selected for a suite of organisms, mutualistic cleaners, which base their livelihoods around the presence of these large consumers and their parasites. Such cleaning mutualisms are intrinsic to the maintenance of organism health or body condition (Poulin and Grutter 1996). Although these mutualisms can range dramatically in their complexity, both savannas and coral reefs host cleaner mutualists, which affect the dynamics of animal populations.

The most obvious cleaning mutualism that exists in African savanna systems is that between oxpeckers (*Buphagus erythrorhynchus* and *Buphagus africanus*) and herbivorous ungulates (figure 4c, box 1; Davison 1963, Grobler 1976). The oxpeckers clean the ungulates of ticks and other parasites including flies and lice, whereas the ungulates provide not only the meal but also a roost (Palmer and Packer 2018). Similarly, several species of obligate cleaner wrasse (*Labroides* spp.) have analogous functions in coral reef systems (figure 4d; Bshary et al. 2008, Adam 2012). The wrasses remove parasites, especially blood-sucking gnathid isopods, from the client fishes, often at specific cleaner stations around the reef.

In savannas, these cleaning mutualisms directly influence herbivore fitness by reducing tick-related disease and mortality (Davison 1963, Grobler 1976). Similarly, the removal of cleaner wrasses from a reef increases the parasite load on larger fishes and can result in a marked decline in local diversity of fish species (Bshary 2003). These mutualisms can also indirectly regulate top-down processes through their influences on consumer abundance and species diversity (Adam 2012). Given that these large consumers play important roles in the ecosystem as we describe above, the promotion of ungulate and fish diversity by these cleaning mutualisms likely plays an underappreciated role in affecting ecosystem function.

However, both oxpeckers and cleaner wrasse can cheat their hosts, turning this mutualism into a parasitism. Although cleaner wrasses mostly remove parasites, they actually prefer mucus and scales of their client fish and will often take a bite of the preferred tissue rather than a parasite (Grutter and Bshary 2003). Similarly, oxpeckers also deviate from tick removal and feed on the blood from open wounds on ungulates, often actively preventing the wounds from healing to facilitate this easy meal (Weeks 2000). These parasitic behaviors are often much less common than the mutualistic ones, likely representing only a nuisance for the clients with minimal impact on the beneficial relationship.

## Conclusions: Finding your comparative ecosystem

So, are parrotfish like wet wildebeest? Do the same general ecological principles underlie African savannas and coral reefs? Clearly, there are inherent differences in these systems. For example, fire is a dominant feature of savannas but is not that relevant to coral reefs. However, these differences should not prevent us from recognizing and appreciating the myriad of similarities that do exist. For example, the positive feedback loops between herbivores and primary production appear similar in both ecosystems, with similar mechanisms driving these processes. Research in each ecosystem has deepened our knowledge of how grazing ecosystems function. The diverse predator communities in both ecosystems have facilitated fundamental work on the impacts of how the fear of predators affects herbivore behavior and, consequently, plant communities. Future advances in understanding how ecosystems function, especially in our era of global change, can only benefit from the cross-fertilization of ideas beyond the boundaries between water and land.

Understandably, many of us will not have the time or funding to conduct research in multiple different ecosystems. But we encourage those that have the opportunity, to explore other ecosystems. Reach out to people studying your analogous system for discussions and potential collaborations. At the very least, get lost in the literature of a different system. If you work on plant–insect interactions, the literature on herbivorous crustaceans and seaweeds will be illuminating. If you work on dugongs or turtles and how their herbivory and disturbances affect seagrass beds, examining the literature on how bison and elk affect grasslands will stimulate new ideas. If you work on the landscape ecology of terrestrial forests, then kelp forests may be your perfect analog. Scientists that study the ecology of spatially isolated deep-sea communities may find similarities in the ecology of high-altitude alpine lakes. Whatever your ecosystem of study, its analog in another environment is probably out there waiting for you to discover it. So, we encourage scientists to explore research in a different ecosystem. Marine biologists, go bash through the bush. Terrestrial ecologists, go jump in the ocean. You never know what insights you will find or how it may enliven your career.

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