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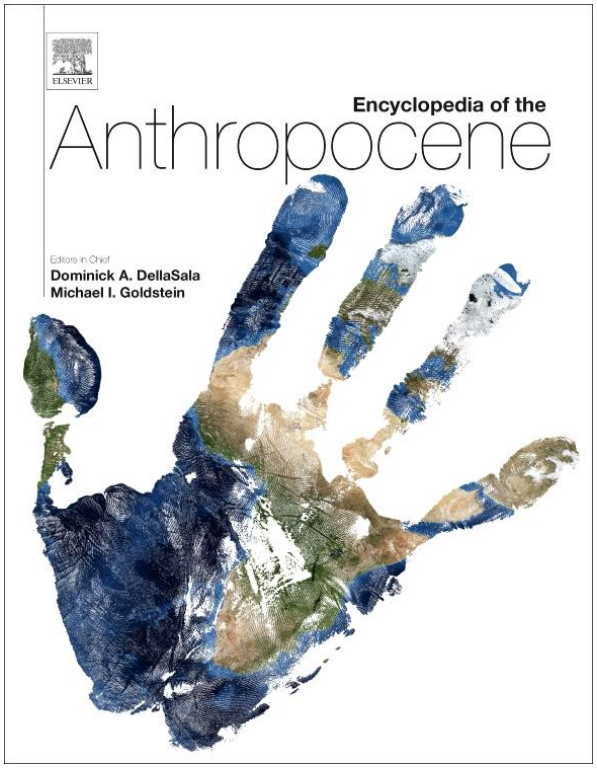

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Novelty in Ecosystems

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Novelty, Self-Organization, and Evolution

A variety of physical factors such as climatic and geologic conditions and the ecological processes that take place within habitats such as succession, self-organization, and evolution generate novelty in ecosystems (sensu Radeloff et al., 2015). Hutchinson (1965) united the physical and ecological sources of novelty in his classic essay titled *the ecological theater and evolutionary play*. In Hutchinson's construct, ecological novelty was the result of an evolving process (the evolutionary play) taking place within the ecological context of the habitat (the ecological theater). Hutchinson's students later modified this construct to include the effect of the evolutionary play on the theater, that is, the evolutionary play was not only affected by changing environmental conditions but also affected the conditions under which the plot was developing. In the Anthropocene, the fundamental processes for generating novelty in ecosystems have not changed, but the theater has significantly changed because the increased scale of human activity has unraveled new forces of change made possible by the combustion of fossil fuels. As a result, the plot of the evolutionary play (i.e., the evolutionary process) has accelerated (Cox, 2004) in the ecological theater of contemporary ecosystems directly or indirectly shaped by humans.

An ecosystem fundamentally involves "the circulation, transformation, and accumulation of matter and energy through the medium of living organisms and their activities" (Evans, 1956, p. 1127). We see no compelling evidence to expect that this essence of the ecosystem will change regardless of the geologic epoch under consideration. For example, after studying the development of floras and faunas over geologic time, Behrensmeyer et al. (1992) discerned that community dynamics were modern in nature by the Westphalian Stage in late Carboniferous, about 300 Mya. They showed that since that time, the species composition of floras and faunas has changed many times in response to changing environmental conditions and dispersal of species. Is it possible then, that while organismal communities were changing and experiencing novelty through geological time, the attributes of ecosystems as described by Evans (1965) did not change? Novelty in species composition facilitates the flux, transformation, and storage of matter and energy in ecosystems as they encounter and adjust to environmental change. Thus, novelty has a key duality: at the ecosystem scale it reflects the adjustment of ecosystem storages and fluxes to change, at the scale of organisms it becomes a driving force of adaptive evolution to changing environmental conditions.

Novelty in ecosystems is revealed ecologically through processes such as succession, self-organization, and evolution—processes that are activated by disturbance events. Novelty is an emerging property of communities in which organisms are subject to the selective forces of evolution and the laws of energy and matter that regulate ecosystem functioning. When processes of succession, evolution, and species dispersal result in novel combinations of species interacting at a particular location, these novel combinations of species form ecosystems through the process of self-organization (sensu Camazine et al., 2001). Self-organization is a process that contributes to the development of ecosystem order and structure by means of internal interactions among the components of the system, in this case the novel mixture of species. Odum (1988) developed the energy basis for the coupling of succession, evolution, and self-organization of ecosystems. Over successional or evolutionary time, species of plants, animals, and microbes converging as a community where the novel system is developing have the opportunity to interact, be it competitively and/or facilitatively. Those combinations of species that reinforce the community by maximizing the energy flow of the ecosystem are the most likely to emerge as members of the novel ecosystem (Odum, 1988). In changing environments, we expect such process of community reinforcement and membership to be, by default, very dynamic.

Because all ecosystems, past and present, are exposed to environmental change, all generate novelty and self-organize along unique successional paths to maturity, organismal adaptation, and resilience. Radeloff et al. (2015) conceptualized the novelty in ecosystems as a multidimensional attribute of ecosystems involving both biotic and abiotic deviation from a baseline, within a defined time frame. This definition is consistent with the idea that novelty is a natural response of all ecosystems to environmental change and allows for estimating levels of novelty among ecosystems. With this approach, Radeloff et al. (2015) eliminated the need to use human agency, self-perpetuation, and irreversibility of change as criteria for defining novel ecosystems. Ironically, these criteria are the ones that led to the emergence and current use of "novel ecosystems" and for defining them in the context of the Anthropocene (Hobbs et al., 2013).

The generation of novelty in ecosystems through geologic time was probably as dramatic as we are experiencing today in the Anthropocene, but such comparisons appeal mostly to specialized ecological and evolutionary fields such as evolutionary paleoecology (Behrensmeyer et al., 1992). The criteria of human agency as one of the causes of novelty generation in present ecosystems contrast with nonanthropogenic forces of ecosystem change, which generated novelty under pre-Anthropocene conditions. Similarly, criteria of self-perpetuation and irreversibility of change apply to all ecosystems, whether they formed before or during the Anthropocene Epoch because all ecosystems are responding to environmental change constrained by the same ecological and evolutionary mechanisms and processes. Today, many argue that human-agency changes the speed of ecosystem response

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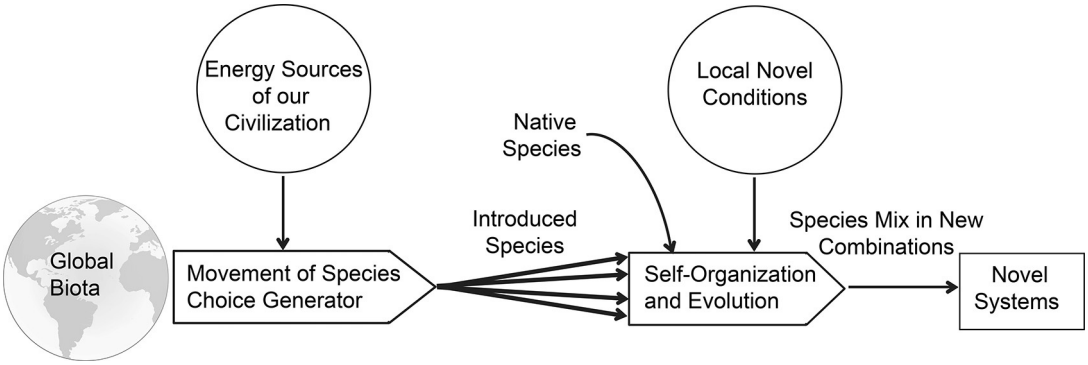

Fig. 1 Global and local causes (*circles*) and processes (*arrow symbols*) of novelty in ecosystems. The mechanism for generation of novelty involves four steps: (1) The introduction (choice generator) and (2) mixing of native and nonnative species in particular habitats with (3) local novel environmental conditions (product of human activity and environmental change). (4) Natural selection and self-organization forces act on the diversity of choices represented by the mixed species assemblage, and those groups of species that maximize energy and material flow and are best adapted to local conditions are favored over maladapted ones. The resulting novel system contains native and nonnative species in novel combinations.

because human-induced environmental change itself is accelerated. Such claims can be true, but ecosystem response to perturbations depends on the type, intensity, frequency, spatial distribution, and duration of the disturbance (Turner et al., 2003), be it anthropogenic or not. Thus, from the point of view of ecosystem functioning and response, what matters are the characteristics of the disturbance regime rather than the cause of the disturbance. To the degree that the disturbance regime contains novel ecological challenges, organisms will respond with novel adaptive solutions.

Our conceptual model for the assembly of novelty in forest ecosystems (**Fig. 1**) is based on human agency, which accelerates the global dispersal of species. Increased species dispersal increases species interactions and the number of alternative pathways toward self-organization, succession, and organismal evolution. The process plays out at local scales in the face of large-scale changes, such as climate change. Anthropogenic activities modify the environmental conditions to which species (native or nonnative) must adapt to avoid local extirpations that can lead to global extinction. Thus, it is precisely at the local scale of species' interactions that most of the novelty is generated and scaled up to the ecosystem through mechanisms and processes of self-organization, succession, and evolution.

In this essay, we address some of the mechanisms that generate novelty in tropical forests and urban environments. We focus attention on three contributing causes of novelty involving human agency: (1) modification of the environment and generation of novel forests, (2) evolutionary processes, and (3) the role of biota in community regeneration. We also discuss the implications of novelty in ecosystems to conservation.

Novel Environments

Human activity has always modified the environment as discussed extensively in historic accounts (e.g., Chazdon, 2014). Human activities during the early Holocene Epoch had planetary-level effects including extinctions of large organisms and species in vulnerable locations such as oceanic islands. Also, humans and other animals have always moved organisms across their biogeographical limits. Human activity increased in intensity and global effects with the advent of fossil fuels and associated technology, leading to the development of extensive urban and agricultural systems. Human activity not only changed the land cover of the planet (Ellis et al., 2010) but has also increased the diversity of habitats available to organisms by introducing novel environmental conditions. In short, human activity is responsible for increasing the environmental heterogeneity of the planet, which is now in the Anthropocene Epoch—a time period dominated by human activity and its effects on climate, environment, and biota.

A list of human activities that now sustain the heterogeneity of environments in the Anthropocene Epoch includes:

- Land deforestation and cultivation dynamics
- Changing the physical and chemical properties of soils
- Changing topography through cutting and filling activities
- Hunting wild animals and rearing domesticated species
- Global dispersal of species
- Altering watershed hydrology and local and global water cycles
- Altering global and local temperature patterns
- Mining the ground for materials
- Manufacturing new chemical compounds that are toxic and/or difficult to decompose and recycle

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- Circulating wastes generated by human activities
- Constructing structures and transportation systems
- Altering landscape connectivity via fragmentation and urbanization
- Constructing impervious surfaces with effects on thermal patterns and hydrology

The global scope of this list of human activities leaves no doubt that the planet is heavily influenced by anthropogenic activity. For example, Sterner and Elser (2002) found that human activity drove the global biogeochemical cycles of the primary elements that regulate the functioning of the biosphere (C, N, P, S, H, and O). The anthropogenic global fluxes of N, P, and S are larger than the combined nonanthropogenic fluxes of those elements (Sterner and Elser, 2002). In the case of carbon, while the human-generated flux was only 13% of the global flux, such influence is sufficient to cause climate change with global consequences.

Consequences of the activities of people that lead to novel habitat formation for organisms include: alteration of vegetation cover, compaction and nutrient depletion of soils, changes in topography, filling of wetlands, altered hydrological cycles, changes in the composition of the atmosphere, altered habitat stoichiometry, presence of toxic materials, and altered patterns of species harvesting, distribution, and colonization. These novel environments add to the existing heterogeneity of the planet and provide new ecological niches available for the establishment of novel communities of organisms. The modification of the planet by humans has led Ellis (2015) to propose a new ecology that he termed anthroecology, which deals with the anthromes that have replaced historic biomes. Ellis proposes, and we agree, to change the ... "classic paradigm of 'natural systems with humans disturbing them' to ... 'societies sustaining an anthropogenic biosphere' (p. 321)." Such an anthropogenic biosphere is driven by human activity, involves considerable land dedicated to cities, and systems used in direct support of human activity such as agricultural systems. In this biosphere, the wilderness or wildness Higgs (2006) will be dominated by novel ecosystems and will constitute the new wild (sensu Pearce 2015).

Novel Versus Historic Forests

The predominant focus of the novel forest literature has been the comparison of their successional state with historic and hybrid forests and seeking ways for restoring, or not, novel forests into historic forests (Hobbs et al., 2013). The main question asked when attempting to convert novel forests into historic ones is whether or not the conditions that sustain novel forests have passed a threshold beyond which it is difficult or impossible to restore the conditions that supported historical forests. With the advent of the Anthropocene and continuing dominance of humans over the ecosystems of the planet, it becomes less likely that novelty can be reversed, suggesting that novel forests are here to stay. If so, the question is how do novel forests compare to historic forests both structurally and functionally? We already know that these forests differ in their species composition.

Age Differences

When comparing novel with historic forests, it is critical to consider the age of forests, an often-overlooked factor. Kennaway and Helmer (2007) aged the forests of Puerto Rico, which Martinuzzi et al. (2013) showed to be 75% novel. Kennaway and Helmer (2007) found that in 2000, 55% of novel forests were less than 13 years old and only 13% were 41–55+ years old. Similarly, Martinuzzi et al. (2013) found historic forests belonged in the oldest age class of 55–64+ years.

It stands to reason that novel forests are younger than historic forests because novel forests emerge from the conversion of mature forest vegetation. Odum (1969) contrasted the characteristics of mature versus successional systems and emphasized changes in their ecological attributes as they matured. This approach can be applied to the comparison of novel versus historic forests because the age difference between novel and historic forests is similar to that between successional and mature forests, $<$100 years old for novel forests and 100–400 years old for mature historic forests. Many attributes of mature forests, such as the high density of endemic species or a well-developed soil humus layer, are almost impossible to find in successional or novel forests because they require time to develop—an unavoidable "time tax." However, the path to maturity and to those particular attributes is through successional mechanisms, and comparing a young forest with a mature one is like comparing a child with an adult. Therefore, even if younger systems appear ecologically inferior to mature systems for not possessing the attributes of mature systems, it must be realized that younger systems will gain the attributes of maturity through succession (Chazdon, 2014). This conclusion is applicable to not only novel forests but also novel ecosystems in general in the Anthropocene, including heavily modified ecosystems such as cities.

Comparison of Ecosystem-Level Attributes

Mature novel forests are more similar to developing novel forests than they are to mature historic forests. Building on Odum's (1969) synthesis, we developed **Table 1**, which compares novel and historic forests and attempts to eliminate normative criteria from the comparison. We found that attributes of developing novel forests generally align with those of developing historic forests with a few notable differences. With regard to community energetics, the main difference was the role of detritus in mature historic forests, which is not prominent in novel forests. Also, mature novel forests retain high net primary productivity at maturity, while mature historic forests have lower net primary productivity and approach 1 in their photosynthesis (P) to respiration (R) ratio (P/R).

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Table 1 A tabular model of ecological succession: trends to be expected in the development of ecosystems *sensu* Odum (1969)

	Developmental stages		*Mature stages*	
Attributes	*Historic*	*Novel*	*Historic*	*Novel*
	Community energetics			
P/R	>1<	>1<	≅1	>1
P/B	High	High	Low	Intermediate
B/E	Low	Low	High	Intermediate
NPP	High	High	Low	High
Food chains	Mostly grazing	Mostly grazing	Mostly detritus	Mostly grazing
	Community structure			
Total organic matter	Low	Low	High	High
Soil profile	Some disturbance	Degraded	Intact	Degraded
Soil organic matter	Moderate	Low	High	Low
Species richness	Low	Low	High	Intermediate
Species dominance	High	Very high	Low	High
Physiognomy	Low stature and low diversity	Low stature and low diversity	High stature and diverse	High stature and diverse
	Life history			
Niche specialization	Broad	Broad	Narrow	Broad
Life cycles	Short	Short	Long	Intermediate
	Nutrient cycles			
Storage in plants	Low	Low	High	High
Nutrient fluxes	Fast	Fast	Slow	Fast
Role of detritus in nutrient regeneration	Small	Small	High	Intermediate
	Selection pressure			
Growth form plant adaptive strategies	r selection	r selection	K selection	Both r and K selection
Xenodiversity	Very low	Very high	Zero	High
	Overall homeostasis			
Internal symbiosis	Undeveloped	Undeveloped	Developed	Developing
Aboveground nutrient pools	Low	Low to high	High	High
Information	Low	Low	High	Intermediate

Some entries in the original table were modified, and two columns were added to include novel forests. Developmental stages range from 0 to 50 years old and the mature stages >50 years. The mature historic forests can reach 400 years old, but the oldest novel forests are <100 years old. Inferences are based on research on puertorrican moist to wet subtropical forests. Gross production to community respiration is P/R, P/B is gross production/standing biomass (a measure of turnover of biomass), B/E is biomass supported per unit energy flow, and NPP is aboveground net primary productivity.

The difference may be due to age, as the oldest mature novel forests are yet to approach the levels of structural complexity that lead to high respiration rates and lower P/R ratios.

The role of detritus in nutrient cycles also separates novel from historic forests, as does the velocity of nutrient fluxes. Cycling of nutrients from detritus is greater in mature historic forests than in novel ones, while novel forests (both young and mature) maintain faster rates of nutrient fluxes than historic forests. Novel mature forests have lower species richness, higher species dominance, and less soil organic matter than historic mature forests. These ecosystem attributes also separate developing novel forests from developing historic forests. Paradoxically, mature novel forests can accumulate more aboveground carbon than both mature and successional historic forests (Lugo et al., 2012).

The high xenodiversity (sensu Cox, 2004) in novel forests differentiates novel from historic forests regardless of age. This parameter—richness of introduced species—has implications for selective pressures and community assembly because the presence of introduced species opens new opportunities for species interactions not present in historic successional processes. This favors the possibility of allowing new adaptive strategies and processes to evolve. Mature novel forests contain native tree species present in various proportions in relation to the dominant nonnative species. The mixing of native and nonnative species broadens life history attributes.

Comparison of Plant Traits

Species and ecosystems are optimized among three life-history strategies as they adjust and adapt to prevailing conditions. Grime and Pierce (2012), who expanded on Odum's r and K selection ideas (**Table 1**), defined these as the CSR strategies: maximization of resource acquisition (C), maintenance of metabolic performance in variable and unpredictable niches (S), regeneration or the rapid completion of the life cycle (R). A particular system can exhibit more than one of the three strategies. Moreover, each strategy is associated with particular plant traits and ecosystem effects that allow us to further refine the distinctions between historic and novel forests (**Table 2**). In **Table 2** we compare mature historic forests with mature (but still younger) novel forests in Puerto Rico using

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Table 2 Plant traits (from Table 6.1 in Grime and Pierce, 2012) and their dominance in novel (N) and historic (H) subtropical moist to wet forests

	Primary strategy		
	C-selected	*S-selected*	*R-selected*
Plant traits			
Life history	Long (H)	Very long (H)	Very short (N)
Life span of leaves and roots	Short (N)	Long (H)	Short (N)
Potential growth rate	Rapid (N)	Slow (H)	Very rapid (N)
Concentration of nutrients in leaves	High (N)	Low (H)	High (N)
Concentration of carbon in leaves	Low (N)	High (H)	Low (N)
Leaf toughness	Low (N)	High (H)	Low (N)
Palatability	High (N)	Low (H)	High (N)
Leaf decomposition rate	Rapid (N, H)	Slow (H)	Very rapid (N)
Seed or spore production	Delayed (H)	Very delayed (H)	Early (N)
Some effects on ecosystems			
Primary production	High (N)	Low (H)	Moderate
Carbon concentration in vegetation and soil	Moderate	High (H)	Low (N)
Retention of nutrients and pollutants	Weak (N)	Strong (H)	Very weak
Resistance to physical damage	Low (N)	High (H)	Low (N)
Recovery from damage	Rapid (N)	Very slow (H)	Very rapid (N)

The dominance of different traits in novel and historic forests shows different adaptive strategies driven by trade-offs in natural history. The assignation of plant traits to N and H forest type is based on research cited in the text, and the differences are relative to each other. The historic forest is a mature old forest (>100 years old), while novel forests range between 30 and 50 years old.

the plant traits and plant adaptive strategies of Grime and Pierce (2012). This table shows historic forests as consistently exhibiting an S-selected adaptive strategy, while the novel forests exhibit two primary strategies (C- and R-selected) and in no plant trait do the novel forests fall within the S-selected strategy. These generalizations apply to the plant trait level as well as the ecosystem effects shown in Table 2.

Slow Variables

The picture that emerges from the comparison of novel and historic forests is that certain attributes and plant strategies of mature historic forests are not present in mature novel forests. The differences have to do with the slow variables (sensu Walker and Salt, 2006) of the ecosystem, which even after 100 years are not as developed in novel forests as they are in historic forests of greater age. These slow variables include the development of the soil profile, robust organic matter layers and humus in soil, the accumulation of rare species, the abundance of large trees (>70 cm dbh), and the development of extensive belowground root systems. These slow variables take a long time to develop (i.e., the "time tax" on succession) and are still lacking in the oldest novel forests in Puerto Rico.

Degradation processes due to human activity have led to the exhaustion of slow variables with ecological consequences. One consequence is the absence of mature forest attributes in novel systems, even after 100 years of growth and succession. The degradation of slow variables in novel forests, particularly soil structure and chemistry, alters the successional development of forests by selecting for species able to grow under degraded soil conditions. Usually, native species cannot grow after soil degradation and depend on nonnative species to reestablish suitable growing conditions after degradation. Resulting combinations of nonnative and native species are better suited to cope with degraded environments in terms of basic ecosystem functions than a purely native community. The result is that in spite of growing on degraded sites, novel forests accumulate large aboveground biomass and nutrient pools and exhibit high primary productivity, rapid rates of litter decomposition and nutrient fluxes, and high turnover of species. High velocity of processes, including regeneration, and high turnover of species and mass are the sources of resilience of novel forests, in contrast to historic forests which depend on accumulated stores associated with slow variables. Both system types achieve resilience, but the speed and turnover of novel forests is an advantage for adaptability in light of a changing environment.

Evolution in Novel Environments

Although drastic anthropogenic habitat modifications and shifting ecological processes in the Anthropocene may paint a picture of a future biosphere lacking in flora and fauna, this is far from reality. Plants and animals of the Anthropocene are proving to be remarkably resilient and adaptable to novel environments of all types, not just novel forests. Urban habitats provide case studies for understanding evolution in the Anthropocene as they are drastically modified from their historical state, can last for centuries and

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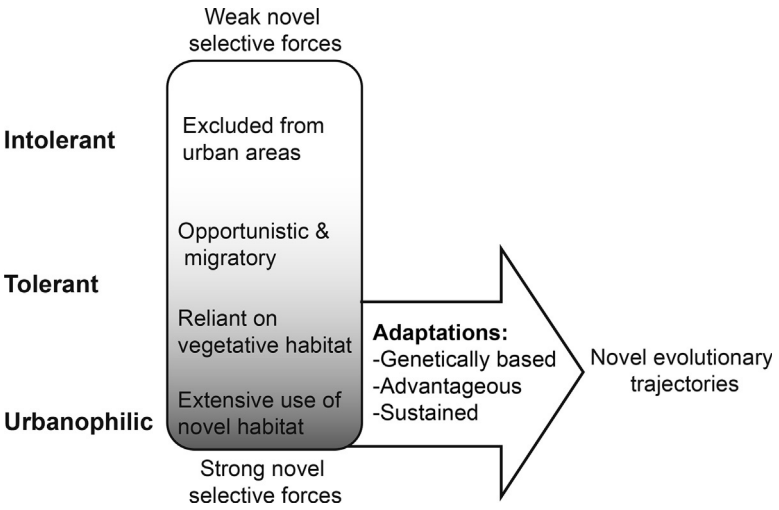

Fig. 2 Urban habitats facilitate novelty. Many species are intolerant to urbanization, some tolerate the novel habitat but are still reliant on historical aspects, and some thrive by extensively utilizing the novel habitat. The more extensively a species uses the novel habitat the more likely they will adaptively respond (*darker gray* represents stronger novel selective forces). Over time, if adaptive traits (represented by the *large arrow*) in urbanophilic and some tolerant species are genetically based, advantageous on longer time scales, and sustained, novel evolutionary trajectories may arise.

millennia, and present novel selection pressures on plants and animals. We propose that the altered, and often intense, selective pressures associated with urban habitats facilitate adaptive evolution in the Anthropocene.

The direct effects of humans on traits of plants and animals have long been appreciated. Through domestication, pest control, and antibiotic use we have caused rapid shifts in phenotypes, many unintentionally. What is only now truly being appreciated is that humans are affecting evolutionary trajectories of plants and animals via drastic modification of the natural habitat. Returning to the analogy of the evolutionary play, not only have the stage and the pace of the play changed, but the actors themselves are changing. As a result, new characters are introduced, old characters are taking on new roles, and some characters exit the stage. The earliest example of such a change is the well-known observations of H.B.D. Kettlewell, who linked industrial pollution with increased melanism in the Peppered Moth (*Biston betularia*), an adaptation to enhance camouflage against substrates darkened by soot. This foundational work demonstrated not only that humans can indirectly and inadvertently affect the phenotypes of wild animals, but also that these changes can occur on rapid, observable, contemporary timescales.

However, not all species are present in urban areas and even closely related species differ in their tolerance and adaptability in urban ecosystems. Species fall into three general categories describing their ability to persist and utilize resources in human-dominated habitats: urban intolerant, urban tolerant, and urban exploiting (Fig. 2). Species that have highly specific niches and habitat requirements are generally intolerant to human-dominated habitats. Often, these intolerant species are excluded from urban habitats leading to elevated local extinction, reduced diversity, and communities dominated by a few urban-tolerant species. Species that tolerate certain aspects of the urban habitat but still rely heavily on resources associated with historical habitat present in urban areas (e.g., most vegetation) persist in the urban landscape but are restricted to urban forests, green spaces, or clusters of vegetation. Urban presence alone is not enough to result in urban adaptation if the most successful individuals persist by avoiding urban stressors. To what extent opportunistic or transient urban exploiters are subject to urban selection pressure and how this compares to selective regimes of historical forests is a subject worthy of further research.

Urban exploiting, or urbanophilic, species are unique in that they utilize the novel urban habitat extensively, taking advantage of anthropogenic resources such as food subsidies and novel structural and climatic microhabitat. Many of these species have a core set of traits in common: broad physiological tolerances, generalists in diet and habitat use, rapid reproduction, high survival rates, and tolerance by and of human activity, even if population control measures are implemented against them. These species must cope with novel selection pressures and unique adaptive landscapes leading to divergent phenotypes and rapid contemporary adaptation at rates of change that can exceed those observed in natural habitats (Hendry et al., 2008). The more a species ventures into and benefits from the urban environment, the more likely it will be to experience adaptive shifts. Ultimately, if these phenotypic shifts are sustained over longer time periods, the potential for novel evolutionary trajectories arise. As novelty in ecosystems arises with anthropogenic habitat modification, plants and animals are responding with rapid shifts in behavior, morphology, and physiology. Over time, if these shifts remain beneficial and are genetically based, they result in a floral and faunal community adapted to the novel anthropogenic environment (Fig. 2).

Behavioral Shifts

Perhaps the most labile traits to respond to human pressures are behavioral, and these are the most commonly reported adaptive shifts in response to anthropogenic habitat modification (Fig. 3). We highlight three well-documented areas of behavioral

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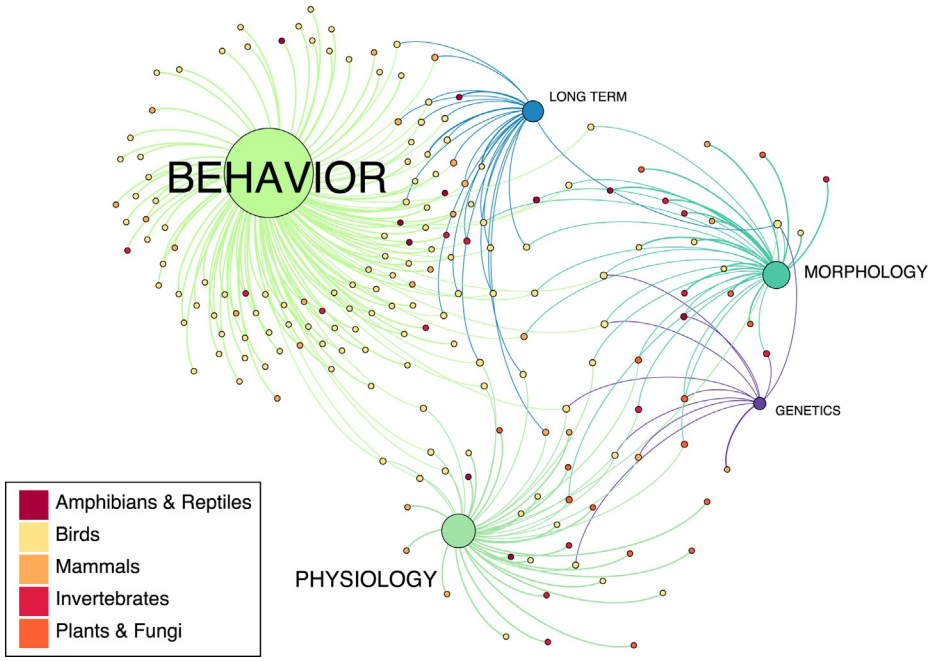

Fig. 3 A visualization of publications describing urban adaptation based on a Web of Science search for "(urban* OR anthropo*) AND (evol* OR adapt*)" conducted in October 2016. Urban adaptive shifts have been documented for a variety of taxa relating to behavior, morphology, and physiology (including reproduction). Few studies have also addressed the genetic basis or long-term implications of such shifts. Here we represent categories of adaptive shifts by the large labeled nodes and edges and individual papers (colored by taxon) by the small nodes. Note the majority of research has been done on behavioral shifts in birds.

adaptation that exemplify how these types of adaptive responses are facilitated in urban habitats: vocalization, resource use, and habituation.

Anthropogenic sound creates a strong selective pressure for vocally communicating species. Adaptive responses to urban sound have been documented in a variety of vertebrate and invertebrate species (and have been extensively described elsewhere) though they have been most studied in birds. The urban environment produces loud and low-frequency ambient sound that can mask vocal signals. Species with naturally higher pitch calls may be preadapted to tolerate urban habitats, while those with lower pitch calls may be more susceptible to the masking effects of urban sound. Some species alter their spatial or temporal use of the habitat in response to anthropogenic sound. For example, urban Mienten tree frogs (*Kurixalus idiootocus*) call from inside storm drains, which enhance call duration and amplitude (Tan et al., 2014). In addition, a number of bird species have altered song characteristics in urban populations compared to nearby nonurban populations. Commonly, urban vocalizations are higher in frequency but may also differ in complexity and song characteristics (Slabbekoorn and den Boer-Visser, 2006). These shifts enhance the vocal signal in the noisy urban environment enabling effective communication.

Resource use is another major facilitator of urban behavioral shifts: various taxa utilize anthropogenic sites and materials and many also consume anthropogenic food sources. Animals forage at waste piles and scavenge meat, fruit, and crops, and various species consume insects attracted to lights. The prevalence of dietary shifts is unquestionable, but to what extent are they correlated with cognitive shifts? Urban animals have been found to solve food-reward problems faster than rural animals (e.g., Liker and Bokony, 2009). Thus the ability to recognize unfamiliar food resources and take advantage of them may require flexibility in diet and cognition in relation to problem solving abilities.

Humans themselves are potent selective agents for behavioral adaptation to urbanization. Habituation to human presence confers protection from predators, reduces unnecessary energy expenditure, and may reduce physiological stress. Animals that do not perceive humans as threats will allow them to approach closer before fleeing (i.e., they have a shorter flight initiation distance, FID). In birds and small mammals, urban animals typically have reduced FID in general, and time since urbanization is correlated with increased habituation (e.g., Møller, 2008). Moreover, some species are able to modulate this response based on experience and visual cues from the potential threat, in some cases even recognizing individuals as threats. Other species capitalize on the wariness of other species. For example, predatory birds flee at a greater distance from humans than prey species, so species that tolerate close proximity to humans benefit from reduced predation and higher nest success (Møller, 2012).

Behavioral shifts may represent an important first step in urban adaptation. The urban habitat creates novel conditions in which different behaviors and personalities are favorable, facilitating novel adaptive responses. If animals are able to behaviorally mediate urban stressors, this enables their persistence while natural selection acts on more hard-wired traits such as morphology.

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Morphological Shifts

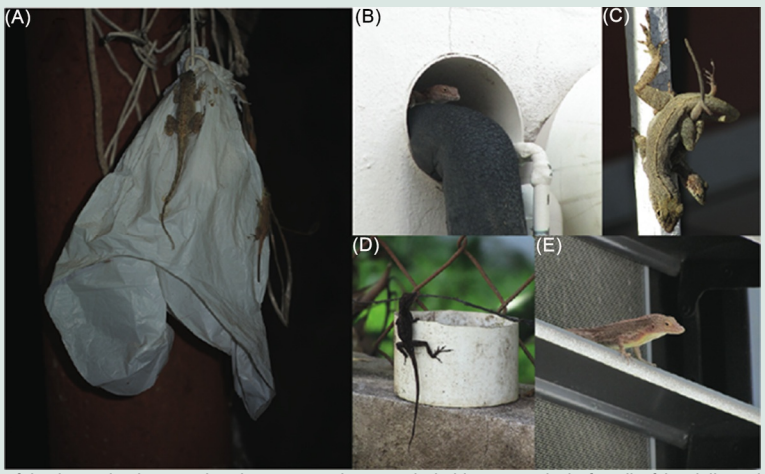
Unlike behavioral shifts, only a handful of studies have documented morphological differences in urban species (Fig. 3), but this is certainly not reflective of the prevalence of such shifts. Traits such as body size and body condition may differ in urban populations but these differences are often plastic and related to food availability. However, differences in the structural habitat, food resources, and other novel aspects of the urban habitat facilitate more complex morphological trait shifts.

Functionally important traits are likely targets of natural selection in urban habitats because of their importance to locomotion and resource use. Effectively utilizing urban substrates such as buildings has implications for skeletal morphology. Similarly, the openness and fragmentation of urban habitats may favor locomotion and dispersal traits. For example, anole lizards in urban areas have relatively longer limbs compared to rural conspecifics, an adaptation that is related to locomotory performance on smooth vertical substrates (Kolbe et al., 2015; Winchell et al., 2016; **Box 1**). In birds, bill morphology is related to both song and foraging, with shifts occurring in response to altered food resources requiring different bill structure (Badyaev et al., 2008) or acoustic environments that favor different song characteristics (Giraudeau et al., 2014).

Body coloration is also likely a target of natural selection in urban areas because of its importance for crypsis and intraspecific recognition. Melanic forms may be favorable when it enhances crypsis or when it correlates with immune function or health. For example, some species are able to sequester toxic metal ions into melanic coats or feathers, facilitating detoxification and reducing toxin burdens, traits favorable in polluted urban environments (Chatelain et al., 2014). More complex shifts in body color and pattern have also been documented.

Cognitive shifts may accompany or enable urban adaptations. Novel foraging techniques, habituation, and problem solving tasks are all behavioral adaptations that fall into this category. In some species, brain size is correlated with urban persistence and colonization of novel habitats. For example, Carrete and Tella (2011) found that flight initiation distance was correlated with relative brain size in urban South American birds, suggesting behavioral flexibility underlying habituation is related to cognition.

Box 1 Linking Behavior and Morphology in an Urban-Adapting Lizard



Anolis cristatellus is a successful urban-adapting species that uses anthropogenic habitat extensively for all of its daily activities, including: (A) sleeping, (B) seeking refuge, (C) interacting, (D) foraging, and (E) basking.

For decades, *Anolis* lizards ("anoles") have been used as models of vertebrate evolutionary change. Evolutionarily, this group has diversified in response to ecological change and opportunity resulting in repeated evolution of similar morphological forms ideally suited for specific microhabitats. Novel ecosystems of the Anthropocene provide a natural experiment to witness this type of evolutionary change on contemporary timescales and in novel directions driven by anthropogenic activity. Recently, a group of researchers has been investigating phenotypic shifts of anoles in urban habitats in their native and expanding ranges. This body of research has demonstrated that species differ in their use of the urban habitat, with some species exploiting the urban habitat and others relying on natural aspects of the urban habitat. Urban species also differ markedly in their habituation and escape behaviors, with urban animals fleeing at closer distances and using different escape tactics compared to forest lizards (Aviles-Rodríguez, personal communication). These same species appear to differ in their ability to effectively locomote on smooth substrates typical of urban habitats, but oddly the urbanophilic species (*Anolis cristatellus*) is less adept than the tolerantavoider species (*A. stratulus*; Kolbe et al., 2015). Within *A. cristatellus*, response patterns are beginning to emerge from this research. Despite their poor performance in laboratory trials, *A. cristatellus* still chooses anthropogenic habitat such as painted walls and metal fences at high frequency (Kolbe et al., 2015; Winchell et al., 2016). Preliminary results suggest that locomotory performance is poor on metal and painted concrete, regardless of the origin of the population (urban or forest) but that urban lizards perform better than the forest lizards on these smooth substrates (Winchell et al., in prep; **Video 1** and **Video 2**). How learning or locomotory "training" factors into this ability is not yet clear, but sprinting ability is correlated with both body size and relative limb length on smooth vertical substrates, with lizards with relatively longer limbs able to sprint faster (Kolbe et al., 2015). These findings are consistent with the phenotypic patterns observed in this species of urban lizards with longer limbs and more subdigital lamellae, specialized scales important for vertical clinging in anoles (Winchell et al., 2016). Urban adaptation in this species, therefore, appears to be determined via a complex interaction of behavioral flexibility (novel habitat exploitation), cognitive ability (habituation and locomotory "training"), and morphology, resulting in measurable performance differences in urban animals.

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Cognitive components of behavioral plasticity have also been documented in two species of small mammals (*Microtus pennsylvanicus* and *Peromyscus leucopus*), which have larger cranial capacity compared to rural conspecifics (Snell-Rood and Wick, 2013). As researchers continue to explore urban adaptations, correlated shifts in brain morphology are likely to be more common than we presently recognize.

Physiological Shifts

The urban environment, with higher temperatures, toxic pollutants, and chronic stressors, necessitates physiological changes for tolerance of this novel habitat. Key adaptive responses involve higher thermal tolerance, enhanced abilities of dealing with toxins and unfamiliar pathogens, and changes in hormones related to stress.

Urban areas experience significantly elevated daily and seasonal temperatures compared to nearby forested areas (urban heat island). Adaptive thermal responses to global climate change are well documented in a variety of taxa though few studies have focused specifically on such shifts in urban habitats. For example, Angilletta et al. (2007) found urban ants in São Paolo were able to tolerate higher temperatures compared to ants outside of the city.

Unfamiliar pathogens and toxins in urban areas create selective pressures for immunological responses leading to enhanced immunocompetence in urban animals. This has been documented in white-footed mice (*P. leucopus*), which have signatures of selection in genes related to immunocompetence and toxin metabolism (Harris et al., 2013). Expressed proteins of these immunological genes act without antibody activation to continuously remove pathogens, and expression of genes associated with xenobiotic metabolism and detoxification acts to deal with elevated levels of environmental contaminants.

Lastly, chronic exposure to stressful situations can facilitate hormonal adaptive responses. Some species are physiologically adapting to higher baseline stress-hormone levels by reducing their acute stress response, a beneficial adaptation that may enable urban persistence and that appears to have a genetic basis (Partecke et al., 2006; Atwell et al., 2012). This decrease in acute corticosterone secretion is associated with urban behavioral adaptations including habituation and boldness. Other hormones, such as dopamine and serotonin, are linked to fear in animals, and shifts in genes related to these hormones are correlated with reduced wariness (van Dongen et al., 2015).

Adaptive Shifts in Plants

We have primarily focused on evolutionary shifts in animals, yet plants are also adaptively responding to the novel urban habitat. Plant species that physiologically tolerate urban conditions and are able to find suitable soil to grow will be subject to natural selection if they naturally propagate and persist (i.e., are not cultivated). We touch on some examples here related to dispersal, growth, and physiology.

Because so much of the urban environment is composed of impervious surface, passive plant dispersal may result in a large number of lost propagules. In general, urban plants should face selective pressures favoring reduced dispersal because of this cost. Cheptou et al. (2008) confirmed this for the plant *Crepis sancta*: dispersal comes at a high cost for urban plants because the high probability of a seed randomly landing on concrete. This strong selective pressure has resulted in greater production of nondispersing seeds by urban plants, ensuring that offspring stay close to the parent plant where they are more likely to land on fertile soil. However, the opposite pattern is observed when we consider animal dispersal. Animals provide directed seed dispersal that in hostile or heterogeneous environments increases movement at long distances to suitable recruitment sites (Carlo et al., 2013, Carlo & Tewksbury, 2014). Recruitment is common under "nursing" structures such as perches and different types of fence lines that abound in urban and other anthropogenic environments.

Environmental stressors such as pollution and thermal and water stress also present challenges and opportunities for adaptive responses in urban plants. Despite an overall decrease in biomass in response to pollution from traffic, urban plants adaptively respond by shifting investment into aboveground leaf and shoot production instead of belowground roots (Gratani et al., 2000). In response to reduced light levels caused by particulate deposition on leaves, some plants have higher chlorophyll content or larger light-harvesting complexes (e.g., Gratani et al., 2000). Thermal and hydric conditions of urban habitats also create selection pressures for urban plants. For example, white clover (*Trifolium repens*) experiences a trade-off between cold tolerance and cyanogenesis, an antiherbivory trait. In city centers, where soil reaches lower temperatures and is not insulated by snowpack, fewer cyanogenic plants grow (Thompson et al., 2016).

Genetic Basis of Shifts

Urban adaptations may be genetically based or may be the result of phenotypic plasticity. For example, although behavioral shifts are often culturally transmitted, certain behaviors have a genetic basis (Mueller et al., 2013; Atwell et al., 2012). Bird song is related to bill morphology in some species (Badyaev et al., 2008), and habituation and boldness may involve genetically based shifts in stress-hormone regulation (Partecke et al., 2006). Plastic responses can have significant evolutionary implications if they permit species to persist in novel habitats, while natural selection acts on heritable attributes. Thus both heritable and plastic responses are relevant to urban adaptation.

The genetic basis of phenotypic shifts in urban flora and fauna has been demonstrated for relatively few species. Some have demonstrated a genetic basis to observed trait shifts based on their maintenance in common garden rearing experiments (Atwell

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et al., 2012; Winchell et al., 2016). These studies demonstrate that adaptive shifts can have a genetic basis, but questions remain regarding the precise genetic mechanisms generating these patterns. Others have found evidence for genetic basis of traits by looking for genetic signatures of change. For example, blackbirds (*T. merula*), which demonstrate multiple behavioral trait shifts in urban populations (relating to circadian rhythm, harm avoidance, stress response, and neophilia), also experience genetic shifts in traits associated with these behaviors (Mueller et al., 2013). Along the same lines, Harris et al. (2013) determined that gene regions in the white-footed mouse (*P. leucopus*) were under direct selection in urban populations, and that these genes were mainly associated with metabolic and immunological functions.

Long-Term Perspectives

Adaptations to conditions when urbanization is recent may not be advantageous as the age of urbanization increases (Snell-Rood and Wick, 2013). Urban adaptations that provide short-term fitness benefits may actually be evolutionary traps on longer timescales if there is a mismatch between immediate benefit and long-term cost. For example, some birds incorporate cigarette butts into their nests, resulting in lower ectoparasite loads and increased hatching and fledging success (Suárez-Rodríguez and Macías García, 2014). The downside of this seemingly beneficial behavior is that hatchlings in nests composed of cigarette butts have greater genotoxic effects, potentially decreasing their long-term fitness. Similarly, many species that feed on anthropogenic resources suffer from longer-term negative side effects including increased genotoxic effects, greater disease susceptibility and prevalence, and higher parasite loads. In any case, novel pressures on urban species will lead to novel types of tradeoffs affecting fitness of organisms and the possible evolutionary outcomes.

Phenotypic shifts, even those shaped by natural selection, are not necessarily adaptive and do not necessarily alter evolutionary trajectories in the predicted direction on longer time scales. Selective pressures can shift from year to year resulting in oscillations between different beneficial trait states over long periods of time. Over evolutionary timescales adaptations like those described above will be fixed in urban populations if they are sustained and provide a true benefit or lost if not. In time, the fauna of anthropogenic ecosystems will be ideally suited for novel environments in the Anthropocene. As organisms evolve along novel trajectories and native species mix with nonnative species, the ecological theater will continue to change, facilitating additional adaptive change under novel selective pressures. We are already witnessing the power of this evolutionary driver in adaptive responses to the ecological interactions of novel species assemblages in anthropogenically dominated areas such as cities and novel forests (Cox, 2004).

Natural Regeneration in Novel Environments

Novel environments, composed of plant and animal species that historically did not co-occur, are now common in the Anthropocene, where compositional novelty and function are driven by human-induced disturbance regimes. Adaptive novelty plays a key role in regeneration following anthropogenic disturbances, and the higher the intensity of the disturbance, the more important novelty becomes to the process (Fig. 4). This is due to positive correlations between the introduction rates of nonnative species, and the severity, extension, and frequency of human disturbances and activity. Nonnative species have traits that make them successful colonizers. Thus, the mixing of native species and the addition of nonnative species into novel functional assemblages become a

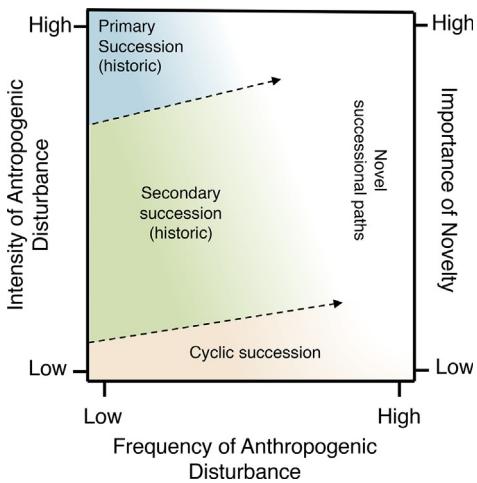

Fig. 4 Diagram showing the hypothesized importance of novelty of species assemblages for successional communities in coping with the frequency and intensity of anthropogenic disturbance regimes. As the intensity of disturbances increases, the spatial scale (e.g., local to global-scale stressors) and the duration of the disturbances also increase.

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critical component of the successional process. This is the type of outcome embodied in the Eltonian concept of succession: to predict the trajectory of succession it is necessary to understand the biological and environmental context in which it takes place.

The contemporary environmental context (i.e., Hutchinson's *theater*) provided by anthropogenic disturbance leads to a dominance of novelty in primary and secondary forest regeneration. But novelty does not imply that the general mechanisms guiding succession will change in the Anthropocene. Connell and Slatyer (1977) identified three general models of forest succession—facilitation, tolerance, and inhibition—defined by interactions between early- and late-arriving species groups. In the facilitation model, early-arriving species modify the environment in ways that increase its suitability for late-arriving species, while in the tolerance model the habitat modifications of early-arriving species have neutral effects on late-arriving species. The inhibition model predicts that early-arriving species modify the environment in ways that reduce the suitability of the habitat for late-arriving species. A remaining challenge is thus to understand the degree to which these three successional models change in relative importance under Anthropocene conditions as each reflects mechanistic differences in the way species naturally interact and assemble into communities. For example, it is still unclear whether novel successional chains are dominated by facilitative or inhibitory interactions among species, which has consequences for the quantity and conditions under which species could coexist or not.

At its onset, natural forest regeneration is controlled by the interplay between seed dispersal processes that allow plants to reach disturbed sites and abiotic/biotic postdispersal filtering of species (Chazdon, 2014). In turn, seed dispersal is regulated by the availability and distance to seed sources and the agency of the dispersal process. Human disturbances—especially those of high intensity, duration, and/or extent—have a joint effect on native and nonnative species that affect the relative contribution of both types of plant species to forest regeneration in novel environments. For example, nonnative species commonly gain dominance in early regeneration over native ones because rates of species introduction and loss of native ones go hand in hand with increased rates of human disturbance. Such conditions make many nonnative species to be less limited as potential sources of seed for early regeneration than many of the original native species, promoting novelty of community assembly.

Defaunation and landscape change also affect the relative role of different agents of seed dispersal during the forest regeneration process. The agents of seed dispersal most commonly involved in regeneration are the wind and animals. For example, wind-dispersed plant species can reach disturbed sites more easily as wind agency is generally unlimited; thus, wind-dispersed species are more likely to serve as novel forest pioneers. Animal agency, in turn, is limited by the availability of animal vectors and by the toll that anthropogenic disturbance regimes take on them. This is because disturbances such as hunting, forest clearing, and fragmentation commonly eliminate large animals and habitat specialists, creating conditions in which common generalist and smaller-bodied species thrive. This creates severe dispersal limitation of large-seeded species in regenerating forests as they exclusively rely on large-bodied animals for dispersal. The loss of large animals with human disturbance also affects plant recruitment and forest regeneration by triggering trophic cascades in which smaller animals that predate seeds and seedlings experience release from predation and/or competition and increase in abundance. The result in both cases is novel species assemblages, new dominance hierarchies, and new community assembly rules during regeneration.

Although the loss of seed-dispersal agents has been a major focus in the literature, the case in which nonnative animals serve as novel agents of seed dispersal remains understudied. Nonnative animals have the potential to restore seed dispersal mutualisms that have been lost, or to change the structure of mutualistic networks by adding novel links to seed dispersal networks. For example, nonnative horses can effectively disperse the seeds of plants originally dispersed by the extinct American mega fauna (Janzen, 1981), and other large nonnative mammals such as cattle and wild boars effectively disperse the seeds of native trees in Argentina (Campos and Ojeda, 1997). Nonnative fire ants (*Solenopsis invicta*) create new types of seed shadows for native plant species in North America (Ness, 2004), and green iguanas (*Iguana iguana*) become novel dispersal agents for native plants in Puerto Rico (Burgos-Rodríguez, 2014). Thus, new actors in the ecological play result in novelty in seed dispersal processes underlying forest regeneration, and alternative pathways for community assembly.

Changes in relative abundance of native animal seed dispersers also represent sources of ecological novelty of key functional importance in the face of anthropogenic disturbances. The disturbances increase the dominance of generalist species of seed dispersers that commonly include birds, bats, and medium-sized to small carnivorous mammals. Network theory predicts that such generalists are key for the stability and resilience of mutualistic plant–animal communities (Bascompte and Jordano, 2007). Further, empirical studies show that just a handful of bird generalist species can disperse seeds of $\geq$70% of the surrounding plant community in areas at the early stages of secondary forest succession (Carlo and Morales, 2016). These generalist seed dispersers consistently mix fruiting species in their diet, resulting in overrepresentations of rare plant species in the seed rain. The plant communities produced by this type of nonrandom dispersal are also nonrandom subsets of the surrounding communities and include representation of both native and introduced fruiting species. Such novel successional assemblages can be considered as ecologically functional as they have been naturally formed by the patterns of animal foraging and seed dispersal and include positive feedbacks between the animal agents and the novel habitats.

Implications to Conservation

As long as the environmental conditions under which ecosystems develop continue to change, i.e., under typical Anthropocene conditions, it is necessary to acknowledge the pervasiveness and importance of novelty in forests and other ecosystem types such as cities. In fact, the conditions under which conservation actions take place in the Anthropocene are riddled with conundrums,

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paradoxes, and surprises. For this reason, conservation actions in the Anthropocene require a new focus, while continuing to implement actions that have proven effective regardless of the geologic epoch (Lugo, 2014). The following conservation approaches follow from the findings of this review on novelty:

- Conservation actions need to be adaptive and deal with uncertainty, continuous change, and novelty. A new paradigm for conservation in the Anthropocene was summarized by Lugo (2014) as follows (p. 54): "Applying adaptive conservation to all human activities."
- Rather than a focus on only protected areas or green spaces such as parks, it is critical to focus conservation activities on all lands and all organisms, including human-dominated lands, such as anthromes sensu Ellis (2015).
- Anthropogenically dominated habitats such as roadsides or even heavily built-up areas should not be discounted as "lost habitat" but should be managed to improve ecological functions of urban-tolerant and urbanophilic species.
- All species have the potential to play an important role during periods of uncertainty and environmental change; this is why all require conservation.
- Species should not be persecuted or eradicated by default just on the basis of biogeographic origin or normative bias.
- The role of adaptive evolution needs to be considered both to prioritize species conservation efforts and to understand long-term consequences of phenotypic change in the Anthropocene.
- Conservation practitioners need to be closer than ever to science, as scientific knowledge will be required to monitor biodiversity, develop and test adaptive interventions, and anticipate disturbance events and biotic trends that influence social needs and interests.
- Scientists need to adjust and assure that science inquiry be transdisciplinary, combining all available knowledge, in addition to traditional disciplinary, interdisciplinary, and multidisciplinary approaches.
- Because of limited resources and knowledge, conservation activities and interventions need to be focused to specific reachable objectives (knowing when or not to intervene is critical).

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