REVIEW

Plastic ingestion as an evolutionary trap: Toward a holistic understanding

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Human activities are changing our environment. Along with climate change and a widespread loss of biodiversity, plastic pollution now plays a predominant role in altering ecosystems globally. Here, we review the occurrence of plastic ingestion by wildlife through evolutionary and ecological lenses and address the fundamental question of why living organisms ingest plastic. We unify evolutionary, ecological, and cognitive approaches under the evolutionary trap theory and identify three main factors that may drive plastic ingestion: (i) the availability of plastics in the environment, (ii) an individual's acceptance threshold, and (iii) the overlap of cues given by natural foods and plastics.

We live in a rapidly changing world, where human activities are altering our biophysical environment and leaving a persistent and substantial footprint on Earth (*1*). The pervasiveness of human-driven impacts has moved key environmental parameters (e.g., CO_2 and CH_4 atmospheric concentrations and soil nitrogen and phosphorus inventories) outside of the ranges found throughout the rest of the Holocene, prompting claims that we are now living in a different geological epoch—the Anthropocene (*1*, *2*). This new epoch is characterized by a range of global phenomena, including changes in Earth's climate (*3*) and a global loss of biodiversity (*4*, *5*). The Anthropocene is also notable for the production of enormous levels of plastic pollution on a scale that will leave identifiable fossil and geochemical records (*1*).

Industrial-scale production of plastic began in earnest in the 1940s (*6*) and scaled up considerably in the 1950s (*7*) during the period known as the great acceleration (*8*), which was characterized by growing pressures on the world's ecosystems. The increasing production and use of plastic were inevitably followed by its accumulation in the natural environment (*7*). Although most of our knowledge on plastic pollution was generated from marine ecosystems, the ubiquity of plastic pollution is now also claimed to be similar across freshwater, terrestrial, and atmospheric systems. Some rivers show concentrations of microplastics that are orders of magnitude higher than those found in marine ecosystems (*9*). Soils store more plastic than ocean basins, and thousands of tons of plastics circulate throughout the atmosphere (*10*, *11*). Although marine ecosystems are generally considered to be sinkholes for plastic (*12*), atmospheric transportation of microplastics and their exchange between soil and bodies of water indicate that oceans are only one component of the global plastic cycle (*11*, *12*).

Plastic is also accumulating in living organisms. Although considerable attention has been given to marine organisms, plastic ingestion is not restricted to these animals, having also been reported in several freshwater species (*13*) and land animals ranging from the Antarctic collembolan (*14*) to African elephants (*15*). Over the last four decades, extensive research has been conducted on the ingestion of plastic in wildlife (*13*, *16*). However, most studies have been limited to quantifying which species are ingesting plastics. After gathering a growing body of evidence showing the ubiquity of plastic pollution and its deleterious effects on living organisms (*17*)—including potential risks to human health (*18*)—we have reached the point where a unifying explanation for plastic ingestion is needed. Here, we directly address this issue by reviewing plastic ingestion through an evolutionary and an ecological lens. Specifically, we link ecology, behavior, and evolution, under the evolutionary trap concept, to provide a unifying framework for understanding why animals ingest plastics.

A widespread problem

The fast pace of plastic-ingestion records can be depicted by the sevenfold increase in the number of marine species ingesting plastics compared with the first comprehensive assessment published in 1997 by Laist (*19*). We have now reached 1288 marine species reported ingesting plastics (Fig. 1). Our Review indicates that 277 terrestrial and freshwater species have also been documented ingesting plastic, which increases the global total to at least 1565 species across environments (Fig. 1 and table S1). Terrestrial and freshwater ecosystems are still understudied (fig. S1) (*10*, *20*, *21*), which may contribute to the disparity in the number of reported species ingesting plastic when compared with marine ecosystems (Fig. 1A). The broad range of taxa known to ingest plastics demonstrates wide contamination across numerous branches of the tree of life—including eight phyla and more than half of the vertebrate orders (Fig. 1B). The sharp rise in the number of studies of plastic ingestion in wildlife is likely related to the increasing load of plastic waste accumulated in the environment combined with the growing interest of scientists and the development of new analytical tools (*22*).

Terrestrial ecosystems

Plastics are manufactured and mainly used and discarded in terrestrial habitats, where their accumulation in the natural environment begins. Although research on plastic pollution in terrestrial habitats is relatively scarce, evidence suggests that it may be potentially interfering with plant-pollinator interactions and soil function by altering the terrestrial geochemistry and biophysical environment (*10*). We find that plastics have been ingested by a diverse group of land animals, including insects, reptiles, birds, and mammals, from the tropics to the temperate and polar regions. Most of the species reported ingesting plastics are often restricted to anthropogenic landscapes, where high volumes of plastic waste can be found (*10*).

Plastic flow is different in terrestrial and aquatic landscapes and is mainly shaped by the properties of the surrounding medium. The greater viscosity and density of water, when compared with those of air, favor plastic dispersion over long distances. However, new evidence has revealed that microplastics can be transported through the atmosphere across thousands of kilometers (*11*) (Fig. 2).

Freshwater ecosystems

Freshwater habitats are among the most rapidly changing and threatened ecosystems on Earth (*23*). Although they serve as an important pathway for the spread of plastics from land to oceans (*24*), the effects of these pollutants on freshwater organisms and ecosystems have been relatively neglected (*25*). Despite the relatively low number of studies, the documented degree of plastic pollution shows that freshwater habitats are highly contaminated (*9*), and documented plastic ingestion in freshwater organisms ranges from insects to mammals, affecting most orders of freshwater vertebrates, including 20% of waterbird and 27% of fish families (Fig. 1C). Plastic ingestion encompasses all food-web levels, from filter feeding and grazing invertebrates to apex predators, and nearly all nodes of river and lake food webs are contaminated by plastics (Fig. 2).

Marine ecosystems

Plastic pollution is widespread in the marine realm, and coastal and ocean ecosystems are still considered the main plastic sink (*12*). The increase of plastics in marine ecosystems was accompanied by a growing number of studies on its ingestion by marine organisms in species distributed from tropical estuaries to cold, deep waters. Data suggest that, for well-studied taxa, plastic consumption seems to be increasing

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over time (26, 27). Plastics have also been shown to be ingested by a diverse group of species at the bases of trophic webs, such as planktivorous and herbivorous fish (Fig. 2), which suggests that trophic transfer could result in further plastic distribution across food webs.

Plastic ingestion as an evolutionary trap

Ecosystems are rapidly changing in response to multiple human pressures, creating a great number of low-quality options that mimic cues of high-quality ones, which draw animals into evolutionary traps as they are misled into make maladaptive choices (28). In this sense, plastic ingestion can be considered as an evolutionary trap, where the sudden appearance of plastics in the environment created several low-profit options that mimic cues of food items, triggering a maladaptive feeding behavior response (28, 29). The evolutionary trap concept was first evoked to explain plastic ingestion in leatherback turtles (29), arguing that transparent plastics were likely to mimic jellyfish, the turtles' main food item. This so-called jellyfish hypothesis has been applied to explain plastic consumption as being a result of a mistaken identity given similarities (e.g., color, size, or shape) with natural prey across a broad range of marine organisms (30), although the debris ingested across individuals are often different in their physical characteristics (31). More recently, plastic-ingestion studies began to evoke the evolutionary trap concept when referring to the similarities between plastics and food (32–34). This idea of a close resemblance between plastics and food items is only part of the story, and by using the evolutionary trap framework, we me may be able to disentangle the "plastic ingestion trap."

Two types of evolutionary traps are proposed: (i) the equal-preference trap—a mild trap where a relatively poor option is indistinguishable from a high-quality one—and (ii) the severe trap—in which a lower-fitness choice is preferred over a higher-fitness resource (28). Results from laboratory studies have found that plastics are often equally or less-than-equally preferred compared with food items (32, 35, 36), but selective ingestion of plastics over food is also reported (37, 38). We have little understanding of the relative attractiveness of plastics and how it varies in wildlife; therefore, determining in which trap type plastic ingestion may be classified is a difficult task. In this sense, animals' evolutionary response and plastic availability are key to understanding the trap severity, as these variables will influence the likelihood of plastic ingestion and the accumulation in the organisms.

The unifying framework

Creating a holistic understanding of plastic ingestion is necessary to unify evolutionary, ecological, and cognitive approaches through the perspective of the evolutionary trap theory. To move toward this unifying framework, the use

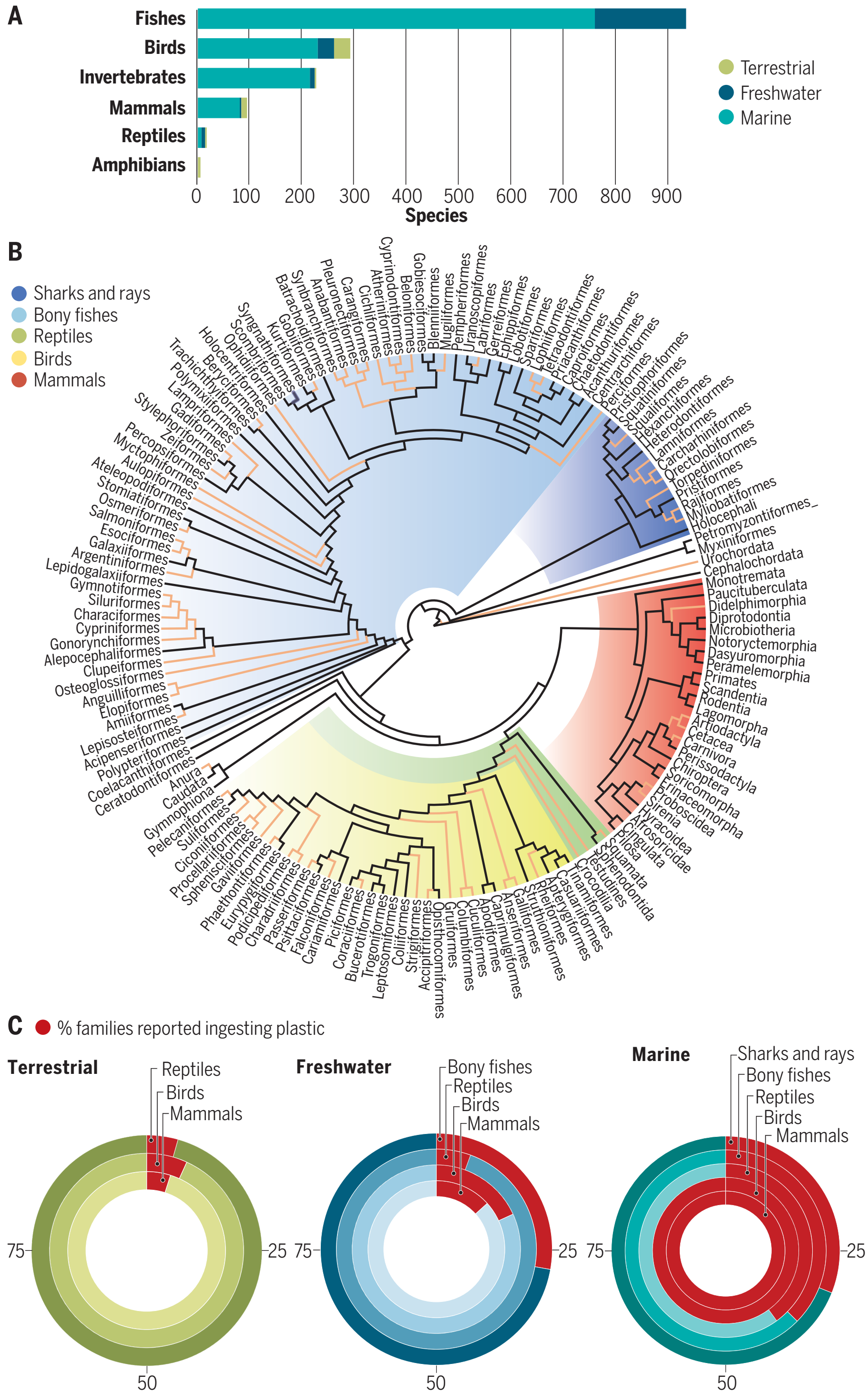

Fig. 1. Global evaluation of plastic ingestion by animals. (**A**) Number of species reported in the literature from 1980 until early 2021 ingesting plastics (macro- and microplastics). Species were classified as either terrestrial, freshwater, or marine (here as estuarine, coastal, and offshore marine seascapes) according to the ecosystem from which the plastic-ingestion record was made. (**B**) Cladogram showing vertebrate orders, with each color representing a different vertebrate group (cartilaginous fishes in dark blue; bony fishes in light blue; reptiles—Lepidosauria + Testudines + Crocodylia—in green; birds in yellow; and mammals in red). Orange branches indicate an account of plastic ingestion for at least one species of the clade. (**C**) Percentage of vertebrate families with plastic ingestion (red bars) reported for at least one species in the terrestrial, freshwater, and marine systems. We classified each family according to living habitat following FishBase (77), Vitt and Caldwell (78), Rasmussen *et al.* (79), Wetlands International (80), Croxall *et al.* (81), Veron *et al.* (82), Burgin *et al.* (83), and Feldhamer *et al.* (84).

of signal detection theory and its evolutionary application [i.e., acceptance threshold (*39*)] are key to understanding and linking the drivers behind plastic ingestion.

Organisms are faced with the challenge of accurately discriminating between beneficial and detrimental actions at the expense of frequent costly mistakes (*40*). Evolutionary history highlights that species are constantly subjected to a tradeoff between two types of errors: accepting low-profit options or rejecting high-profit ones. Plastic pollution can be seen as the rapid addition of a great variety of low-profit options, challenging the ability of organisms to differentiate food items from detrimental plastic pieces.

The recognition of a profitable food item relies on cues perceived by an individual and its acceptance threshold—the cue level at which it switches from rejecting to accepting an item (*39*, *40*). The acceptance threshold is selected on the basis of the balance between the costs of accepting a poor option and the costs of rejecting a good one. As the ability of an organism to distinguish between sensory stimuli is limited, we should expect some overlap in the distribution of cues between low-profit and high-profit items. Additionally, the acceptance threshold may also be influenced by circumstances, such as risk perception at any given moment (e.g., predation or starvation risk) (*41*).

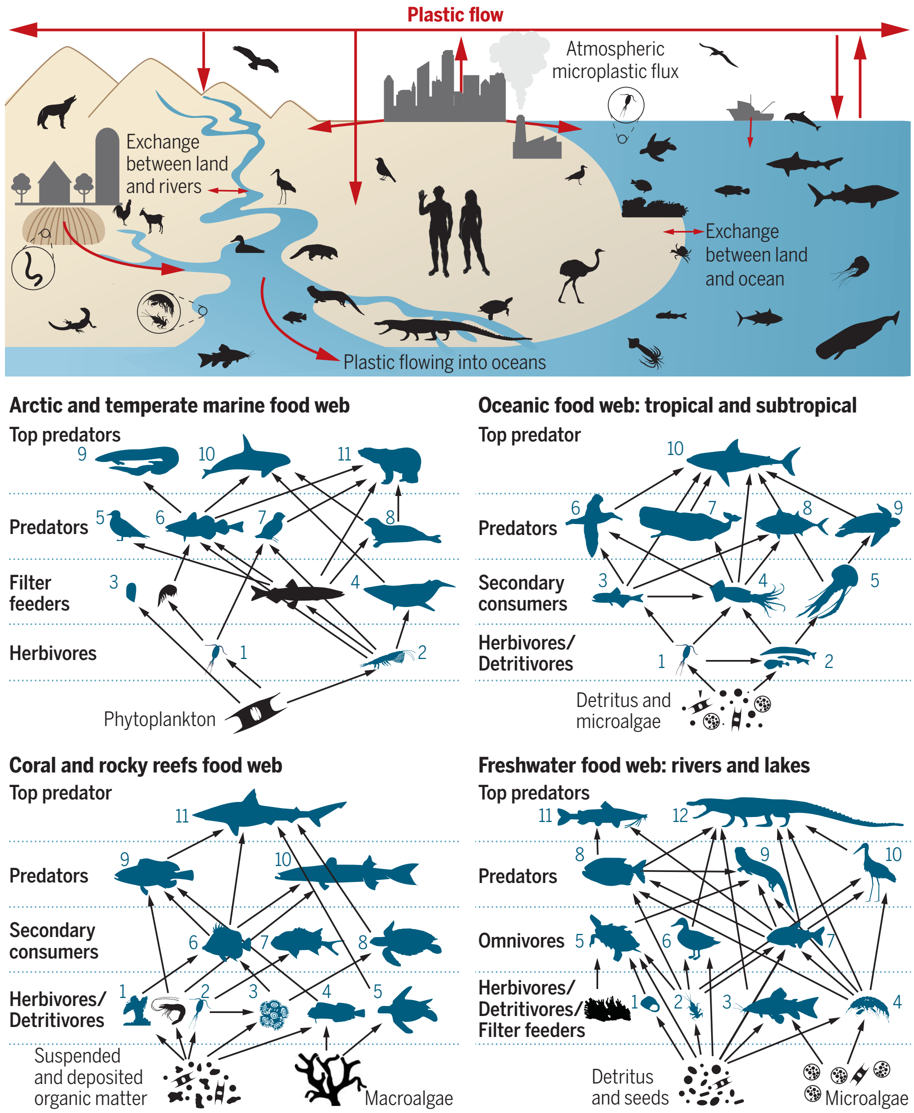

Fig. 2. The pervasiveness of plastic pollution. (**Top**) Plastic flux and accumulation in the environment are shown by red arrows. Plastics are circulating through all Earth systems and have been affecting animals with diverse niches and ecological traits. All depicted animals have a record of plastic ingestion. (**Bottom**) Plastics are ingested (teal silhouettes) by wildlife species distributed across several nodes of aquatic food webs. Arrows denote expected food chain pathways and potential routes for plastics trophic transfer. References used to draw food webs and plastic ingestion are in table S2. Animal silhouettes used are available under a Public Domain 1.0 license at Phylopic (http://phylopic.org), unless otherwise indicated in table S4.

In this context, plastics can be seen as a widespread poor food option. Once encountered, the likelihood of ingestion will be determined by an individual's acceptance threshold and the overlap between plastics and food cues. High cue overlap and/or low acceptance thresholds will increase the chances of an individual accepting a detrimental option (*28*). Interacting with these two drivers is the abundance of plastic "prey" items in the environment. As plastic availability increases, there will be an inevitable increase in the diversity of feeding cues emitted by plastics [i.e., materials, sizes, shapes, and colors (*42*)] and correspondingly higher encounter rates.

The volume and distribution of plastics in the environment combined with the foraging strategies of organisms determine the plastic-encounter rate (i.e., plastic availability), which is an important factor driving their ingestion. In support of this pattern, recent studies have documented a positive relationship between plastic debris abundance and rates of ingestion (*26*, *43*), although this pattern remains to be further explored. The relationship between the increase of plastic in the environment and its ingestion may be of particular importance to filter-feeding animals (*44*).

Acceptance threshold and cues overlap are theoretical parameters from signal detection and acceptance threshold theories (*39*, *40*), but they can be evaluated through some empirical proxies. In the case of plastic ingestion, we proposed that three traits are particularly associated with cues overlap and acceptance thresholds: (i) level of prey resemblance to plastics (physical and chemical), (ii) food selectivity (generalist to specialist), and (iii) nutritional state (e.g., risk of starvation). We suggest that these traits, combined with measures of plastic availability, should become the foundation for risk assessments for plastic ingestion (Fig. 3A). Despite the relatively low number of studies with an appropriate design to test the effects of these traits (n = 43; table S3), our framework is consistent with the current empirical evidence (Fig. 3B).

The dietary generalist-specialist distinction plays an important role in understanding foraging behavior, nutrition, and food selection. In general, specialist species are known for consuming a narrow range of foods and are likely to accept only the most profitable ones (i.e., high acceptance threshold), whereas generalists are known for ingesting a broad range of foods and mostly accepting all encountered prey when foraging (i.e., low acceptance threshold) (*45*). Under similar plastic availability in an environment, we would therefore expect generalist foragers to be more likely to ingest plastics than specialists, which seems to be supported by the literature (*46*–*49*).

The acceptance of a broader range of food items can be also triggered by circumstances, particularly those related to the risk of starvation, such as resource unpredictability (*50*) and the level of hunger (*51*). Starvation can thus induce poor foraging performance and fluctuations on feeding thresholds, leading to the consumption of less-profitable foods (*52*, *53*). Under these circumstances, an increase in opportunistic feeding behaviors could be expected (*50*). We would thus predict that the risk of plastic ingestion may increase as the risk of starvation increases. Moreover, resource unpredictability is also linked with an increase in generalist (*50*) and opportunistic (*47*) feeding behaviors. Scavenging is a good example of such a behavior—being relatively common among many terrestrial and aquatic species (*54*, *55*)—and has recently been suggested as a possible pathway for plastic ingestion by marine animals (*47*). Additionally, our Review of the existent literature shows that a third of terrestrial species that consumed plastics are obligatory or opportunistic scavengers.

The level of resemblance of plastics to natural food items (i.e., feeding cues overlap) has been thought to influence their ingestion by marine animals (*28*, *30*) and was also implicated in the ingestion of plastics by freshwater (*56*) and terrestrial (*57*) species. This general perception based on the similarities of foods and plastics can likely be related to the limited discriminatory capacity of sensory organs (*58*). Visual cues can both influence plastic detection (*31*) and their ingestion (*59*). Plastics in the environment have different degrees of similarity to natural foods, from a very precise match (*60*) to a vague (e.g., size) (*46*) or no obvious resemblance. The size of food also represents a nonvisual cue, influencing selection, capture success, and handling time (*61*). Animals' body sizes influence the range of plastic sizes ingested; however, more studies are needed to better understand how this applies to the smallest ingestible pieces (*62*). Filter, suspension, and deposit feeders are the most susceptible species to plastic ingestion because of prey size similarity (*44*, *63*). Nonphysical plastic characteristics are no less important, with chemical signatures overlapping those produced by prey also playing a role in plastic ingestion (*32*, *34*, *35*). Misleading infochemical cues emitted by the plastisphere (*34*) are often comparable to chemical signatures produced by natural foods and have been implicated in accounts of plastic ingestion by vertebrates and invertebrates (*34*, *64*).

Nevertheless, prey resemblance is quite difficult to evaluate; even the Eleonora's falcon (*Falco eleonorae*), which has the ability to capture fast-moving prey, has been documented misjudging plastics for natural foods (*57*). Thus, the unfortunate great diversity of plastic characteristics may provide endless nonexclusive possibilities for feeding cues overlap.

The number of studies on plastic ingestion are rising, as are the number of species affected and the knowledge about the impacts on multiple biological and trophic levels. However, only a small fraction of these studies is dedicated to understanding the potential drivers of plastic ingestion. Additionally, most of them are focused on evaluating taxa-specific ecological traits, which commonly lack parallels among species and are usually embedded with multiple potential drivers (e.g., plastic-encounter rate and food selectivity), which undermines their use in a broader risk-assessment evaluation. As a global problem that is spreading at a fast pace throughout diverse ecosystems, a general agreement on how to build a comprehensive risk assessment is needed.

Plastic ingestion can affect animals by a diverse set of mechanisms, such as nutritional dilution, physiological disruption, and impairment of gastrointestinal functions, all of which affect health, growth, and reproductivity output (*17*), which may ultimately lead to demographic effects (*65*). Lethal and chronic physiological health effects on the individual level have been reported in laboratory and field studies (*17*), but potential effects on the populational level are just beginning to emerge (*65*).

We live in a world where the co-occurrence of multiple anthropogenic stressors is the norm, and the risks posed by the plastic ingestion trap need to be examined in this context. Chronic effects of pollutants are hard to estimate at a population level in natural environments, but some studies are present in the literature (*66*). For example, the chronic exposure to organochlorine-persistent pollutants has left worldwide populations of vultures and killer whales (*Orcinus orca*) at the risk of extinction (*67*, *68*). These studies provide unsettling examples of how years of conservation efforts can be severely compromised by diffuse threats. It is possible that some of the threats to wildlife posed by the exposure to plastic pollution are yet to emerge, but useful lessons can be drawn from these examples.

Can the plastic trap be disarmed?

Demographic and eco-evolutionary simulations suggest that evolutionary traps can lead to population declines (*58*, *65*, *69*). Therefore, teasing apart how these traps can be disarmed is important. Three processes, and their interactions, may help to disarm evolutionary traps (*70*): natural selection, learning, and human management. In the first case, the evolution of an adaptive response to plastic pollution requires the appearance and selection of heritable traits related to sensory and cognitive systems that improve the differentiation between plastics and foods. This could potentially take place over multiple lineages across different evolutionary time scales.

Learning, like selection, potentially provides a mechanism for a population to respond to changes in the environment, enabling them to escape from an evolutionary trap (*70*). However, the ability to learn and pass on learned behaviors (cultural transmission) varies among species. To evaluate the feasibility of learning to escape a trap, we consider several factors: (i) animals may have the ability to distinguish cues from plastic and food items and (ii) the plastic ingestion trap offers multiple opportunities to do so, which increases the chances of learning through experience. Studies reporting a negative outcome as a result of plastic ingestion commonly highlight the chronic nature of the deleterious

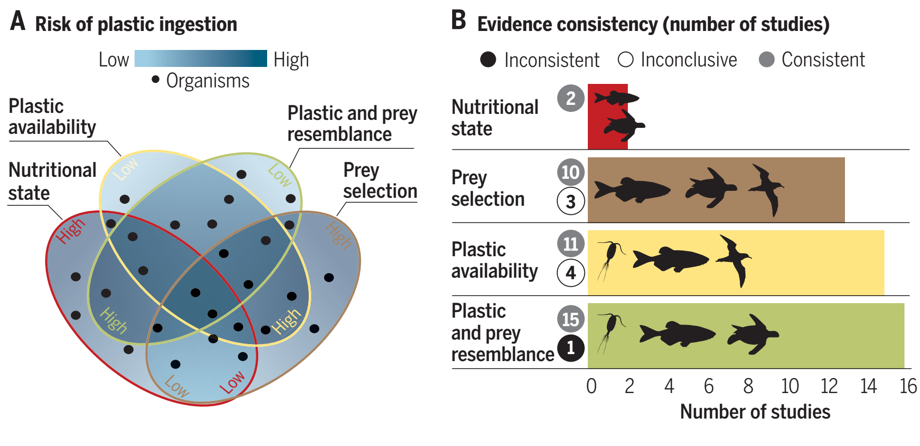

Fig. 3. Plastic ingestion risk assessment and the strength of evidence. (**A**) Diagram showing how the availability of plastics in the environment, the nutritional state of an organism, the prey resemblance with plastics, and prey selection can interact, thereby increasing the risk of plastic ingestion by hypothetical individuals (black dots). (**B**) The number of studies that provide empirical evidence regarding the proposed traits associated with risk of plastic ingestion. Data were collected from a systematic review. Evidence was selected when the study design allowed a credible causal interpretation. Evidence was classified as consistent [statistical results are in accord with the proposed framework (A)], inconclusive (statistical results did not allow a conclusion about causal interpretation), or inconsistent (statistical results contrast with our proposed framework). Depicted organisms indicate the animal groups present in the studies: invertebrates, fishes, reptiles, or birds. Animal silhouettes are available under a Public Domain 1.0 license at Phylopic (http://phylopic.org), unless otherwise indicated in table S4.

effects (*17*, *71*, *72*). This temporal disconnection between the act of ingesting plastics and their negative outcome decreases the possibility for an individual to obtain feedback on the poor payoff of plastic ingestion; therefore, the process of learning through experience is compromised (*70*).

The challenge of relying on natural selection and/or learning highlights the need for human intervention. Two human-mediated actions have been proposed to reduce the risks of animals falling into an evolutionary trap (*28*): (i) decreasing the attractiveness of the low-fitness option and (ii) reducing encounter rates with the trap. Although a reduction in the attractiveness of plastics has been previously proposed (*34*), a wide range of taxa with individual sensory and cognitive systems will prevent a one-size-fits-all solution. Therefore, decreasing plastic production is needed to reduce the encounter rate with the plastic trap.

Conclusions and outlook

The ingestion of plastics has been increasingly reported throughout diverse branches of the tree of life. Much research has reported deleterious effects of plastics in organisms, although research concerning their impacts at the population level is still in its infancy. Models suggest that evolutionary traps can severely affect population viability, and it is therefore imperative that we identify individuals, populations, and species at the greatest risk.

Although several advances in the understanding of plastic-ingestion drivers and effects have been made in the last years (*17*, *31*–*35*, *47*, *65*, *73*, *74*), we suggest that future research focuses on expanding the studies on nutritional and sensory ecology and evaluating animals' behavior within an evolutionary perspective. Studies should be designed to evaluate the relative attractiveness of plastics and their preference related to food under realistic scenarios. The interaction of the plastic-ingestion drivers, as proposed in our framework, should also be integrated in future studies to evaluate the risk of ingestion. Additionally, the threats posed by this evolutionary trap must be considered under the current context of growing pressures on the world's ecosystems, where, combined with the increase in plastic pollution, wildlife populations are exposed to multiple threats and are experiencing the degradation of their habitats (*4*, *5*), which also affects the quality and abundance of their food in relation to plastic debris.

As there are limited options for escaping the plastic evolutionary trap, mitigation efforts should heavily focus on reducing the encounter rates for at-risk populations. We cannot turn back the clock on plastic pollution, but we can adopt measures to minimize the consequences of this ubiquitous trap. Plastic pollution continues to rise, and, even if we were able to scale up the boldest mitigation policies in place today, millions of tons of plastics will still accumulate in the environment each year (*75*, *76*). This scenario calls for international steadfast commitment to transformative change, which must include pre- and postconsumption solutions guided by science, such as substantial decreases in plastic production and use—shifting toward a circular economy—and investments in waste management and recovery around the world (*75*, *76*).

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SUPPLEMENTARY MATERIALS

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