

Interrelated Causes of Plant Invasion

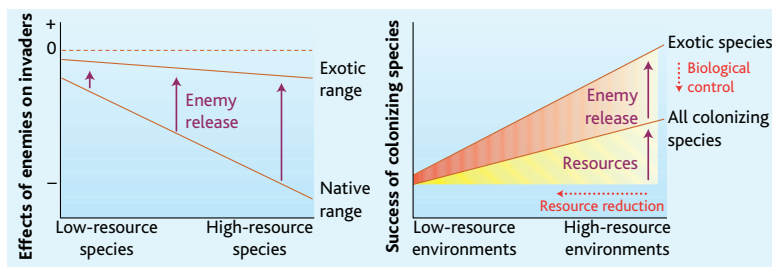
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An occasional stem of leafy spurge in the prairie would not threaten native species. Nor would it bother ranchers. But the millions of hectares of this Eurasian species that inhabit western North America have displaced native plant species and reduced forage for both wild and domestic animals, costing hundreds of millions of dollars annually (1). The problems caused by such invasive species are the direct result of their success in colonizing new habitats, and understanding why they are so successful is essential to controlling their spread. Although there are many competing ideas to explain invasion, it is possible that two of the most important are interrelated: The plant species that benefit the most from high resource availability may also gain the most from escaping enemies upon moving to a new range. This proposal predicts that resources may influence the success of biological control (the introduction of enemies from an invader's native range). It also implies that anthropogenic increases in plant resources may play a larger role in invasion than previously thought.

Due to the enormous variety of invasive plants, attempts to explain invasion have led to an array of partially overlapping hypotheses. Hypotheses explaining the exceptional success of exotic species are based upon ways in which a species' new range differs from its native range: fewer insects and diseases (2, 3), less competitive environments (4), and competitors that are more susceptible to chemicals produced by the invader (5). Hypotheses explaining colonization in general, irrespective of whether the colonizing species are native or exotic, rely on characteristics of the colonizer or the colonized

plant community. For example, fast-growing species with high seed production make good colonizers (6, 7). Plant communities with lots of disturbance, high resource availability, or reduced species diversity tend to be easily colonized (4, 8).

Of primary interest are two mechanisms of invasion that are particularly well supported by existing studies of plant invasions: release from natural enemies and



Resources and enemy release may interact to cause invasion. (Left) Species adapted to high resource availability are inhibited by enemies in their native range, and therefore have great potential to benefit from escaping those enemies in their exotic range. (Right) Although all high-resource species will benefit from high resource availability, high-resource exotic species will also benefit from enemy release. Therefore, increasing resource availability will increase the advantage of exotic over native species.

increased resource availability (2–4, 8). The enemy release hypothesis attributes the success of exotic species to their escape from diseases and herbivores upon moving to a new range (2, 3). This gives them an advantage when competing with native species still burdened by enemies. Not only are enemies missing in exotic species' new ranges, but the absence of enemies is correlated with invasiveness (3, 9). Enemy release provides the greatest benefit to exotic species that are highly susceptible to enemies in their native range (2).

The resource hypothesis suggests that plant invasion is caused by availability of resources such as light, water, and soil nutrients (8). Resources become available when resource supply increases, as with atmospheric nitrogen deposition, or when resource capture by other plants decreases, as with disturbances such as fire or plowing (8). High resource availability benefits fast-growing native or exotic species.

The reason that enemy release and resource availability may interact is that fast-

growing, high-resource species also tend to be highly susceptible to enemies. When introduced to a new range, these species are likely to benefit from both high resource availability and enemy release. Where resources necessary for plant growth are scarce, growth is slow and the metabolic cost of producing new plant tissue is high; therefore, plants from such habitats have evolved defenses to protect that tissue (10). Conversely, plants from high-resource habitats grow quickly, produce tissue at low metabolic cost, and invest little in defense (10, 11). Such high-resource species are also nutritious, with little structural material and high tissue nutrient concentrations (11, 12). Poorly defended, nutritious, high-resource species tend to be preferred by herbivores (10, 13), to lose more tissue to herbivory (14), and to be more strongly regulated by herbivory (13, 15) than low-resource species. They may also be particularly susceptible to pathogens (16).

If, as the evidence indicates, high-resource plant species are more strongly affected by enemies than are low-resource species, they should also gain more from leaving those enemies behind. The effect of enemy release in a new environment should therefore increase with the resource availability to which a species is adapted (see the figure, left). This concept, referred to here as the resource–enemy release hypothesis, predicts that enemy release and increased resource availability may act in concert to cause invasion (see the figure, right). Consequently, successful management of plant invasions may require both biological control, which aims to reduce enemy release by introducing enemies from an invader's native range, and methods aimed at limiting or reducing resource availability.

Explaining plant invasions is likely to involve not only multiple mechanisms of invasion, but also understanding the conditions under which each mechanism tends to be important. The resource–enemy release hypothesis predicts those conditions for two of the principal mechanisms of invasion, and in turn suggests how we could manage invasive species. For example, the effects of enemy release may be strongest for high-resource species. It follows that biological control may be most effective against high-resource invaders. Furthermore, unlike the resource hypothesis which

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applies equally to native and exotic species (8), the resource–enemy release hypothesis predicts that high resource availability will help exotic species more than native species (see the figure, right). Consequently, anthropogenic increases in resource availability, ranging from small-scale disturbances to global climate change, may not just facilitate invasion, but facilitate invasion by exotic species in particular. In fact, exotic species tend to outperform native species in high- but not low-resource environments (17). Humans may therefore play

an even larger role in invasions by exotic species than previously thought.

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10.1126/science.1114851

PALEONTOLOGY

Shaking the Earliest Branches of Anthropoid Primate Evolution

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Although chimpanzees are our closest living relatives, humans also share many important anatomical and biochemical characteristics with a large group of extant and fossil primates that taxonomists have named “anthropoids.” All living humans, apes, baboons, macaques, leaf monkeys, and New World monkeys, together with numerous fossil anthropoids, share a common ancestor that originated in either Africa or Asia, both continents having yielded primitive fossil representatives of this group (see the figure). In Africa, mostly through the work of Simons and his team in the Fayum desert in Egypt, numerous distinctive taxa of primitive anthropoids have been described from sediments dated at between 35 and 32 million years old (1). Not only did Simons discover *Aegyptopithecus*, the ancestor of later and more derived anthropoids (catarrhines, which includes the Old World monkeys), but he also recovered and described a diversity of more primitive anthropoid taxa, some of which appear to be endemic to North Africa while others are considered to be closely related to New World monkeys (2). Therefore, for several decades, North Africa was considered as the center of anthropoid origin and early diversification. But this classical Fayum record begins abruptly, at about 35 million years ago, when an ecologically diverse anthropoid community was already in place. Very little was known about earlier African anthropoids dating from closer to the beginning of the African anthropoid radiation.

Now, on page 300 of this issue, Seiffert *et al.* (3) describe the most complete known remains of the earliest African anthropoids from the oldest fossiliferous level of the Fayum desert, Birket Qarun Locality 2 (BQ-2), precisely dated from 37 million years ago. These anthropoids are represented by two distinct and small species of the genus *Biretia* (4) whose body masses have been estimated to be 273 and 376 g, respectively. Their dental morphology agrees with what had been predicted for a common ancestor of later African anthropoids. It is also one step more evolved than that of any contemporaneous Asian anthropoid. The smaller of these two new species (*Biretia fayumensis*) is similar to a contemporaneous Algerian species (*Biretia piveteani*) from the Bir-El-Ater locality, which is known from a single tooth (4). But the larger of these new species, *Biretia megalopsis*, whose dentition is very similar to that of the smaller one, displays a surprising and unexpected specialization. Its ocular orbits are strongly enlarged, being similar in size and morphology to those of *Tarsius*, a modern small-bodied nocturnal primate from Southeast Asia, suggesting that *Biretia* displayed a nocturnal activity pattern as well.

Unfortunately, in the smaller new species this bony area below the orbit is not preserved. The enlarged orbits of *Biretia megalopsis* conflict with the classical notion that the earliest anthropoids were diurnal primates with well-developed stereoscopic and color vision (5), and with the oldest Asian fossil record. Seiffert *et al.* (3) consider this species as a specialized, early branch of African anthropoids, because no later Fayum anthropoid displays such a character. For these authors, *Biretia* sug-

gests an ancient evolutionary history in Africa that allowed enough time for some anthropoids to develop such specialized adaptations. Alternatively, all of the Algerian and Egyptian anthropoids of this age may have shared enlarged orbits, because their similar dental characters suggest that they are closely related. But such a specialized adaptation would then exclude these fossils from the ancestry of their later Fayum relatives. Nevertheless, the dental morphology of these fossils undoubtedly documents an early stage of African anthropoid evolution, pinpointed by some uniquely shared specialized characters.

In addition to the description of these two new species, Seiffert *et al.* (3) present the results of an outstanding cladistic analysis using 360 morphological characters of 102 extant and fossil primate taxa, which supports some interesting hypotheses. The two new Fayum species appear as the sister groups of a well-known extinct anthropoid family, the Parapithecidae, which is only known from North Africa. They derive, according to that cladistic analysis, from an older Saharan primate, *Algeripithecus*, which was described several years ago on the basis of a couple of teeth (6), as the earliest (more than 45 million years old) and most primitive African anthropoid. In addition, both new Fayum species and *Algeripithecus* are considered as related to a late Paleocene (60 million years ago) Moroccan primate, *Altiatlasius*, known only from a dozen isolated teeth (7). According to that result, the anthropoids would have had a very long evolutionary history on the African continent, and this ancient origin is supported by several molecular analyses that suggest similar antiquity for the branching events between extant anthropoid lineages. Unfortunately, these older African putative “anthropoids” are extremely fragmentary, and many of their morphological characters remain undocumented. Needless to say, this hinders efforts to obtain a strong and accurate phylogenetic tree, and convergent evolution is a common pitfall of cladistic analyses.

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