

## Chapter 15

# Role in ecosystems

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### Introduction

Galapagos giant tortoises have transformative effects on the ecosystems they inhabit. Giant tortoises are the largest native terrestrial animal in the Archipelago, with dome tortoises reaching up to 350 kg. Tortoises inhabit most vegetated ecosystems on the larger islands, with their historical densities likely reaching at least 2.5 tortoises/ha (Chapter 12: Population Biology), which, combined with individual size, leads to substantial biomass, possibly greater than 500 kg per hectare (Lovich *et al.* 2018). As generalist herbivores, giant tortoises consume at least their own body weight each year (Hamilton and Coe 1982) from dozens of different plant species (Blake *et al.* 2015, 2012b; Cayot 1987; Hamilton and Coe 1982). In their search for food, water, mates, and nesting sites, tortoises trample vegetation and create permanent trails, which generate heterogeneity in plant communities. Through digging to create resting and nesting sites, tortoises can expose large areas of bare soil, which affects plant regeneration rates and community dynamics. The combination of tortoise herbivory and movement results in the dispersal of seeds and the transportation of nutrients within and among ecosystems (Blake *et al.* 2012a; Ellis-Soto *et al.* 2017). Through these combined effects, tortoises are considered the “ecosystem engineers” of terrestrial ecosystems in Galapagos, affecting ecological

processes and impacting many other species with which they co-occur.

Although there is consensus that giant tortoises play an important role in Galapagos ecosystems, the extent of tortoise impacts and when and where tortoise effects are most important to ecosystem functioning remain to be resolved. Experimentally, one of the methods used to estimate the effect of large herbivores on an ecosystem is to quantify key variables of community composition and ecosystem function, then remove the herbivores from the ecosystem and measure how the system changes (e.g., Augustine and McNaughton 2004; Bakker *et al.* 2016). An unplanned “removal pseudo-experiment” occurred when whalers and pirates removed huge numbers of tortoises in the 1800s (Chapter 4: Exploitation). Overharvest by mariners led to tortoise population declines throughout the Archipelago, with present-day populations many times smaller than the estimated prehuman contact densities (Chapter 20: Population Status). Although these losses theoretically could have afforded the opportunity to study tortoise–ecosystem interactions in detail, there are no “before” data. That is, there are no scientific data on ecological conditions before the overexploitation, with which to compare conditions after the tortoise decline (although new techniques using soil carbon isotopes are beginning to uncover some of these past conditions [Box 21.1 in Chapter 21: Española Island]). Furthermore, populations of

nonnative herbivores (primarily goats, but also donkeys and pigs) increased dramatically on some islands after tortoise populations declined, reaching a peak in the latter half of the 20th century (Campbell *et al.* 2004; Carrión *et al.* 2011; Hamann 1993b). The destructive effects of these nonnative herbivores on plant communities confound signatures of tortoise effects on ecosystems, even as tortoise populations rebound. For these reasons, the study of the role of giant tortoises in Galapagos ecosystems is a work in progress.

This chapter synthesizes what is known regarding the ecological role of Galapagos giant tortoises. It begins with a review of the interactions between tortoises and plants, followed by an investigation of how these interactions might “scale up” to affect the spatial distribution of other species, in other words, how tortoises can engineer their ecosystems. Understanding ecosystem engineering effects of these mega-herbivores, and how tortoise actions differ from those of nonnative herbivores, can help guide restoration of fully functioning ecosystems in the Galapagos Islands.

## Mega-herbivore effects

Megafauna have traditionally been defined by an absolute body size (e.g., >1000 kg, Owen-Smith 1988); however, there is a strong argument to be made that this distinction should be context-dependent, especially in island ecosystems where the largest vertebrates are typically smaller than in continental systems but still have large ecosystem impacts (Hansen and Galetti 2009). At their historical (prehuman contact) densities, Galapagos giant tortoises likely consumed the greatest total amount of plant biomass compared to any other native herbivore (although the native rice rats [both extant, *Aegialomys galapagoensis* and *Nesoryzomys* spp., and extinct, *Megaoryzomys curioi*], once widespread and now highly reduced in range in Galapagos, may once have also consumed large quantities of plant biomass, Gregory and Macdonald 2009). At an order of magnitude larger than the next largest vertebrate—land iguanas, *Conopholus* spp.—tortoises can be considered the mega-herbivores of Galapagos, on par with better known examples from continental systems such as elephants and large-bodied ungulates (Hansen and Galetti 2009; Owen-Smith 1988). Like other mega-herbivores, tortoises likely exert substantial control over the growth and biomass of the plant species they consume. All giant tortoise species are generalist herbivores, consuming a wide variety of species and vegetative forms (i.e., grasses, forbs, cactus, fruits, and leaves from shrubs and trees). In part because of their large body size and seasonal changes in food availability, tortoises forage over relatively large areas (Burt 1943), and their movement patterns and herbivory combine to shape the ecosystems they inhabit.

Saddleback and dome species of Galapagos tortoises have distinct foraging habits and food item preferences, with consequences for tortoise effects on ecosystems. Dome tortoises are primarily grazers, feeding on grasses, sedges, and fallen fruit (Fig. 15.1); they are rarely observed to raise their heads above their carapace when foraging (Cayot 1987; Rodhouse *et al.* 1975). In contrast, saddleback tortoises browse in addition to grazing, feeding on low-hanging cactus pads and leaves of shrubs and small trees, often stretching to their full height to reach these food items (Cayot 1987; De Roy 1979; Fig. 15.1). Grazing and browsing exert different pressures on the plant community. Grazing dome tortoises often crop plants close to the ground surface (Rodhouse *et al.* 1975), which may favor grazing-adapted species such as grasses and produce grazing “lawns” (Coe *et al.* 1979; Gibson and Hamilton 1983; McNaughton 1984). Browsing by tortoises is likely a selective agent for traits in plants that provide physical protection (e.g., spines on cacti) or chemical protection (e.g., latex-producing poison apple or manchineel tree, *Hippomane mancinella*). Tortoise foraging may also alter growth rates and growth forms in plants, for example, that enable plants to quickly grow past the browsing reach of saddleback tortoises (Herns and Mattson 1992).

The differences in feeding behavior between saddleback and dome tortoises appear to be labile according to forage availability, as both forms receive the same food items in captivity (primarily nonnative, leafy green plants; Márquez *et al.* 1999) and thrive in terms of weight gain and reproductive output (Furrer *et al.* 2004; Snell *et al.* 1986). However, when given a choice in the wild, saddleback and dome tortoises select different food items. The introduction of nonnative tortoises to Pinta Island (Chapter 23: Floreana and Pinta Islands) has provided a “common garden” experiment to investigate these preferences. Such experiments involve introducing different forms of organisms to the same environment to determine whether preferences and traits are innate or plastic (Hunter 2012; Hunter *et al.* 2013). In 2010, 39 adult sterilized tortoises (of saddleback, dome, and intermediate forms of several species) were introduced to the same location in the transition zone on Pinta Island. Although all the tortoises had spent most of their lives in captivity, the saddleback tortoises immediately sought out *Opuntia* cactus pads that were readily available near the introduction site, whereas dome tortoises moved rapidly upward in elevation to the more restricted humid highlands where they grazed on grasses and forbs (Hunter *et al.* 2013). It is not clear whether the dome tortoises were selecting this habitat based on available food items or whether they sought a cooler and moister climate. This experiment did demonstrate that the combination of habitat and foraging preferences of the two phenotypes are, to a certain extent,



**FIGURE 15.1** Galapagos giant tortoises as mega-herbivores. Dome tortoises are primarily grazers (A) and can maintain “grazing lawns” in humid highland habitats (D), whereas saddleback tortoises are also browsers (B). Saddleback tortoises can depend heavily on *Opuntia* cacti and will often wait under large adult trees until pads or fruits fall (E). All tortoises consume fruit when available of both native (e.g., *Heliotropium* spp., C) and invasive species (e.g., guava, *Psidium guajava*, F). Consumption of fruit leads to dispersal of seeds in dung, which may potentially fertilize and promote seed germination and growth (G), but the effectiveness of tortoise seed dispersal needs further study in both greenhouse experiments (H) and in the field. Exclosure experiments in the field can be an effective method for quantifying tortoise herbivory and trampling effects on plant communities (I). Photos: Frank Sulloway (A, B), Francisco Laso (C), GTRI (D, I), James Gibbs (E), Stephen Blake (F), Linda Cayot (G), Christian Ziegler (H).

“ingrained” and conserved across species that share phenotypes, even when maintained in captivity for decades if not their entire lives.

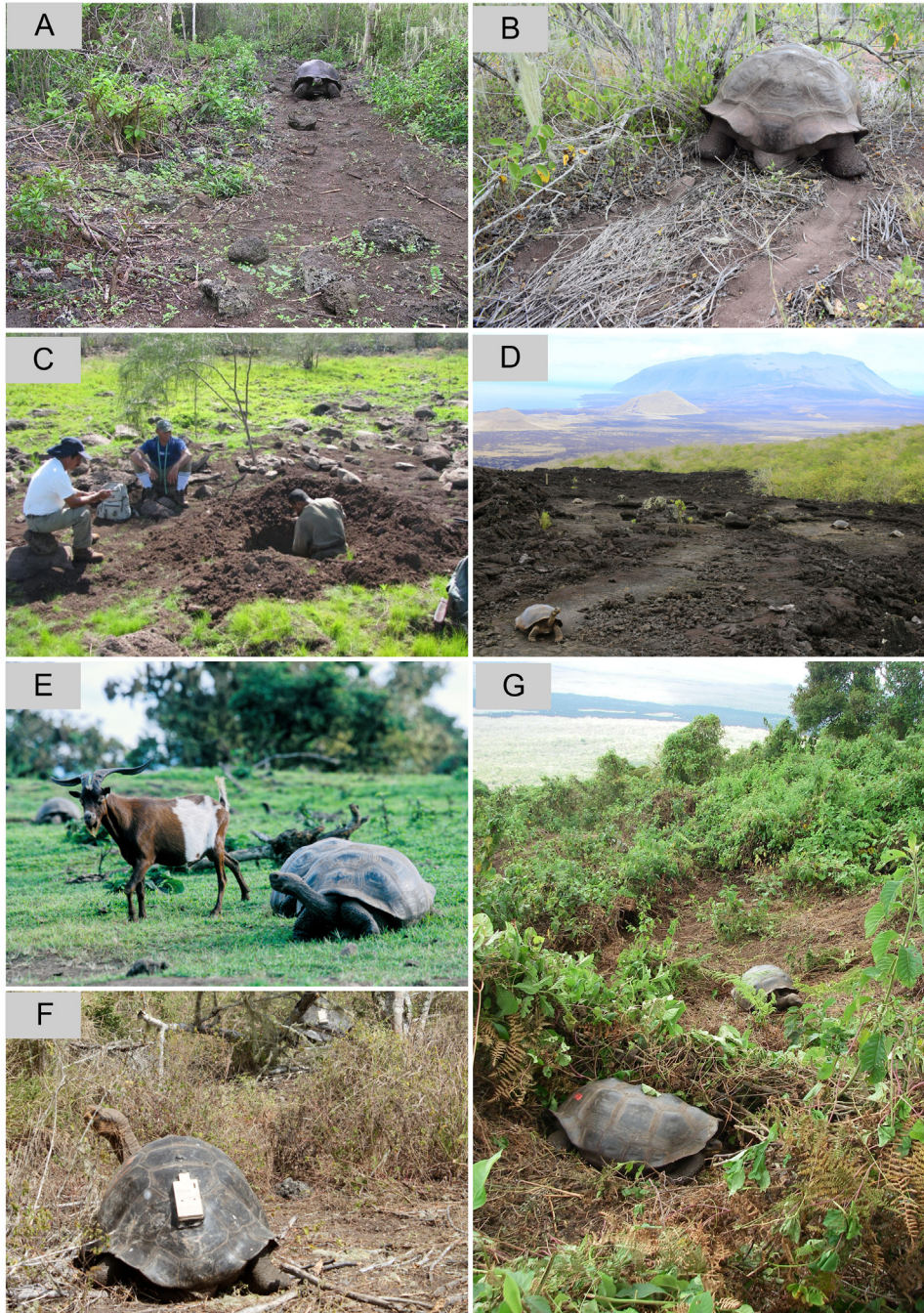
Saddleback and dome tortoises differ also in the extent of their movements among habitats in search of food. Saddleback tortoises (especially those species inhabiting flatter, more arid islands, e.g., Española Island) are more sedentary and will wait in place for seasonal plant growth (Bastille-Rousseau *et al.* 2017b; Chapter 13: Movement Ecology). Dome tortoises inhabiting larger islands with greater elevation change exhibit a broader range of movements, ranging from sedentarism to nomadism to migration (Bastille-Rousseau *et al.* 2019, 2017b; Blake *et al.* 2012a). Many tortoises on larger islands migrate from near sea level into humid highlands and back again annually in response to seasonal flushes of plant growth (Blake *et al.* 2012a), traversing along an up to 45-km round trip through multiple habitat types over individual paths that converge,

creating permanent tortoise trails (Bastille-Rousseau *et al.* 2017b; Fig. 15.2). Such long distance movements in search of food resources link tortoise-related ecosystem impacts such as nutrient recycling, trampling, herbivory and seed dispersal over otherwise disparate isolated habitats, likely increasing species diversity and habitat heterogeneity (Blake *et al.* 2012a; Campos-Arceiz and Blake 2011; Holdo *et al.* 2011: 131–143; Hunter and Gibbs 2014).

## Tortoise–plant interactions

### Interactions with *Opuntia*

The heavy dependence of tortoises on *Opuntia* cactus (and perhaps vice versa) has triggered several, still poorly evaluated hypotheses about coevolution between tortoises and cacti (Dawson 1966). The primary hypothesis is that saddleback tortoises evolved longer limbs and necks to better enable



**FIGURE 15.2** Tortoises' physical activities shape the ecosystems in which tortoises live. Their movements and trampling create trails through dense vegetation (A, B) and can create large disturbances (F, G). Over time, tortoises can even create trails through inhospitable lava fields (D). The combination of tortoise movement and herbivory can maintain grassland ecosystems, as has been discovered through the analysis of carbon isotope data from soil pits (C). Tortoise impacts on ecosystems are fundamentally different from those of invasive herbivores, such as goats (E) (see [Box 15.2](#)). Photos: GTRI (A–C, G), Paul Gibbons (D), Frank Sulloway (E), Francisco Laso (F).

them to browse on the low-hanging pads of arboreal *Opuntia* trees (Fig. 15.1), thereby accessing much needed water and nutrients in arid lowland ecosystems (Cayot 1987; Dawson 1966; Fritts 1984). At the same time, tortoise herbivory may provide a selective pressure for well-defended (spiny) juvenile cacti and tall, out-of-tortoise-reach stature in adult cacti (Dawson 1966; Hicks and Mauchamp 1996), leading to a classic evolutionary arms race (Endara *et al.* 2017). The arboreal growth form of *Opuntia* may also be driven by

competition with other plant species for light, because the height of *Opuntia* species in Galapagos matches well that of the tallest woody plants present across different islands (Arp 1973; Hicks and Mauchamp 1996; Racine and Downhower 1974). In addition, the spiny nature of juvenile *Opuntia* does not completely deter tortoise herbivory (Cayot 1987), and it may provide a multitude of other benefits, including condensation of water vapor, shade production, heat radiation, or a shield against ultraviolet light (Arp 1973). Therefore although

it is clear that tortoises and cacti do strongly interact, the case for coevolution is weak and circumstantial.

*Opuntia* is an important food resource for all tortoises during dry parts of the year, but especially so for saddleback tortoises on arid islands. On Española Island, the population of saddleback tortoises reaches its highest densities in areas with adult *Opuntia* cacti, as opposed to areas with just juvenile and subadult cacti, or no cacti (Gibbs *et al.* 2014, 2008), and enclosure experiments indicate that tortoises rapidly consume fallen pads and fruits when available (Box 15.1). *Opuntia* pads and fruits are the primary food item for saddleback tortoises on Pinzón Island during the dry season (Cayot 1987), a period during which tortoise mortality is more likely to occur. On Pinta Island, saddleback tortoises introduced in 2010 (Chapter 23: Floreana and Pinta Islands) chose habitats with high cactus densities and consumed *Opuntia* pads and fruits more than any other food type. The introduction of tortoises to Pinta Island and subsequent monitoring occurred during the transition between the wet and dry seasons, when green grasses and forbs were still available, suggesting that when *Opuntia* is readily available, saddleback tortoises prefer it over other food sources (Hunter 2012; Hunter *et al.* 2013).

The negative consequences for *Opuntia* of tortoise herbivory on live pads and stems may be counterbalanced by the benefits of seed dispersal by tortoises. *Opuntia* seeds are quite large compared to seeds that are bird-dispersed in the Galapagos (Dawson 1966). The large seed size of some *Opuntia* species may be a tactic to avoid seed predation by birds—only large-beaked finches and mockingbirds can crack and consume seeds of some *Opuntia* species (Heleno *et al.* 2011). Given that *Opuntia* seeds are too large to be dispersed by most birds, and are generally cracked and eaten (and thus not dispersed) by larger-beaked birds, tortoises, as well as land iguanas, are likely important seed dispersers for *Opuntia* and may facilitate persistence of *Opuntia* throughout the Archipelago.

### Seed dispersal

In addition to *Opuntia* cactus, tortoises disperse the seeds of several dozen other plant species that run the gamut from tiny grass seeds that are likely unintentionally consumed to large seeds encased in fruits that tortoises seek out (Blake *et al.* 2012b; Heleno *et al.* 2011; Fig. 15.1). Other animal species disperse as many or more species of plants (particularly lava lizards and finches, Heleno *et al.* 2013), but none travel as far as tortoises between feeding on the seeds and

#### BOX 15.1 Enclosure experiments to measure tortoise impacts

Disentangling the complex ways tortoises interact with their ecosystem is challenging. One approach is to study this by excluding tortoises (and all their activities) from certain areas and comparing those “enclosures” with areas where tortoises are allowed to roam. For example, decades of enclosure experiments in African savannahs have revealed the critical importance of mega-herbivores in reducing woody plant cover and maintaining open areas (e.g., Augustine and McNaughton 2004; Bakker *et al.* 2016). These effects are often context-dependent (e.g., on foraging habits and preferences of herbivores, on soil types, and on plant community composition) and involve complex pathways of interactions (Bakker *et al.* 2016).

Enclosure experiments were initiated on Española and Santa Fe Islands in 2015. Fences that could withstand tortoise bulldozing were erected around square plots, with unfenced plots acting as “treatment” plots where tortoise impacts would occur (Fig. 15.1). On Española Island, a primary goal was to determine whether tortoise movement and herbivory would be sufficient to reduce woody plant density (Chapter 21: Española Island). By comparing woody plant density in enclosures and open plots, scientists can quantitatively measure the effects of tortoises on woody plants—in effect putting numbers on something that has only been qualitatively measured or conjectured about in the past. Preliminary results indicate that tortoises reduce woody plant recruitment and increase grass cover. They remove and disperse virtually all the large volume

of cactus pads and fruits that fall. Outcomes of these experiments will allow managers to estimate how many years it would take for tortoises to reduce woody vegetation density across the island, and determine if the timeline for restoration is sufficient, or whether tortoises will need human help to restore their ecosystem.

Woody plant encroachment is less of a concern on Santa Fe Island due to overall lower woody plant density although the reason for this is still unclear. Here, *C. hoodensis* tortoises were introduced as a replacement species to fill the niche left open by the extinction of the native tortoise species (Chapter 24: Santa Fe Island). Enclosure experiments will allow scientists to understand how reintroducing this ecosystem engineer will change the ecosystem in the coming decades. Of particular interest is the potential for interactions among tortoises, pallid land iguanas (*C. pallidus*), a species endemic to Santa Fe Island, and the island’s vegetation. Some of the enclosures erected on Santa Fe have fencing that excludes tortoises but not iguanas, and others exclude both species. Thus, the experiment will be able to differentiate the effects of herbivory, trampling, and seed dispersal by tortoises and iguanas. Preliminary results from this experiment are provided in Chapter 24, Santa Fe Island as well as Selles Rio (2019). As the reintroduced tortoises grow to adult size, these enclosures will continue to provide insights into tortoises’ effects on the island’s ecosystem.

depositing them, due to both distances traveled and the varying rates of passage through the gut, making tortoises the most effective agents of long-distance seed dispersal. Large seeds may take up to 28 days to pass through the guts of tortoises (Blake *et al.* 2012b; Sadeghayobi *et al.* 2011; Vásconez 2018), and small seeds may take much longer as they get stuck to intestinal walls (L. Cayot, pers. comm.), during which time a tortoise could move hundreds of meters to several kilometers. Thus, long-distance seed dispersal is common for seeds ingested by tortoises, with potentially important positive impacts on recruitment and altering vegetation patterns (Nathan and Muller-Landau 2000).

In addition to dispersal, passage through the tortoise gut may aid in seed germination through four potential routes: seed scarification, removal of fruit pulp, provision of a moist, protected environment, and deposition in a nutrient-rich packet of dung. Several studies have investigated whether passage through a tortoise's gut (a potential route for seed scarification) aids in seed germination (Fig. 15.1). Tortoise gut passage of Galapagos tomato seeds (*Solanum cheesmaniae*) produced extraordinary results for germination: 60%–80% germination rates for gut-passed seeds versus 1% germination rates for seeds not passed through a tortoise (Rick and Bowman 1961). Water treatments barely improved germination over the control, so it appears that some chemical or physical process that occurs during passage through the tortoise gut is responsible. However, Galapagos tomatoes do grow on islands where tortoises have never been present (Darwin *et al.* 2003), so other animal dispersers may also fill this important role, such as Galapagos mockingbirds (Rick 1966). Passage through the tortoise digestive tract also enhances the germination rate of some *Opuntia* species (Estupiñan and Mauchamp 1995). Numerous studies have shown that fruit pulp can inhibit germination (e.g., Samuels and Levey 2005, and references therein). Studies in Galapagos have shown more equivocal results, with gut-passed seeds of many plant species germinating at similar rates to controls (Blake *et al.* 2012b; Nogales *et al.* 2017). The Galapagos tomato may therefore be unusual in its strong response to tortoise gut passage, but many other species clearly benefit from the moist environment of the tortoise gut. Most Galapagos arid zone plants germinate after exposure to water, such as after a rainfall event (e.g., Hamann 2004, 1985, 1979); therefore the wetting that occurs through tortoise gut passage may facilitate seed germination during the drier parts of the year. In addition to providing moisture, tortoise dung may provide physical protection and a nutrient-rich environment for germination and early development of seedlings (Moolna 2008; Rick and Bowman 1961); however, Blake *et al.* (2012b) found no support for improved seedling growth and survival as a result of dung “fertilization.”

A potential negative impact of high-volume seed dispersal that is infrequently discussed in the literature is density-dependent mortality of seeds and seedlings. Galapagos giant tortoises may disperse hundreds or even thousands of seeds from a single species in a dung pile (Blake *et al.* 2012b). If germination is effective, competition for light and space will be intense and may negate advantages provided by tortoise gut passage and tortoise dung fertilization. The seed dispersal literature is replete with information on the quantity of seeds dispersed in ecosystems, but there are few data to estimate the effectiveness of dispersal. Thus, hypotheses on the impact of giant tortoise seed dispersal on Galapagos ecosystems remain largely untested.

### Tortoise trampling and woody plants

Giant tortoises have complex interactions with woody plants. Some woody plant species are browsed by saddleback tortoises when of small stature (e.g., *Croton* spp.; Cayot 1987), but most biomass reduction is likely through trampling effects. As tortoises move through their living areas, they avoid densely vegetated areas that are too difficult to push through (Hunter and Gibbs 2014). However, saddleback tortoises in pursuit of *Opuntia* cactus will push through dense thickets of woody plants, causing biomass reduction and occasional mortality of small shrubs and trees through the breaking of stems and branches (Hamann 1993b; Hunter and Gibbs 2014). Most tortoise-induced mortality is likely of young woody plants with stem diameters less than 1 cm; larger shrubs and trees can resist tortoise trampling and browsing. Repeated movement along the same “trails” that may connect large *Opuntia* cactus, along migration routes, and at the edges of these paths likely reduces the recruitment rate of small woody plant seedlings (Gibbs *et al.* 2014, 2008; Fig. 15.2).

Details of the extent and mechanism of tortoise effects on woody plants within arid lowland ecosystems come from two recent lines of evidence: data from enclosure experiments on Española and Santa Fe Islands (Box 15.1), and information on past vegetation communities through investigation of soil cores on Española Island (Box 22.1 in Chapter 21: Española Island). Soils contain the molecular signature of the dominant plants present at a certain point in history—digging deeper into a soil pit is a journey back in time. Soil cores (Fig. 15.2) suggest tortoises can fundamentally alter plant communities in Galapagos. Española Island soils indicate that historical populations of tortoises suppressed woody plant growth throughout the island (likely also the case in arid lowland zones of other islands). Soils that developed hundreds of years ago reveal a markedly different plant composition than present day soils, with woody plants being far less dominant than they are today (Gibbs *et al.* 2014). The

recent shift (within the last 100 years) to a more woody-plant–dominated system is likely a consequence of the temporally linked processes of the severe population reduction (and near loss) of tortoises on Española Island and the decades-long presence of invasive goats. Without the constant trampling by giant tortoises, and the destructive herbivory of goats (Box 15.2), the entire plant community may have shifted to a new state, demonstrating how the effects of tortoises on biomass reduction of woody plants can have broad-scale repercussions for arid ecosystems of Galapagos (Fig. 15.3).

Once an ecosystem in Galapagos transitions to a woody plant–dominated one, it may be slow to transition back to a more open grassland or savannah, even after restoring the tortoise population. The restoration of the Española Island tortoise population following the eradication of goats has begun this process on the island, but initial data indicate that tortoise movement may be restricted to a core area where woody plant density is lower (Bastille-Rousseau *et al.* 2016; Gibbs *et al.* 2014; Chapter 21: Española Island). Pinta Island, where tortoises were functionally extinct throughout the last century and where goats were also introduced, did

### BOX 15.2 Nonnative herbivores in tortoise country

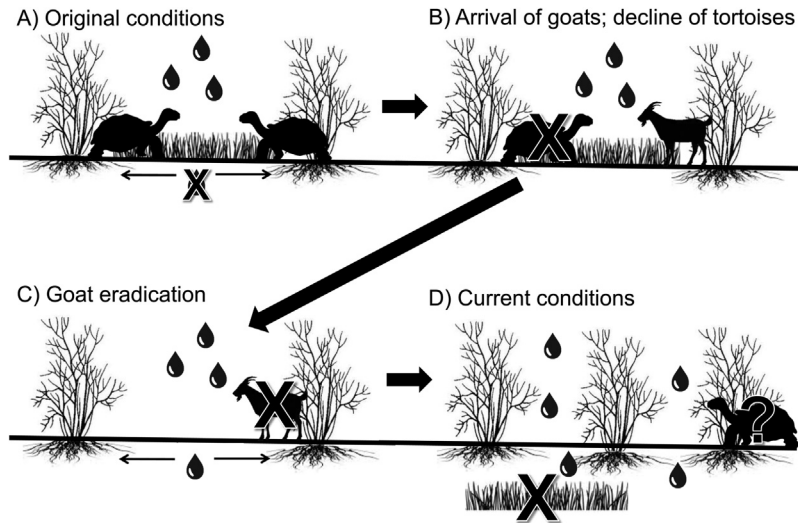
Botanical studies in the 1970s–1990s attempted to document the ecological destruction wrought by introduced herbivores in Galapagos. For instance, goats caused drastic reductions in vegetation density through their pervasive herbivory, including toppling of trees once they had eaten all other available forage—a pattern repeated on Pinta, Santa Fe, Santiago, and Santa Cruz Islands, among others (Calvopiña 1980, 1977; Hamann 1993a,b, 1975). Following the eradication of nonnative herbivores, plant communities rebounded but often with different species assemblages (Hamann 1993b, 1979). This rebound was likely impacted by changes in soil chemistry and physical processes created by compaction from ungulate hooves, making seed germination and water retention more difficult (Hamann 1979; Ortíz-Alcaraz *et al.* 2016). As some species recovered slowly, certain woody species expanded their ranges into what had previously been a mosaic of open grasslands and closed woodlands (Gibbs *et al.* 2014; Hamann 1993b).

Tortoises and ungulates, though both large herbivores, differ in their effects on plant communities in important ways. First, tortoise population growth rates are substantially slower than those of ungulates. When a gravid female tortoise arrives on an uninhabited island, it will take many decades for the population to reach ecologically-effective numbers of tortoises (Gibbs *et al.* 2014). However, when a small collection of goats is introduced to an island, population growth is explosive—as has been witnessed time and again—with goat populations reaching thousands of individuals from a few individuals in as little as a decade (Chapter 19: Invasive Species).

Another key difference is that tortoises are poikilothermic (i.e., “cold-blooded”) and therefore have slower metabolisms than endothermic (i.e., warm-blooded) mammals, allowing tortoises to “wait out” drought conditions without feeding or drinking for long periods of time. Nonnative ungulates are not well equipped to wait out the long stretches of resource unavailability characteristic of Galapagos dry seasons and therefore must forage on anything they can find. Goats have been observed toppling *Opuntia* cacti and woody trees to eat their stems and branches (Hicks and Mauchamp 1996), typically after more nutritious plant resources have been

devoured. Ungulates tend to eat a wider variety of plant species than tortoises (although there is substantial overlap) and switch readily between grazing and browsing (Fowler 1983), and with their teeth and multichambered stomachs, ruminant ungulates (such as goats) convert more plant energy into animal biomass. In effect, ungulates are much more efficient and destructive herbivores than tortoises, especially in ecosystems like Galapagos that did not coevolve with ruminant ungulates. Tortoises may have less of an effect on plant communities through direct herbivory and more through their trampling. Here again, ungulates are more likely to be destructive given their faster movements, sharp hooves, herding behaviors, and their need to continue to search for food during drought. The greater activity of ungulates in the dry season has led to massive soil erosion in Galapagos (Schofield 1989), which further influences which, if any, plants may regenerate following ungulate removal. A Galapagos ecosystem with tortoises as its dominant herbivore is controlled (slowly) from becoming overrun with woody vegetation, whereas an ecosystem where the dominant herbivore is a nonnative ungulate is quickly destroyed (Gibbs *et al.* 2008; Hamann 1993b, 1979), leaving it open to the rapid spread of woody plants once the nonnative species is removed (Fig. 15.3).

Bastille-Rousseau *et al.* (2017a) attempted to shed light on the interactive impacts of tortoises and nonnative herbivores on vegetation across the Archipelago using a combination of satellite data, historic estimates of tortoise distributions, current tortoise presence data, and goat eradication data. They found that tortoise presence is associated with increased vegetation productivity (i.e., vegetation productivity within the current range of tortoises is higher than expected compared to productivity outside tortoise range). Productivity was high in historic tortoise ranges and even higher in current tortoise ranges. Given the nature of the data, however, it is impossible to determine whether the high productivity within tortoise ranges was due primarily to tortoise selection for productive habitat (Chapter 14: Habitats), tortoise ecosystem engineering effects, or a combination of the two. As expected, a strong negative effect of goats on vegetation productivity was supported, with clear rebounding of vegetation cover and productivity following goat removal.



**FIGURE 15.3** Hypothesized interactions among herbivores and herbaceous and woody plants in the context of ecosystem restoration. Woody plants and grasses are in constant competition for water resources in semiarid environments. Grasses form mats that intercept and absorb rainfall before it penetrates the soil and can be used by woody plants (A), giving grasses a competitive advantage (except during heavy rain events) and leading to herbaceous plant dominance (Archer 1995; Brown and Archer 1999). Native herbivores tend to graze grasses sustainably (e.g., beaks and soft feet of tortoises). Nonnative herbivores (e.g., goats) with hooves and teeth overgraze, especially grasses but also woody plants (B). Once grass density is reduced, rain penetrates the soil, continuing to favor woody plants (C). When all herbivores are removed (goats eradicated, tortoises extirpated), woody plants expand, shifting the system into a novel stable state of woody plant dominance (D), which is difficult to shift back to a more open grassland system until woody plant density is reduced, through the bulldozing action of restored tortoise populations (which may take a long time, as stem sizes of woody plants may be difficult for tortoises to break) or human intervention.

not undergo such drastic changes, primarily because the presence of a large goat population lasted for less than 15 years (Chapter 19: Invasive Species; Chapter 23: Floreana and Pinta Islands). When a group of 39 adult tortoises were introduced to Pinta Island in 2010 to act as ecosystem engineers, the changes that had occurred in the island's vegetation were less drastic than on Española Island. Both woody plant density and extent could be reduced in the future on Pinta Island once a reproductive population of tortoises is restored (Hunter and Gibbs 2014).

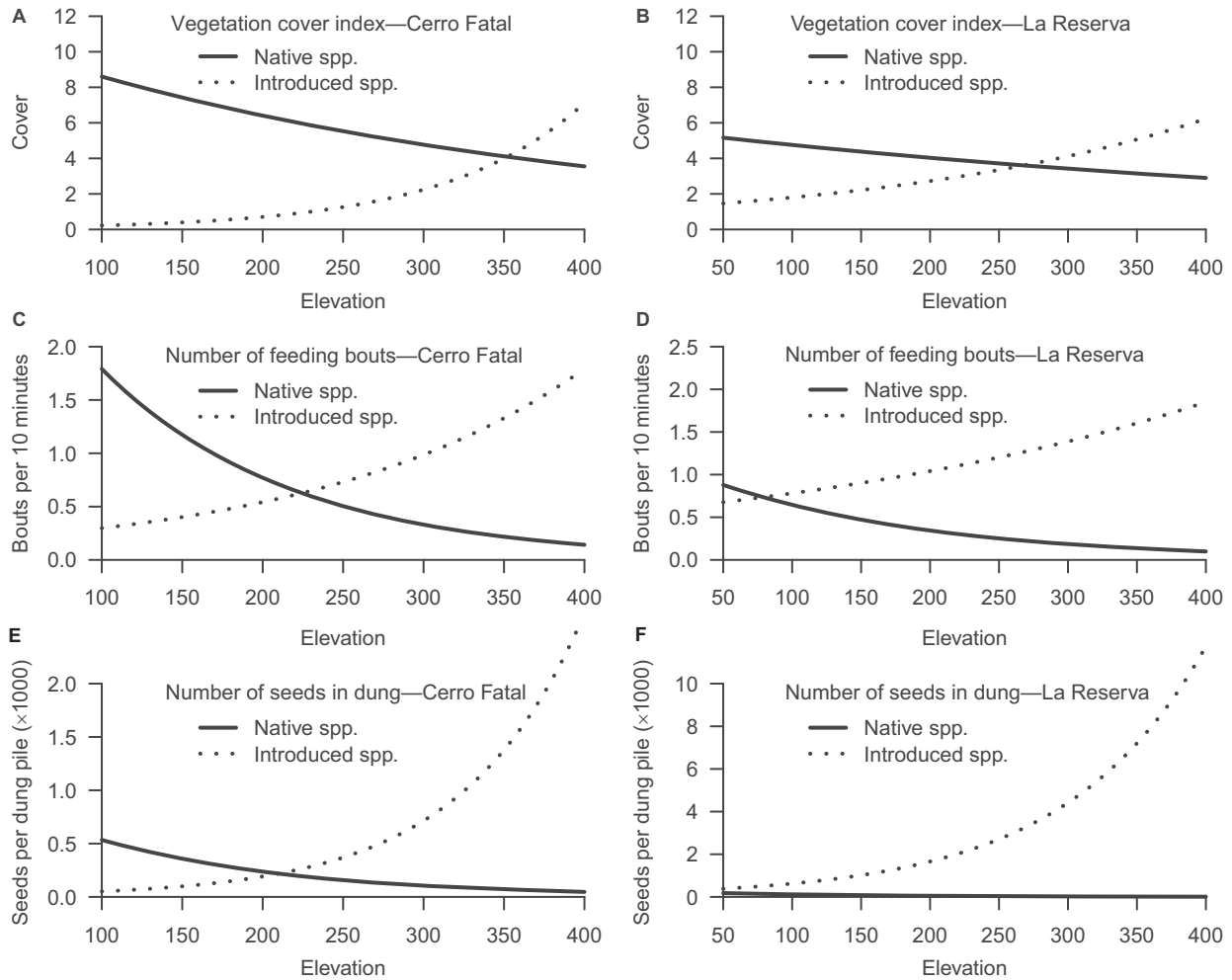
### Nonnative plants

As generalist herbivores, foraging tortoises exploit introduced plant species that have become prevalent in the transition and humid highland zones of many Galapagos Islands. In the highlands of Santa Cruz Island, most biomass consumed by tortoises is comprised of nonnative species (Blake *et al.* 2015, Fig. 15.4). Many introduced plants are highly palatable. Fruits of the endemic guava (*Psidium galapageium*) are ~1 cm in diameter with a thick skin and have abundant seeds and little pulp, whereas those of the invasive guava (*P. guajava*) are 3–5 cm in diameter, with a thin skin and an abundance of sugary pulp. Bite for bite, tortoises obtain many more calories from the invasive guava fruits than from those of the endemic congener. Additionally, and perhaps in part due to seed dispersal from tortoises (Fig. 15.1), invasive guava now covers a much larger area than the endemic species.

Many nonnative grasses, such as elephant grass (*Pennisetum purpureum*), *Digitaria* spp., and *Panicum* spp., were introduced to Galapagos because of their high nutritional value and easy digestibility for cattle (Schofield 1989). Tortoises likely benefit nutritionally from consuming such species in agricultural areas. Invasive plants tend to grow vigorously compared to native species, and it is unlikely that tortoise herbivory or trampling has any impact on such species. Rather, it is likely that tortoises facilitate the spread of introduced species through seed dispersal. Indeed, seeds of nonnative species are now much more abundant than seeds of native species in tortoise dung in areas within or close to agricultural zones (Blake *et al.* 2012b; Fig. 15.4). According to Schultz (2003), gut passage may hinder germination of some nonnative species (e.g., guava) but may aid germination for others (e.g., passion fruit); however, data for Galapagos giant tortoises on this topic are equivocal (Blake *et al.* 2015).

Tortoises may be dramatically increasing the rate of spread of some introduced species. For example, under current climate conditions, most adult guava trees in much of western Santa Cruz occur outside the Galapagos National Park areas at elevations above 200 m, with 150 m the lowest elevation at which adult trees occur. Climate projections suggest that the climatic niche of suitable guava habitat may be moving downslope and by 2070 suitable conditions will occur near the coast. Due to their long distance migrations, tortoises are already





**FIGURE 15.4** The relationships between elevation and properties of vegetation and tortoise diets on Santa Cruz Island. The cover of introduced species as a proportion of total vegetation cover increases with elevation in both Cerro Fatal (eastern Santa Cruz) and La Reserva (western Santa Cruz, A, B), a pattern which is primarily driven by protected status: low elevation areas are highly protected areas of the national park and higher elevation areas are farmlands (with introduced plant species invading park land from the farmlands). In both Cerro Fatal and La Reserva, the number of tortoise feeding bouts on introduced species increased with elevation while bouts on native species decreased (C, D). Finally, consistently across both sites, the number of seeds of introduced fruit species in tortoise dung piles increased with elevation, while numbers of seeds of native species declined (E, F). *Reproduced with permission from Blake et al. (2015).*

planting millions of guava seeds in this area of expansion within the National Park, thus guava will likely “surf the wave” of climate change via tortoises (Ellis-Soto et al. 2017), with new plants sprouting as soon as the climatic conditions become suitable. Finally, the more often tortoises consume fruits of introduced species, the less they will be dispersing the seeds of native species, further reducing the competitive ability of native plants species.

## Impacts on the landscape

### Plant communities

The effects of tortoise movements and herbivory create a web of interactions with broad impacts on the ecosystems

in which tortoises occur (Fig. 15.6). Teasing apart these interactions to understand direct cause and effect relationships is challenging, due to interactions among historical tortoise declines, the effects of nonnative herbivores (both current for those still present and “legacy” for those eradicated, Box 15.2), and the importance of irregular El Niño events for driving plant community dynamics. Current understanding of broad-scale tortoise impacts on plant communities depends on extrapolations from small-scale experiments and observational studies. Evidence derived from these studies of interactions between tortoises and the plant community is beginning to emerge and help elucidate tortoise impacts on the landscape.

The effects of tortoises on plant communities depend on the type of ecosystem (Chapter 14: Habitats). For

**BOX 15.3 Giant tortoises connecting terrestrial and freshwater ecosystems****Author: Diego Ellis-Soto**

Nutrient cycling is a major knowledge gap for predicting the ecological impacts of tortoises (Falcón and Hansen 2018). Galapagos giant tortoises likely have dramatic effects on freshwater ecosystems, which are restricted in number and extent in Galapagos, where tortoises frequently gather in large numbers, yet the ecology of these ponds and the impact of tortoises on them are unknown. Floyd *et al.* (2014) suggested that tortoise activities may have been critical for the maintenance of open water and certain plant species in the wetlands on Santa Cruz Island.

On Santa Cruz, *C. porteri* and *C. donfaustoi* tortoises migrate to track seasonal patterns in vegetation productivity between lowlands and highlands (Bastille-Rousseau *et al.* 2019; Blake *et al.* 2012a). Throughout their journey, tortoises encounter ponds, where they often congregate to wallow and regulate their body temperatures. These water bodies occur naturally within areas of the Galapagos National Park, where they dry out during months without precipitation. Ponds on private lands are often made by humans for livestock, have water year-round, and attract a large number of tortoises, which have become a major tourist attraction. Tortoises can wallow in these ponds for extended periods of time, and in doing so they transport seeds and nutrients that they

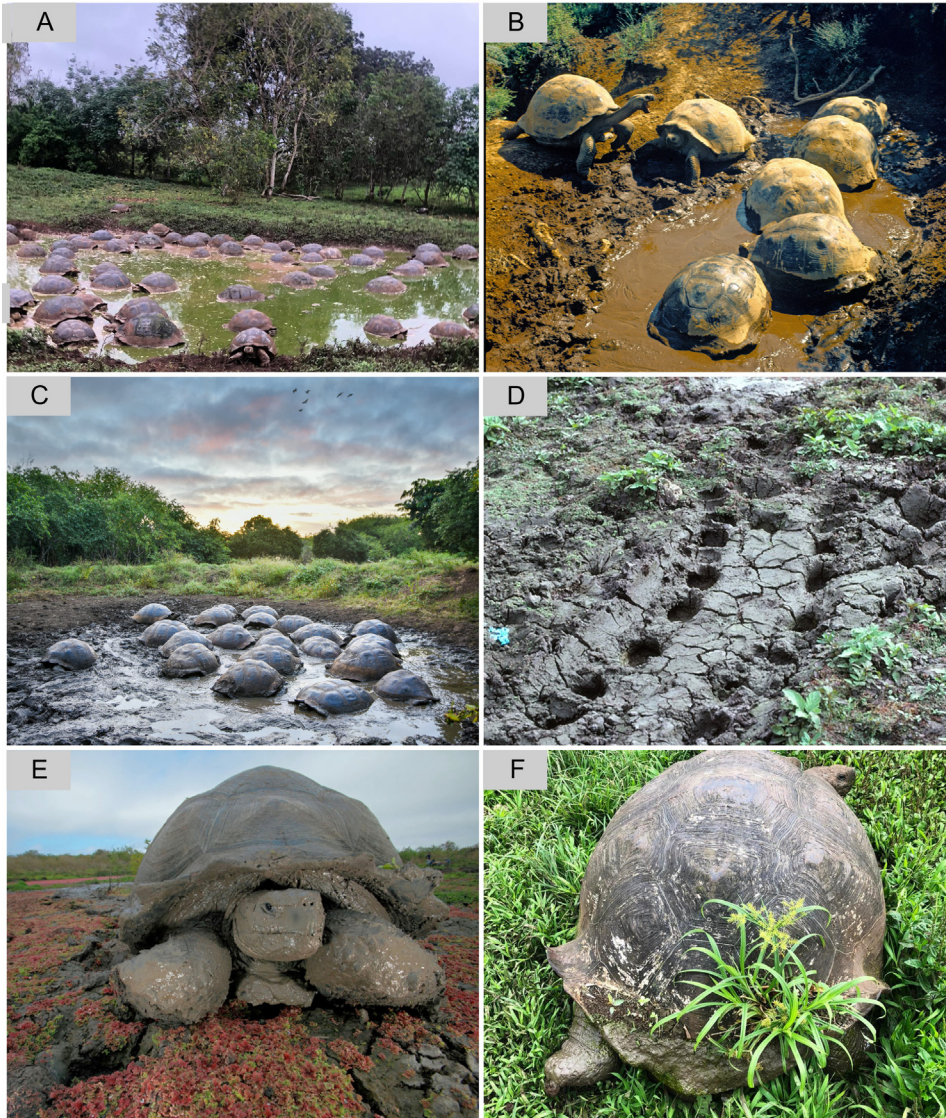
consumed on land into the ponds in the form of feces and urine. As tortoises move in and out of ponds on a daily and seasonal basis (Fig. 15.5), they are actively engineering these freshwater habitats. Tortoises also act as dispersers for aquatic plants (Fig. 15.5), macroinvertebrates, and algae across ponds, which could be important for sustaining populations of these species among ponds and shaping the community of aquatic organisms in ponds. Tortoises often leave ponds with their carapace and legs covered in mud, which they transport into surrounding terrestrial habitats (Fig. 15.5). With these mud burdens, the many tortoises regularly using the ponds may slowly and collectively excavate the ponds. In addition, when entering and exiting a pond, their heavy bodies tend to sink and their legs get stuck in mud on the pond periphery, which expands the pond margin. Preliminary results of an ongoing study of tortoise use of natural and human-made ponds on Santa Cruz Island reveal that natural and human-made ponds are different from one another, with tortoises moving more material into and out of human-made ponds. The presence of tortoises is also linked to lower levels of dissolved oxygen in the ponds, which can negatively influence aquatic life, similar to the ecological effects of hippos wallowing in freshwater pools in Africa (Dutton *et al.* 2018).

example, in the humid highlands of Isabela and Santa Cruz Islands, tortoises engineer wetland communities within temporary pools in which they wallow (Box 15.3). In arid lowlands, high tortoise densities largely promote herbaceous plant growth at the expense of woody plants, through the combined effects of herbivory and trampling (Gibbs *et al.* 2008; Hunter and Gibbs 2014; Fig. 15.6). Without tortoise trampling, the arid zone of many Galapagos islands might be covered with impenetrable thickets of woody vegetation, as has been observed most clearly on Española Island following the collapse of the tortoise population, although cause and effect was complicated by the presence and eventual eradication of goats (Bastille-Rousseau *et al.* 2017a; Gibbs *et al.* 2014). Unlike Española Island, the loss of giant tortoises from Santa Fe Island did not precipitate woody growth incursion, perhaps because foraging by pallid land iguanas (*Conolophus pallidus*) may have a similar impact to foraging by giant tortoises (Cano Rodriguez 2018; Selles Rio 2019).

Tortoises also likely have landscape-scale impacts on the spatial distribution and population structure of plants for which they are seed dispersers. *H. mancinella* (poison apple or manchineel tree) has an unusual disjunct distribution in Galapagos: it is common along coastlines but also sometimes dominant in the transition zone (e.g., on Santa Cruz Island, Cayot 1985: 363–398; Hamann 1984).

*H. mancinella* is a common coastal tree species throughout the tropics, but there are no records of it being found inland, except in Galapagos (Hamann 1984; Randall 1970). The distinct distributional pattern in Galapagos is likely caused by the combination of tortoise migrations and seed dispersal—without movement between these zones by tortoises, it is unlikely that *Hippomane* would have crossed the inhospitable arid zone to the transition zone (Cayot 1985; Hamann 1984). Research from the Mascarene Islands demonstrates clearly the positive impact that tortoise seed dispersal can have on regeneration of native, endangered species (e.g., *Diospyros egrettarum*), with Aldabran giant tortoises (*Aldabrachelys gigantea*) being used in vegetation restoration programs on islands throughout the Indian Ocean where native dispersers have gone extinct (Griffiths *et al.* 2010; Hansen *et al.* 2010).

The spatial distribution of *Opuntia* is also likely affected by tortoise movements. Tortoises move among adult cacti searching for fallen pads and fruits (or, in the case of saddleback tortoises, sometimes browsing on low-hanging pads). Although tortoise movements and trampling at the base of adult cacti inhibit recruitment in the immediate vicinity of the adult (Gibbs *et al.* 2010), tortoises enhance long-distance seed dispersal, possibly contributing to the lower-than-expected genetic differentiation among *Opuntia* cactus populations (Helsen *et al.* 2009).



**FIGURE 15.5** Galapagos tortoise use and engineering of freshwater ecosystems. Dozens of tortoises (tons of terrestrial biomass) may use freshwater pools at the same time (A–C). Through movement into and out of pools, tortoises transport mud (D, E), often making the pools larger and deeper in the process. Tortoises may also transport plants into and out of pools, potentially aiding freshwater plant dispersal (F, *Carex* spp. on tortoise carapace). Photos: Kyana Pike (A, F), Frank Sulloway (B), Pierre Ferron (C), Linda Cayot (D) and Christian Ziegler (E).

Whether tortoises have a net positive or negative effect on cactus population densities remains unclear. Although seeds dispersed in nutrient-rich packets of dung may have a better chance at germination and recruitment (Blake *et al.* 2012b; Moolna 2008; Rick and Bowman 1961), recruitment losses from tortoise trampling and herbivory may outweigh these gains. However, cactus recruitment and survival are negatively affected by woody plant density (Gibbs *et al.* 2008), and competition with woody plants is a strong selective force on cactus populations (Arp 1973; Racine and Downhower 1974). Thus, without tortoise trampling to reduce woody plant densities, cactus populations would likely decline. This has been demonstrated on Española Island: adult cactus density is particularly low and woody plant density is particularly high compared to other arid lowland ecosystems (Gibbs *et al.* 2014, 2008; Márquez *et al.* 2003).

The relative impacts of destruction via nonnative ungulate herbivores versus tortoise population loss on cactus populations are difficult to untangle. On both Floreana and Española Islands, where tortoise populations were decimated and introduced ungulate populations abundant, adult *Opuntia* cacti are very rare, especially when compared with nearby islets. Gardner Islet off the coast of Española Island and Champion and Gardner Islands off the coast of Floreana never had an introduced ungulate population, and all have much higher cactus density than their respective adjacent larger island (Grant and Grant 1989). However, these islets also never had a tortoise population, so perhaps *Opuntia* can grow to abundance in the absence of tortoises. Another case in support of this hypothesis is Santa Fe Island, where *Opuntia* populations reach densities comparable with islands with intact tortoise populations (Racine and Downhower 1974), even though the tortoise

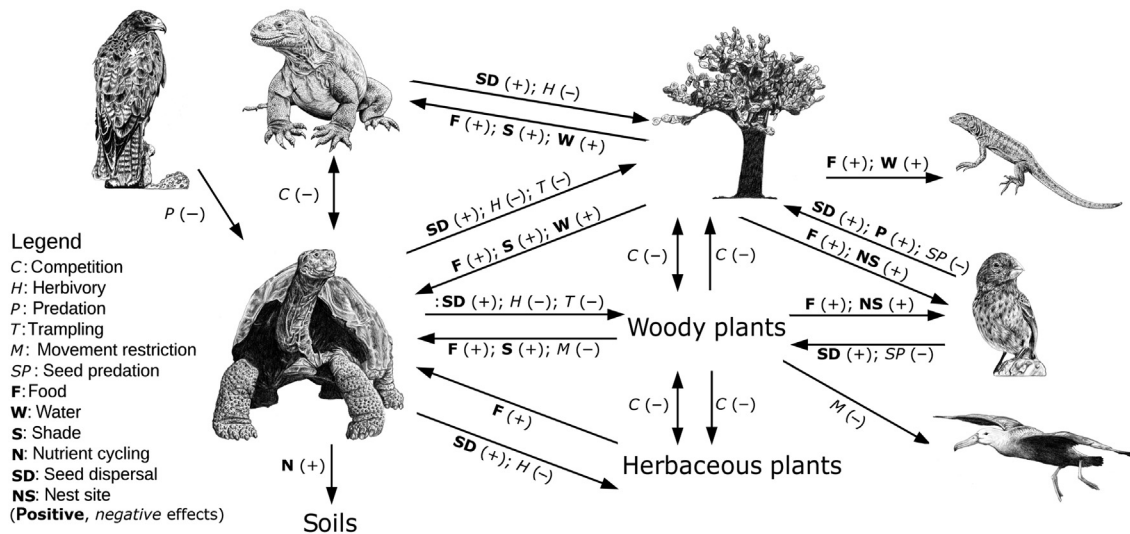
species native to this island was among the first to go extinct (Van Denburgh 1914). It is possible that a smaller goat population of shorter residency time limited the impact on *Opuntia* on Santa Fe (Hamann 1979). It is also possible that land iguanas and rice rats are effective seed dispersers on Santa Fe Island (Cano Rodriguez 2018) and maintain *Opuntia* at high densities. An experimental introduction of giant tortoises (*C. hoodensis*) to replace the extinct species on Santa Fe Island will help to reveal the interactions of these two herbivores in terms of their effects on *Opuntia* (Box 15.1 in Chapter 24: Santa Fe Island).

Tortoises may also interact with another powerful force structuring plant communities in Galapagos: El Niño. Dramatic fluctuations in precipitation resulting from the extremes of drought and El Niño oscillations (ENSO) play one of the most significant roles in when and where plant growth occurs (Cayot 1985; Hamann 1985: 299–330). ENSO precipitation also may cause shifts in tortoise movements and foraging behavior; thus the effects of ENSO and tortoises interact to create distinct patterns. The flush of plant growth following heavy ENSO precipitation causes tortoises to switch their foraging preferences on arid islands from water-rich *Opuntia* cactus to ephemeral, leafy plants (Cayot 1987, 1985). Tortoise movement rates within a given area may slow down in response to this greater resource availability, but mass migrations, for example from the highlands of Santa Cruz to the arid zone, were also noted during El Niño, involving many more tortoises than during normal seasonal shifts (Cayot 1987, 1985). In addition to these

changes in tortoise behavior, excessive ENSO precipitation can increase mortality of larger *Opuntia* (through waterlogging causing them to topple) and woody plant species (Cayot 1985; Hamann 2001), and weaken *Opuntia* trunks so that tortoises can eat directly into them in the immediate post-El Niño period (L. Cayot, pers. obs.).

### Cascading effects on animal species

The culmination of tortoise–plant interactions is an altered landscape for many other animals from what would occur in the absence of tortoises. In a sense, all other animal species that inhabit the larger, tortoise-occupied islands of Galapagos have evolved within tortoise-engineered ecosystems, and changes to the ecosystem caused by tortoise declines may have cascading consequences for them. For instance, tortoises have indirect effects on small land birds and lava lizards through their direct effects on the distribution and abundance of woody and herbaceous plants and cacti (Fig. 15.6). By altering habitats for birds and lizards, tortoises may indirectly influence the population sizes of these smaller animal species. Mockingbirds, some finch species, and lava lizards are effective seed dispersers in that they consume many species of fruit and passage through their digestive tract is likely to improve germination rates (Heleno et al. 2013, 2011; Nogales et al. 2017). So, by altering habitat, tortoises also impact patterns of overall seed dispersal and viability by birds and lizards more than tortoises would on their own. These complex interactions are poorly



**FIGURE 15.6** Observed and hypothesized tortoise–ecosystem interactions in Galapagos, particularly within arid lowland ecosystems (not all potential interactions are depicted). Arrows indicate the direction of impact (e.g., tortoises impact herbaceous plants through herbivory and seed dispersal; herbaceous plants impact tortoises as a source of food). Bold letters indicate positive population-level effects (generally, an increase in survival or reproductive output) and italic letters indicate negative effects. Illustrations depict (from bottom left, clock wise) saddleback giant tortoise, Galapagos hawk (*Buteo galapagoensis*), land iguana (*Conolophus* spp.), *Opuntia* cactus, lava lizard (*Microlophus* spp.), large ground finch (*Geospiza magnirostris* [pictured to represent all small-bodied, fruit- and seed-eating birds]), and waved albatross (*Phoebastria irrorata*). Illustrations by Catherine A. Moore.

understood and should be a focus of future research (see “Research Needs”). Several case studies illustrate the potential complexity of these interactions.

The effects of tortoises on ecosystems differ from those of the other endemic large herbivore in Galapagos, the land iguana. Giant tortoises and land iguanas appear to have substantial dietary overlap (Cano Rodriguez 2018), suggesting potential for competition (Fig. 15.6), especially during times of resource scarcity. Land iguanas also disperse seeds of similar species and at similar rates to tortoises (Traveset *et al.* 2016). However, given the size disparity between tortoises and land iguanas, tortoises likely have a larger overall impact on their ecosystem: tortoises move longer distances, have longer gut passage times, and trample more vegetation in the process of their movements. Therefore it is likely that iguanas are more affected by the presence of tortoises (either positively through the creation of open habitat, or negatively through competition) than vice versa. An additional interaction is seen where land iguanas and tortoises occur together. On Wolf Volcano and Santa Fe, juvenile tortoises use land iguana burrows to escape from high mid-day temperatures (J. P. Gibbs, pers. obs.). Effects of the widespread collapse in land iguana abundance and distribution in Galapagos (Snell *et al.* 1984) on tortoises are unknown. The restoration of giant tortoises to Santa Fe Island will help to further illuminate interactions between tortoises and land iguanas and the impacts of each species on the ecosystem (Box 15.1).

Giant tortoises may also shape the habitats of land-nesting seabirds. The critically endangered waved albatross (*Phoebastria irrorata*) nests only on Española Island (apart from a tiny nesting population on an island closer to mainland Ecuador). With a >2 m wingspan, this seabird needs long and wide “runways” in their nesting grounds to land and take off. Woody plant growth encroaches on these runways if not maintained by a large herbivore—either native tortoises or nonnative goats, which had been maintaining open vegetation throughout the island during the period with few to no tortoises up until their eradication in the late 1970s (Gibbs *et al.* 2014). In the period without a major presence of large herbivores (1980s–1990s), woody plants encroached on the albatross runways, potentially reducing adult survival and breeding opportunities (Anderson *et al.* 2002; Gibbs *et al.* 2014). Thus, tortoises have an indirect influence on albatross mediated through their effects on woody plant density (Fig. 15.6). In addition to this indirect effect, tortoise trampling over centuries potentially affected albatross behavior in a more direct way. Waved albatross do not build nests and have been observed to move their eggs during incubation—a seemingly maladaptive behavior not seen in any other albatross species—often resulting in egg death (Awkerman *et al.* 2005). However, this

behavior may be a tortoise-trampling avoidance strategy in addition to other potential causes such as the avoidance of ectoparasites (Awkerman *et al.* 2005). Thus albatross both benefit from tortoise trampling through the creation of openings in woody vegetation while evolving a mechanism to avoid tortoises trampling their eggs. This interaction may have further, substantial impacts on the ecosystem. Albatross import large amount of nitrogen from marine areas into the terrestrial ecosystem via the copious amount of guano they produce. Any tortoise-mediated changes in abundance of albatross nesting could have major ramifications for the terrestrial food web, which is heavily affected by nitrogen availability.

Tortoise interactions with *Opuntia* cactus also likely have ramifications for many other animals, given the heavy dependence of many Galapagos species on *Opuntia* cacti for food, water, and shade—which is why *Opuntia* cacti are commonly referred to as “keystone species” in Galapagos (Fig. 15.6). Many species of Darwin’s finches (including the aptly named cactus finch, *Geospiza scandens*), mockingbirds, doves, and lava lizards all eat *Opuntia* fruits, seeds, and vegetative pads (Coronel 2002; Grant and Grant 1981; Fig. 15.6). Many birds also build their nests in *Opuntia* trees, where spiny pads act as a predator deterrent (Hernández *et al.* 2003). The reliance of some species on *Opuntia* may be very high. The Floreana mockingbird (*Mimus trifasciatus*) is extirpated from Floreana Island and only exists on two satellite islets. One possible explanation for their extirpation is the severe reduction of the *Opuntia* population on Floreana Island, whereas Gardner and Champion Islands still have abundant *Opuntia* (Grant *et al.* 2000). As tortoises alter the spatial distribution of *Opuntia*, they likely also change the distribution of these *Opuntia*-dependent bird and lizard populations.

## Need for restoration

Although there is still much to learn about how tortoises shape the ecosystems of Galapagos, the evidence is overwhelming that giant tortoises are an integral component of healthy, functioning ecosystems on the islands and volcanoes where they naturally occur. The combined effects of the loss of tortoises from ecosystems and the destructive herbivory by nonnative ungulates followed by their eradication may be pushing many arid zones into novel ecological steady states dominated by woody plants (Gibbs *et al.* 2014; Hunter and Gibbs 2014; Fig. 15.3). Restoring tortoises to their historical distribution and former abundances could help prevent such permanent changes in Galapagos ecosystems and potential losses of species in the process. Many efforts are underway to do just that (Chapter 17: History of Conservation; Section V: Restoration Case Studies). In addition to efforts to rebuild tortoise numbers in extant populations (e.g., on Española

Island [Gibbs *et al.* 2014; Chapter 21: Espanola Island], and Pinzón Island [Jensen *et al.* 2015; Chapter 22: Pinzon Island]), captive-bred, nonnative tortoises have been introduced as replacement populations to Pinta (Hunter 2012; Hunter *et al.* 2013; Chapter 23: Floreana and Pinta Islands) and Santa Fe Islands (Box 15.1; Chapter 24: Santa Fe Island). These efforts represent attempts to not only restore tortoise populations to islands where the endemic species is extinct but to also restore vital tortoise ecosystem functions (Hansen *et al.* 2010; Hunter and Gibbs 2014). Offspring from hybrid tortoises with ancestry from tortoise species native to Floreana Island (*C. niger*, now extinct) will be released on that island to fill the extinct species' niche (Hunter *et al.* 2020; Quinzin *et al.* 2019; Chapter 23: Floreana and Pinta Islands). Outplanting of cactus is also a component of tortoise restoration on both Española and Floreana Islands to rebuild depleted *Opuntia* populations and restore tortoise habitat (Tapia *et al.* 2019). These efforts send a hopeful message about conservation in the Galapagos: species extinction may be forever, but replacement species (Griffiths *et al.* 2010; Hansen *et al.* 2010) can restore lost interactions and help entire ecosystems to recover.

## Research needs

Many of the known and potential interactions between tortoises and the ecosystems they inhabit (see Fig. 15.6) need to be more fully studied to understand the role of tortoises and to determine the cascading effects of tortoises and their historical exploitation on other species in Galapagos. Studying these interactions will help to determine the extent to which tortoise restoration may aid in the recovery of other declining species. Ecosystem processes involving giant tortoises that require further investigation include:

- how seed dispersal and trampling by tortoises affect the spatial distribution of plant species;
- tortoise effects on nutrient cycling and the replenishment of soils;
- how tortoise impacts on plant communities create or remove habitat conditions for other animal species;
- identification of the tortoise density threshold at which tortoise engineering becomes evident in a system (i.e., at what tortoise densities do functional responses in other plant and animal populations occur?); these thresholds likely vary by ecosystem type and could serve as management targets for tortoise restoration to facilitate ecosystem recovery;
- whether and over what time frame tortoise restoration can transition woody plant-dominated ecosystems

back to more open/mosaic systems or whether vegetation management measures must be taken, and

- interaction between climate conditions (and changes in climate) on plant communities and how tortoise movement and herbivory mediate these interactions.

Studying these processes will not only shed further light on the important role that tortoises play in their ecosystems but will also inform management strategies on how to best take advantage of tortoises' engineering to restore Galapagos ecosystems.

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