

Node-by-node disassembly of a mutualistic interaction web driven by species introductions

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Interaction webs summarize the diverse interactions among species in communities. The addition or loss of particular species and the alteration of key interactions can lead to the disassembly of the entire interaction web, although the nontrophic effects of species loss on interaction webs are poorly understood. We took advantage of ongoing invasions by a suite of exotic species to examine their impact in terms of the disassembly of an interaction web in Patagonia, Argentina. We found that the reduction of one species (a host of a keystone mistletoe species) resulted in diverse indirect effects that led to the disassembly of an interaction web through the loss of the mistletoe, two key seed-dispersers (a marsupial and a bird), and a pollinator (hummingbird). Our results demonstrate that the gains and losses of species are both consequences and drivers of global change that can lead to underappreciated cascading coextinctions through the disruption of mutualisms.

biological invasions | community disassembly | seed dispersal | pollination | herbivory

Interactions among species are the ties that bind communities together. Thus, understanding the mechanisms and consequences of both direct and indirect interactions is fundamental to elucidating the assembly and disassembly of ecological communities in a changing world (1–3). Interaction webs are a way to summarize the diversity of interactions among species in a community (4, 5). The properties of interaction webs include the number of nodes (i.e., species richness), links between the nodes (i.e., species interactions), nature of the links (i.e., antagonistic or mutualistic), and the strengths of those interactions (4, 6). The addition of novel species to an interaction web, particularly of invasive species, can have important implications for stability, depending on how the novel species alters the properties of interaction webs (7), especially if these species affect critical nodes of the web, such as keystone species (3, 8, 9) or particular interactions. Species losses, especially those involved in keystone mutualisms, could disassemble an interaction web by triggering a cascade of linked coextinctions (3, 10–12). The idea that connectance promotes stability and that the loss of keystone mutualisms leads to web disassembly relies on the notion that mutualisms and the species engaged in them are fundamental to maintaining the structure and diversity of ecological communities (4, 13–15). Here we show how the addition of novel species from disparate taxa and the ensuing loss of a keystone species leads to the node-by-node disassembly of an interaction web in Patagonia, Argentina. Taken together, these results demonstrate that simultaneous gains and losses of species are both consequences and drivers of global change that can lead to underappreciated cascading effects.

In particular, we take advantage of an ongoing natural experiment triggered by the invasion of a suite of exotic ungulates and wasps to examine whether the disruption of mutualisms and the loss of keystone mutualists leads to the disassembly of an

interaction web (Fig. 1). The pivotal nodes of this interaction web consist of the southernmost hummingbird species (*Sephanoides sephanioides*), a mistletoe (*Tristerix corymbosus*), the dominant understory shrub (*Aristotelia chilensis*) that is the most common host of mistletoe (16), and an endemic marsupial (*Dromiciops gliroides*) (17). The hummingbird pollinates nearly 20% of the endemic woody genera in Patagonian forests, including the mistletoe (18). The nectar produced by the showy flowers of mistletoe (*T. corymbosus*) is the only nectar resource for the hummingbird during the winter throughout much of its range (18–20), and the hummingbird is an important (almost exclusive) pollinator of the mistletoe (21, 22), making this an obligate pollination mutualism for both partners. Additionally, the marsupial (*D. gliroides*) disperses seeds of at least 16 fleshy-fruited species (23) and is the only known disperser of the mistletoe (17, 24), making this an obligate dispersal mutualism, at least for the mistletoe. Marsupial abundance closely tracks the abundance of mistletoe fruits (16, 25), which is consistent with the view that this is an important resource for the marsupial. After passing through the gut of *D. gliroides*, most of the seeds of the mistletoe are defecated on branches of *A. chilensis* and germinate (17). Another important mutualist in this interaction web, the White-crested Elaenia (*Elaenia albiceps*), is the most common seed-dispersing bird, dispersing seeds of most of the fruiting plants in these forests (19, 26), including the seeds of *A. chilensis*, the host of mistletoe. Finally, the germination rate of *A. chilensis* seeds dispersed by birds is nearly three-times higher than for nondispersed seeds (27). Because these interactions are in many instances obligate, any reduction in the abundance or

Significance

Examining the effects of species gains and losses is fundamental to understanding the assembly and disassembly of ecological communities in a changing world. However, field-based empirical studies that demonstrate the disassembly of mutualistic webs are exceedingly rare. In this study, we take advantage of an ongoing natural experiment that links the gain of invasive species (introduced large mammals and wasps), the loss of a native keystone species (a mistletoe), and the ensuing node-by-node disassembly of an interaction web in Patagonia, Argentina. Our results demonstrate that the gains and losses of species are both consequences and drivers of global change that can lead to underappreciated cascading coextinctions through the disruption of mutualisms.

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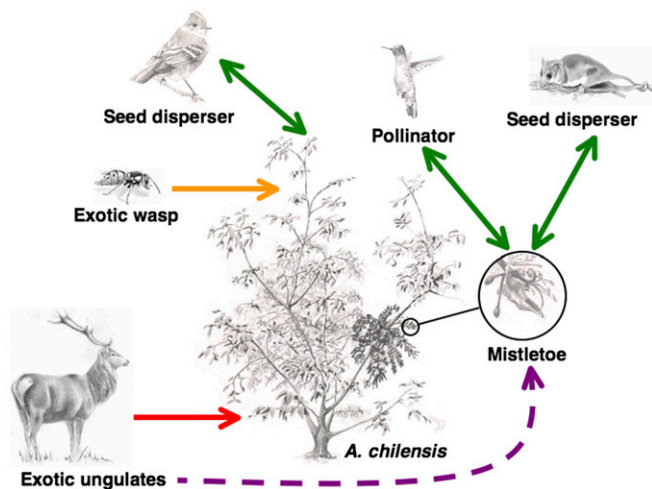


Fig. 1. Interaction web showing the direct effects (solid arrows: yellow, fruit predation and red, herbivory) of exotic species on *A. chilensis* and the indirect effect (dashed arrow, violet) on the keystone interactions (solid arrows: green, pollination and seed dispersal) between a hummingbird, a mistletoe, a marsupial and a bird. (Drawings by Ezequiel Rodriguez-Cabal.)

alteration of the behavior of any of these species has the potential to disassemble this interaction web.

Results and Discussion

Cows (*Bos taurus*) were introduced to this system in the late 18th century (28), and game animals, such as red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), were introduced in 1904 (29). These species are widespread (occupying >50% of the forests in Patagonia) and are significant sources of disturbance in these temperate forests (28, 30, 31). Exotic herbivores are known to modify native plant communities by directly affecting plant survival, growth, reproduction, and recruitment through browsing, grazing, and trampling, and indirectly by altering nutrient cycles, primary productivity, disturbance regimens, and by disrupting interactions with other herbivores, pollinators, and seed dispersers (32–34).

A. chilensis is a preferred forage for both deer and cows (28, 30, 35). As a result, *A. chilensis* is directly affected by the presence of exotic ungulates: the density of *A. chilensis* was 16-times lower in sites where these exotic species are present (hereafter, “invaded” sites) than where the species are absent (hereafter, “intact” sites) (Fig. 2A). We excluded deer for 1 mo and found that 99% of *A. chilensis* leaves outside of the deer enclosures were removed by deer (Fig. 2B) in invaded sites. Mistletoe plants appear to be specialists on *A. chilensis* (16): more than 75% of the plants parasitized by mistletoe are *A. chilensis*. Indeed, the density of mistletoes was 83-times lower in invaded sites than in intact sites (Fig. 2C). Thus, by preferentially browsing on *A. chilensis*, exotic ungulates may indirectly affect the persistence of the keystone mistletoe (30), on which many other species rely, thereby indirectly disassembling this interaction web.

In fact, the ungulates affected more than just *A. chilensis*; they affected the entire plant community (28). Total plant cover in the understory was 35-times lower ($t_{25} = 7.63$, $P < 0.0001$) and habitat complexity was 20-times lower ($t_{25} = 13.99$, $P < 0.0001$) in invaded than in intact sites. Habitat characteristics, such as the abundance and diversity of food resources, nest sites, and distance to shelter can influence the distribution of many vertebrate frugivores (36), and in turn fruit-bearing plants. We found that the density of fruiting plants was three-times lower in invaded than in intact sites (Fig. 2D). The changes in habitat structure and food availability also affected the marsupial (25). In 52

trapping nights, we never captured marsupials at any of the invaded sites, although they occurred at each of the 13 sampled intact sites. Because mistletoe seeds must pass through the gut of the marsupial to germinate and be deposited on branches of *A. chilensis* to establish, the local extinction of marsupials undoubtedly affects mistletoe recruitment (37). Indeed, this was the case: we did not detect any mistletoe seed dispersed by marsupials

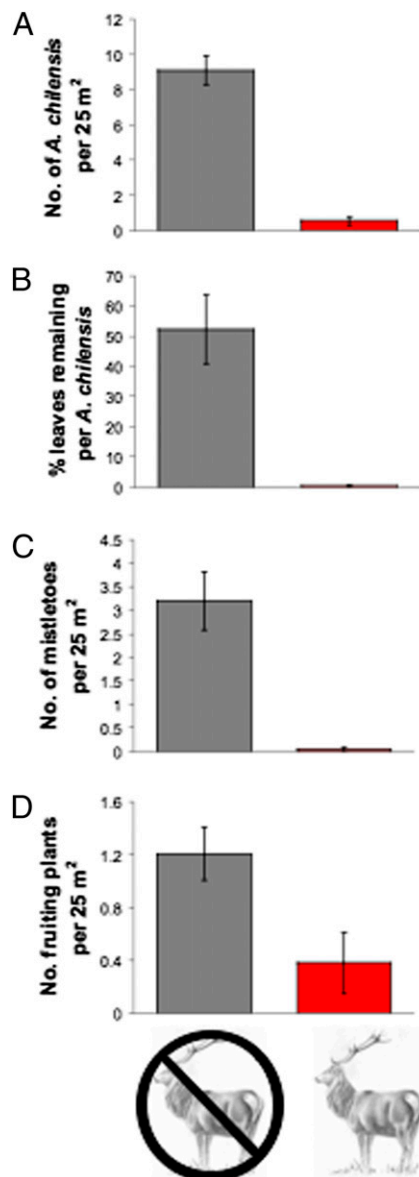


Fig. 2. Direct effects of exotic ungulates. In the austral summers of 2010 and 2011 we examined the direct effects of exotic ungulates at 13 sites with exotic ungulates (invaded sites) and 13 sites without exotic ungulates (intact sites) on the number of reproductive *A. chilensis* (>70 cm in height), number of reproductive mistletoe, and number of fruiting plants. In the summer of 2010 we quantified the effects of browsing by exotic ungulates on *A. chilensis* with an enclosure experiment. We found that: (A) *A. chilensis* were 16-times more abundant in intact (mean ± SD per plot; intact sites 9.12 ± 3.72) than in invaded sites (0.55 ± 1.30; $t_{25} = 12.26$, $P < 0.0001$); (B) Exotic ungulates consume almost 99% of the *A. chilensis* leaves outside the enclosure ($Z_{23} = -3.43$, $P = 0.0006$); (C) Mistletoe was 83-times more abundant in intact (mean ± SD per plot; intact sites 3.21 ± 2.79) than in invaded sites (0.04 ± 0.19; $t_{25} = 8.53$, $P < 0.0001$); (D) Fruiting plants were three-times less abundant at invaded than intact sites ($t_{25} = 3.18$, $P = 0.0041$). (Drawings by Ezequiel Rodriguez-Cabal.)

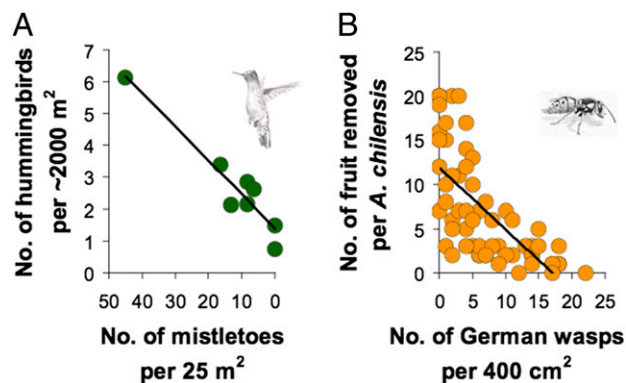


Fig. 3. Direct and indirect effects of exotic ungulates and the German wasp. (A) Exotic ungulates indirectly affect hummingbird pollinators through browsing on *A. chilensis*, which in turn reduced the number of mistletoe. Hummingbird abundance during the austral winter decreases as the number of mistletoe plants decreases ($R^2 = 0.82$, $df = 7$, $P = 0.0021$). (B) German wasps directly affect *A. chilensis* by preying upon its fruits. As the abundance of the German wasp increased the number of seeds removed decreased ($R^2 = 0.56$, $df = 59$, $P < 0.0001$). (Drawings by Ezequiel Rodríguez-Cabal.)

(mean \pm SD per plot; intact sites 5.35 ± 7.18 ; $Z_{25} = 4.32$, $P < 0.0001$) or seedlings at the invaded sites (mean \pm SD per plot; intact sites 2.12 ± 2.48 ; $Z_{25} = 4.33$, $P < 0.0001$).

Because the density of mistletoe was demonstrably lower in sites with, than in sites without exotic ungulates, and because the mistletoe is the primary source of nectar for the hummingbird during the austral winter, the density of hummingbirds should also be lower at invaded sites than at intact sites. In fact, the density of hummingbirds in the winter declined strongly as the mistletoe density declined (Fig. 3A), suggesting that exotic ungulates affect hummingbirds by affecting *A. chilensis*, and in turn the mistletoe. Admittedly, we do not know whether these differences in hummingbird densities arise because either the population size of hummingbirds or the activity of hummingbirds is reduced at invaded sites. However, whatever the case, the pollination services provided by hummingbirds are likely to be indirectly affected by the presence of exotic ungulates.

The effects of the exotic ungulates on this interaction web are dramatic, but perhaps not surprising given the density and sheer biomass of the ungulates ($\sim 3,015$ kg/km 2) (38). However, another exotic species in Patagonian forests may have more subtle but equally disrupting effects on this interaction web. The German wasp, *Vespa germanica*, arrived in the early 1980s (39) and has rapidly spread, becoming one of the most outstanding insect invasions ever recorded in Patagonia (39). In these forests, the wasp feeds on the fruits of *A. chilensis*, with cascading effects throughout the rest of the interaction web. The number of *A. chilensis* fruits removed by seed-dispersing birds and marsupials was three-times lower in sites invaded by *V. germanica* and six-times lower in sites in which we temporarily increased activity of *V. germanica* (by stocking sites with artificial food resources) relative to sites where *V. germanica* was absent (where we applied poison treatments; generalized linear model, $\chi^2 = 218.80$, $P < 0.0001$). Across all sites, the number of seeds removed per individual *A. chilensis* decreased significantly with increasing activity of German wasps (Fig. 3B). Moreover, the abundance of *E. albiceps* was similar across sites before the fruits of *A. chilensis* ripened (generalized linear model, $\chi^2 = 0.16$, $P = 0.934$). However, the abundance of *E. albiceps* during the fruiting season was three-times lower (mean number of individuals \pm SD per site; 5 ± 2.83) at sites where we experimentally increased wasp activity and 1.5-times lower (7.5 ± 3.54) in sites with natural activity of wasps (nonpoison treatment) relative to sites where we

experimentally reduced wasp activity (poison treatment; 18 ± 2.82 ; generalized linear model, $\chi^2 = 17.81$, $P < 0.0001$).

Both direct and indirect interactions can lead to cascading coextinctions and the disassembly of interaction webs (11, 15). Despite the obvious direct effects of exotic ungulates and the German wasp, using metaanalysis, we found that some of the indirect effects were stronger than the direct effects (Fig. 4). Browsing by exotic ungulates on *A. chilensis* reduced the number of available hosts for the keystone mistletoe, thereby indirectly affecting mistletoe and marsupial populations. Furthermore, fruit predation by German wasps reduced the abundance of *E. albiceps*. Consequently, the impact of exotic ungulates and the German wasp cascaded through the interaction web to influence the number of seeds removed by both the marsupial and *E. albiceps*. The only node of the interaction web that appeared not to be affected (at least according to our metaanalysis) was the hummingbird (even though their abundance declined as the density of mistletoe declined) (Fig. 3A). One possible explanation is that the home range of any one hummingbird is much larger than the area affected by our treatments or the effects of the exotic species, and the effects of these treatments on hummingbirds might surface only at larger spatial scales.

The effects of local extinctions are potentially on par with other global change drivers (40). Our results revealed that a suite of exotic vertebrates and invertebrates led to a cascade of linked extinctions, resulting in the disassembly of a mutualistic plant–animal interaction web in Patagonia. Because of the importance of the hummingbird as a key pollinator, and the marsupial and *E. albiceps* as key seed-dispersers in Patagonian forests, we suggest that the decline or loss of these vertebrates (or, the loss of the mistletoe) could lead to a dramatic decline in the diversity of the highly endemic flora of these forests. However, these results are not limited to this special case in which this particular suite of exotic species indirectly affects keystone interactions in Patagonia. Direct and indirect species interactions often play essential roles in the maintenance of community structure in a variety of ecosystems (1, 3, 41). Although more work is needed to elucidate fully the consequences of these potential indirect interactions, our study demonstrates the role that both direct and indirect interactions among disparate taxa can play in maintaining ecosystem integrity.

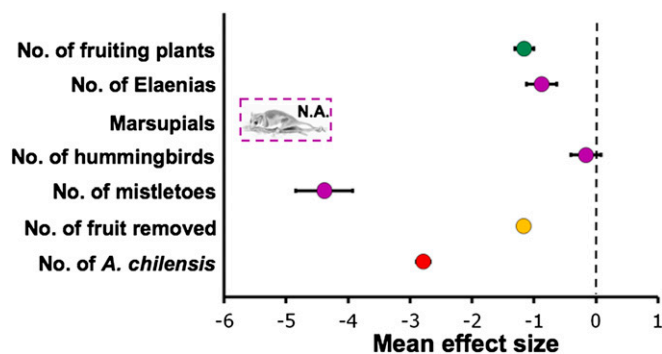


Fig. 4. The effect size of exotic species [$\ln(N_{PE}/N_{AE})$] on the different response variables measured in this study. Error bars are 95% confidence intervals. The effect of exotic species is significant if the confidence intervals do not overlap zero (dashed line). Violet indicates indirect effects, red depicts herbivory on *A. chilensis* by exotic ungulates, yellow shows the effect of German wasps on fruit removal, and green shows number of fruiting plants dispersed by the marsupial and *E. albiceps*. Because we used presence/absence data to evaluate the indirect effects of exotic ungulates on the marsupial, we cannot calculate an effect size. However, we did not find marsupials at any of the invaded sites, but marsupials were present in all of the intact sites.

Material and Methods

Study Area and Natural History. We conducted our research in Nahuel Huapi National Park (705,000 ha) and Arrayanes National Park (1,753 ha) in northwestern Patagonia, Argentina. The native forest vegetation in the study area belongs to the Subantarctic biogeographical region, which is distinctive from the Neotropical biomes of the rest of South America (42). This temperate forest is known for its high endemic flora and number of plant-animal mutualisms (43). For example, more than 50% of the woody plants produce fleshy fruits and their seeds are dispersed by vertebrates (43).

We selected 26 sites for the study. Exotic ungulates are present at 13 of the sites, 7 have only deer and 6 have cows and deer (invaded sites); the other 13 sites have no exotic ungulates (intact sites). Sites were 25 × 25 m and were chosen haphazardly to incorporate the range of habitats found in each treatment. Sites were separated by at least 1–2 km. The most common trees, at all sites, are the evergreen southern beech *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*. The understory is dominated by the shrub *Aristotelia chilensis* and the bamboo *Chusquea culeou*. The two forest layers are well differentiated, with tree canopy reaching up to 40 m in height and understory reaching up to 5 m in height.

Exotic Ungulates. In the austral summers of 2010 and 2011, we examined the direct effect of exotic ungulates on *A. chilensis* and their indirect effects on the interaction between the hummingbird, the mistletoe, and the marsupial. We measured the following set of biotic and physical variables in haphazardly 3-m radius circular plots placed at each site and separate at least by 5 m ($n = 4$ per site): number of reproductive *A. chilensis* (>70 cm in height), number of reproductive mistletoes, number of seeds dispersed [when *D. gliroides* defecates mistletoe seeds, the sticky pulp that surrounds the seeds facilitates attachment to the branch resulting in “necklaces” of up to 20 seeds linked by viscin threads (Fig. S1)] and seedlings established (those presenting the first two true leaves) of the mistletoe, and the complexity of habitat structure. As a measure of habitat complexity within each plot, we counted the number of contacts with a vertical pole (3-m height) for branches 5–10 cm in diameter and oriented <45° relative to the ground and number of fruiting plants.

To quantify the effects of browsing by exotic ungulates on *A. chilensis*, we conducted an enclosure experiment. In 2010, we planted 12 pairs of *A. chilensis* at three sites, each pair consisting of one *A. chilensis* fenced with 1.2-m-high woven wire to prevent browsing by exotic ungulates, and the other *A. chilensis* open to allow browsing (control). The *A. chilensis* used in the exclusion experiment were generally the same sizes as those that are parasitized by mistletoe in these forests. We counted the number of leaves in each *A. chilensis* at the beginning of the experiment and after 30 d. Additionally, using standard dendrochronological techniques, we found that the age structure of the potential hosts for the mistletoe differed significantly between intact and invaded sites (Fig. S2).

To facilitate rapid surveys on the indirect effects of exotic ungulates on the presence or absence of the marsupial, the 26 study sites were grouped by presence or absence of mistletoe (see ref. 25 for a detailed explanation). At sites with mistletoe, we concluded that marsupials were present if we found recently dispersed mistletoe seeds (recall that this marsupial is the only seed disperser of mistletoe in these forests). If no dispersed seeds were found at the site, we used trapping to confirm the absence of the marsupials. We also trapped in sites without mistletoe. At each site, we placed a 5 × 5 grid of Tomahawk-style traps ~5-m apart. Each trap was placed 1–2 m above ground in the shrub closest to the sample point. Traps were baited with apples and bananas. Because the objective was to document presence, once at least one marsupial was trapped, we stopped trapping at the site; we were not trying to estimate population sizes. We continued trapping for four nights if no marsupials were captured. Based on previous capture data for marsupials in this same system (25), and following procedures in ref. 44, the probability of capture was 99.6% in four nights if marsupials were present. Thus, we are confident that marsupials were absent after four nights of trapping if no marsupials were captured.

Finally, during the austral winter of 2011 flowering season of the mistletoe (March–November) (21), the number of hummingbirds (visually and acoustically) was recorded using fixed-radius point counts (45) at eight sites. Because of the eruption of the volcano Puyehue-Cordon Caulle in the fall of 2011, we could not use the same set of sites as these were heavily affected by ash fall. Consequently we selected eight new sites. Additionally, because sites with a long history of disturbance by exotic ungulates do not maintain mistletoe populations, we selected four sites in places where exotic ungulates were present but in very low densities. We paired those four sites with sites where exotic ungulate were absent (intact sites). At each site, point counts were conducted during the morning on days without rain and wind. The

distance between points was always >300 m. Hummingbirds were counted at three 25-m fixed radius plots during a 10-min period (46).

Exotic Wasps. To evaluate the impact of German wasps on the mutualism between *A. chilensis* and seed dispersers, we marked 20 immature fruits with small paper tags on each of 60 plants haphazardly chosen in three different treatments in the Arrayanes National Park. Twenty *A. chilensis* plants were marked in wasp-excluded sites (poison treatment), 20 in invaded sites (nonpoison treatments), and 20 in overabundance sites (protein + sugar treatment). The sites were separated by at least 1 km, because German wasps travel 200 m on average from the nest during foraging (47). We reduced the abundance of German wasps using toxic baits (poison treatment) prepared with 0.1% Fipronil mixed with 20 g of raw ground beef (47). The poison treatment was developed to control only German wasps and does not affect the native fauna. The baits were placed in feeding stations made of 500-mL plastic bottles with both ends cut off. To increase the abundance of German wasps locally (protein + sugar treatment), we added baits containing 20 g of fish-scented cat food bait (Whiskas, Kal Kan Foods) (48), 20 g of raw ground beef, and 20 g of honey. In the two treatments, feeding stations were hung between 1 and 2 m above ground in a shrub on a 25 × 25-m grid. Poison and protein + sugar treatments were carried out before the fruits were ripe and maintained throughout the entire fruiting season. To determine the abundance of German wasps, we hung in each of the 60 *A. chilensis* a 20 × 20-cm sticky trap. At monthly intervals during the fruiting season, we counted the number of German wasps in each sticky trap. Sticky traps were replaced monthly. As a result, the activity of German wasps was significantly lower in plots in which we applied poison treatments (1.95 ± 1.82 mean \pm SD per 20 × 20-cm sticky trap) relative to sites where we experimentally increased wasp activity (11.65 ± 5.14 in protein + sugar baits treatment), and to unmanipulated sites with natural abundance (7.75 ± 5.54 in nonpoison treatments).

At weekly intervals, we recorded the status of each marked fruit and scored it as a developing fruit, ripe fruit, removed fruit, senescent fruit, and eaten fruit. Eaten fruits are those for which the pulp had been consumed without detaching the fruit/seed from the peduncle. We predicted that the German wasp, by feeding on fruits and being aggressive toward native birds, would reduce the number of fruits removed by seed dispersers. To test the impact of German wasps on frugivorous birds, we conducted a biweekly bird census at intact, invaded, and protein + sugar addition sites.

Overall Direct and Indirect Effect of Exotic Species. We compiled the results of each experiment and observational study conducted here and measured the direct and indirect effect of the exotic ungulates and the German wasp. We estimated the effect of these exotic species as the log-response ratio [$\ln(N_{PE}/N_{AE})$] of the mean of the response variable in the presence of the exotic species (N_{PE}) divided by the mean of the response in the absence of the exotic species (N_{AE}) (49, 50). The effect of exotic species is significant if the confidence intervals do not overlap zero.

Data Analysis. To examine the impacts of these exotic species on a suite of response variables, we log- or square-root transformed the response variables as needed to improve normality and reduce heteroscedasticity (see Table S1 for residual diagnosis tests). When data transformation did not meet the assumptions of normality, we used Wilcoxon signed rank tests for analysis continuous data and generalized linear models using a Poisson distribution with a log-link function for count data with zero-inflation. For clarity, we show the untransformed values in figures. In cases when multiple measurements were taken at a particular site over a period of days or weeks, we used the average of all of the observations as the particular response variable in the analyses. Sites were the unit of replication when we investigated the impacts of exotic ungulates. However, we used individual *A. chilensis* trees as replicates only when we examined the relationship between the number of fruits removed per tree and the abundance of German wasps because of logistical challenges that arise when trying to exclude or eliminate wasps from entire forest stands.

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