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Short Communication

Tegu lizard (*Salvator merianae*) disperses the invasive plant *Eugenia uniflora*

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ABSTRACT

Invasive species affect ecosystems all over the world. Their impacts intensify when there are beneficial effects among different invasive species, an invasional meltdown. The Argentine black and white tegu lizard, *Salvator merianae* (Squamata: Teiidae), and the plant *Eugenia uniflora* (Myrtaceae) are native to mainland South America but behave as invasive species in other parts of the world. We tested the effectiveness of *S. merianae* as a seed disperser of *E. uniflora*. Tegu feces containing seeds of *E. uniflora* were collected to compare the seed germination of gut-passed seeds, manually de-pulped seeds, and seeds of whole fruits. Survival analysis indicated that Tegu lizards behave as seed dispersers of *E. uniflora*, and there was a tendency for gut-passed seeds to germinate faster than non-gut-passed seeds. Tegu lizards may carry seeds in their guts for considerable distances, facilitating the spread of *E. uniflora* where both species co-occur as native and invasive (e.g., southern USA). The results indicate a mutualistic interaction between the Tegu lizard and *E. uniflora* in their native range, which should be considered by initiatives to monitor and control the invasion of the lizard and the plant.

Keywords: biological invasion; frugivory; gut passage; invasional meltdown; reptile; seed dispersal; seed germination.

The Argentine black and white tegu lizard, *Salvator merianae* Duméril & Bibron, 1839 (Squamata: Teiidae), is a large lizard reaching up to 5 kg and 1.6 m in length (Fitzgerald 1992; Fig. 1A). It is native to Brazil, Uruguay, eastern Paraguay, and Argentina, occurring in diverse habitats, including forests, savannas, swamps, and cities (Fitzgerald 1992; Jarnevich *et al.* 2018). The species was introduced probably after the pet trade and became invasive in Florida, Southern USA, threatening native wildlife (Mazzotti *et al.* 2015; Haro *et al.* 2020) as well as in islands such as Fernando de Noronha, Brazil (Abrahão *et al.* 2019; Gaiotto *et al.* 2021). Climate niche models suggest that *S. merianae* may expand its current distribution and invade large tracts of the Southern USA and northern Mexico (Jarnevich *et al.* 2018). *S. merianae* is omnivorous, with plant material (including fruits and seeds) and invertebrates comprising the bulk of its diet, but small vertebrates, vertebrate eggs and carrion are also commonly consumed (Mercolli & Yanosky 1994; Kiefer & Sazima 2002; Barreto-Lima & Camilotti 2009; Mazzotti *et al.* 2015; Diniz *et al.* 2021; Gaiotto *et al.* 2021). Although seed dispersal by lizards is thought to be most "an island phenomenon", probably driven by the scarcity of arthropod prey on islands (Valido & Olesen 2019), there is an increasing number of studies showing the potential of lizards to behave as seed dispersers in mainland, especially in xeric environments (Gomes *et al.* 2021; reviewed in Correcher *et al.* 2023). Seed dispersal by lizards often has a positive effect on seed germination

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similar to or even better than those performed by birds and mammals (Vasconcellos-Neto *et al.* 2009), suggesting lizards may contribute to effective seed dispersal and plant recruitment (reviewed in Valido & Olesen 2019). However, seed dispersal may also be a gateway to the spread of invasive species elsewhere, facilitated by frugivorous animals (Traveset & Richardson 2014).

Eugenia uniflora L. (Myrtaceae), known in Brazil as Pitanga, is a shrub/small tree species native from eastern and central mainland South America that produces fleshy fruits (Fig. 1B-C) and whose seeds are dispersed by birds and mammals (Duarte & Paull 2015; Blendinger & Villegas 2011; Jones *et al.* 2022; AV Christianini pers. obs.). *E. uniflora* has been introduced in many tropical and subtropical regions around the world because of its valuable fruit and as an ornamental plant, but it became invasive in places such as Florida (USA), the Bahamas, Bermuda, Queensland (Australia), Hawaii, Fiji, French

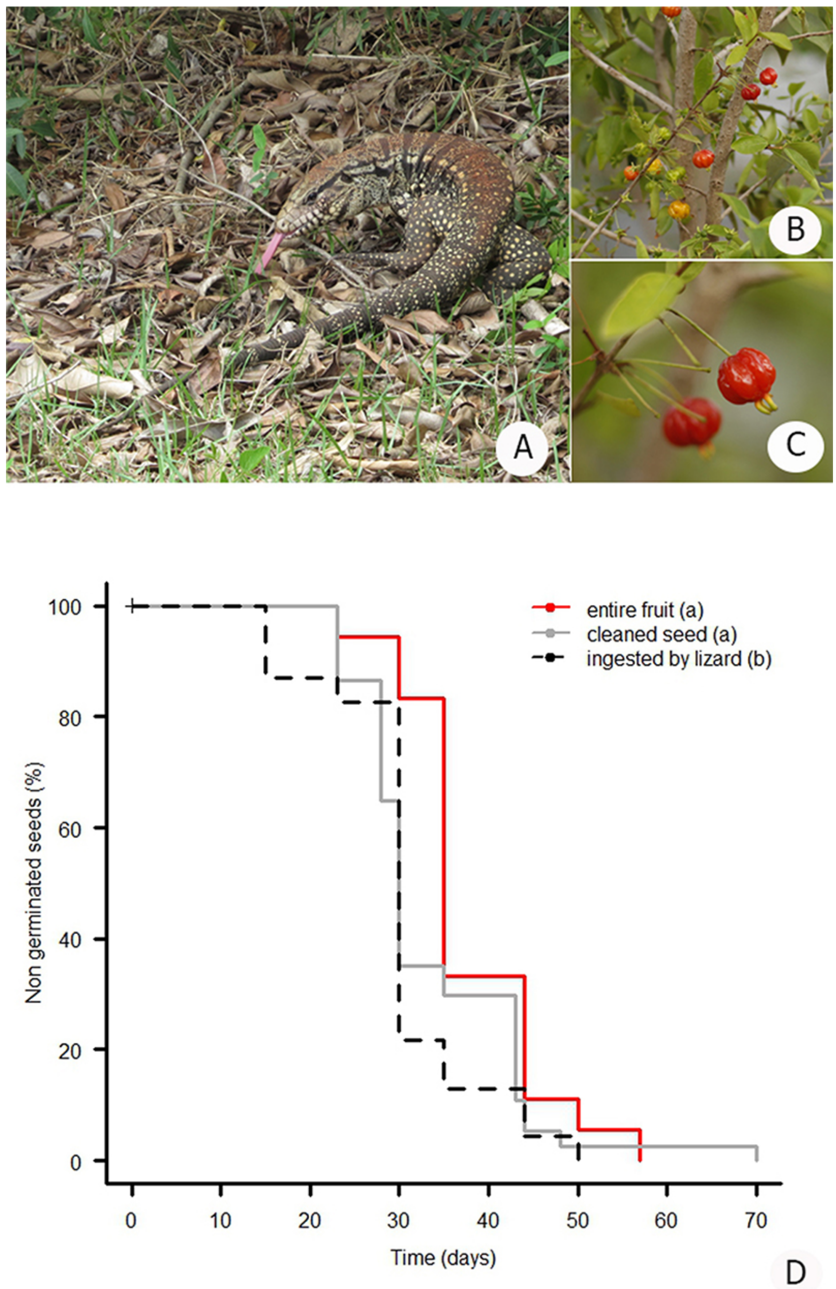

Figure 1. Argentine black and white Tegu Lizard *Salvator merianae* (Squamata: Teiidae) is native from South America, but an invasive species elsewhere (A). The lizard was observed in its native range ingesting seeds of the native fleshy-fruited *Eugenia uniflora* (Myrtaceae), which is also an invasive species elsewhere (view of a fruiting branch (B) and a close up of ripe fruits (C); a fruit is ca 2cm width). In (D), germination curves of the seeds from *E. uniflora* ingested and defecated by Tegu lizard (in black; N = 24) and control seeds (within entire fruits (red; N = 19) and manually de-pulped (in gray; N = 37)) (D). Different letters after treatment names indicate differences in survivorship curves. Photo credits to AV Christianini (*S. merianae*) and M. Alcolea (*E. uniflora*).

Polynesia and Mauritius islands among others (Rifai 1992; Langeland & Burks 1998; Duarte & Paull 2015). Experiments with captive lizards suggest that *S. merianae* may eat and disperse seeds of *E. uniflora* (Castro & Galetti 2004). However, there is no published observation about the Tegu lizard eating *E. uniflora* fruits under natural conditions, nor their potential as long-distance seed dispersers. Furthermore, there is no evaluation of the role of seed treatment in the gut of the lizard on seed scarification or removal of germination inhibitors that may be found in the seed coat or pulp of the fleshy fruit (de-inhibitory effect; Samuels & Levey 2005).

Here, we tested the potential role of *S. merianae* as a seed disperser of the invasive *E. uniflora*. We made observations of a large Tegu lizard (Fig. 1A) that inhabits Federal University of São Carlos, Campus of Sorocaba, southeastern Brazil (47º31'S; 23º35'W). The Tegu lizard was spotted several times exposed to the sun (probably in thermoregulation) around a burrow used as a shelter on October 2021. The entrance of the burrow was between 75-83 m away from the two nearest *E. uniflora* individuals. In one of these occasions one of us (AV Christianini) spotted the lizard feeding on fallen fruits of the nearest *E. uniflora*, 75 m from the Tegu shelter. The Tegu ingested at least seven entire fruits before leaving. On October 27, we collected two Tegu scats around the entrance of its burrow. The samples were taken to the lab and washed in tap water under a sieve. The material was left drying at room temperature and further inspected for contents.

Both fecal samples contained plant material (mostly leaf fragments and seeds), and arthropod remains, including Diplopoda, Coleoptera, Hymenoptera (Formicidae), and Orthoptera, often observed in Tegu diet (Mercolli & Yanosky 1994; Kiefer & Sazima 2002). Scat 1 contained 14 seeds of *E. uniflora* and 20 of *Malpighia emarginata* (Malpighiaceae), while scat 2 contained 11 seeds of *E. uniflora*. The seeds retrieved were rinsed in tap water, planted in germination chambers filled with vermiculite, watered daily, and kept in a greenhouse under natural day-light and temperature. To test if the Tegu lizard improves seed germination of *E. uniflora*, we compared the germination of seeds ingested by the lizard (N=24) with seeds from two control treatments. Control 1 contained seeds we removed from fleshy fruits (i.e., manually de-pulped, N=37), while control 2 contained seeds still embedded in fleshy pulp (i.e., the whole fruits, N=19). Control seeds were sowed following the same protocol for the seeds found in Tegu scats. With three germination treatments, we would be able to answer if a potential improvement in seed germination after gut passage would be due to mechanical/chemical abrasion on the seeds (by comparing gut passed versus manually de-pulped seeds), or release from germination inhibitors commonly found in fruit pulp (whole fruits versus manually de-pulped seeds) (Samuels & Levey 2005). We recorded germination based on the observation of the protrusion of the radicle two weeks after planting and every week for up to 20 weeks (140 days). Observations ended 70 days after the last record of seed germination. Seeds that did not germinate until the end of the experiment were rotted, being unable to germinate.

We used survival analysis to compare seed germination among treatments. Survival curves were analyzed using the Kaplan-Meier estimator. The χ^2 log-rank test tested the general similarity among the curves, and comparisons between the curves were tested using the Bonferroni method to adjust p-values for multiple comparisons. Given our modest sample sizes, we probably had a low power to detect a potential true effect of seed ingestion by the lizard on seed germination (Gotelli & Ellison 2004). Therefore, we did not approach the rejection of the null hypothesis of equal survivorship curves based on a simple cut off probability value of 0.05. Instead, we opted to interpret p-values following the evidence-based language recommendations of Muff *et al.* (2021). Analyses were performed in R (R Core Team 2019) package survival (Therneau 2023). Survival curves were plotted with packages *survminer* and *ggplot2* (Wickham 2016).

Considering all treatments, 98% of the seeds from *E. uniflora* germinated, confirming the high germination rates often observed for this species (Stricker & Stiling 2013). We found a weak evidence (log-rank test χ^2 = 5.6; df = 2; p = 0.06, Fig. 1D) that the lizard improved germination speed. Post-hoc tests suggest a moderate evidence of difference between the germination speed of seeds ingested by the Tegu lizard and those in entire fruits (Bonferroni adjusted post-hoc test: χ^2 = 7.94; p = 0.02). We found no evidence of difference in the germination speed of seeds cleaned by us and ingested by the Tegu lizard (χ^2 = 0.037; p > 0.99). We also found no evidence of difference in the germination of seeds cleaned by us and seeds within entire fruits (χ^2 = 3.67; p = 0.17). Survival curves suggest a successful role of Tegu lizard gut passage in removing seed germination inhibitors found in seeds coated by fleshy pulp, accelerating germination speed compared to seeds within entire fruits, but not cleaned seeds (Samuels & Levey 2005) (Fig. 1D).

E. uniflora overlaps fruit maturation with the time of emergence of the Tegus from their cold/dry season burrows in Southeast Brazil (Sanders *et al.* 2015), which likely intensifies the interaction between Tegus and the fleshy fruits. The finding that *S. merianae* behaves as a seed disperser of *E. uniflora* under natural conditions indicates that the lizard may spread propagules into new sites in native and invasive ranges of this plant. *E. uniflora* and *S. merianae* overlap most of their distribution in their native range (Turchetto-Zolet *et al.* 2016; Jarnevich *et al.* 2018). However, niche models suggest that Tegu lizards may find suitable conditions and invade large tracts of the Southern United States and Northern Mexico (Jarnevich *et al.* 2018), including many sites not currently invaded by

E. uniflora. This beneficial effect among invasive species is a typical example of an invasional meltdown, where an established alien facilitates the invasion by another alien species (Simberloff & Von Holle 1999). Since seedlings of *E. uniflora* may outperform native plant species in the invaded ranges (Stricker & Stiling 2013), seedlings are likely able to establish even when deposited in scats mixed with other seed species ingested by Tegus. The nearest *M. emarginata* individuals, whose seeds were also found in lizard scats, were 97 m away from the Tegu burrow, which suggests that the lizard may carry viable seeds in the gut and deposit them at considerable distances. Given that the home range of Tegu lizards extends over 10 hectares (Abrahão *et al.* 2019) and radio-tracked lizards can move longer than 800 m in subsequent days (Mason *et al.* 2022), these minimum seed dispersal distances are likely conservative estimates, considering also that gut passage times of food in lizards may last a few days (Valido & Nogales 2003; Castro & Galetti 2004). Therefore, Tegu lizards probably deposit seeds farther than our minimum distances recorded (75 – 97 m).

Initiatives to monitor and control the invasion of *E. uniflora* and *S. merianae* should also consider the potential mutualistic interaction between those species. Our results also highlight that it is not advisable to overlook the importance of lizards in seed dispersal and potentially plant regeneration of several other plants in the mainland, in their native (Diniz *et al.* 2021), and invaded ranges. We believe these topics are worth further investigation.

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Author's contribution

Conceptualization, investigation, data curation and formal analysis: MLC and AVC; Writing-original draft and visualization: AVC. Writing – review and editing: MLC, with Supervision by AVC.

Conflict of interest statement

Authors have no conflicts of interest (personal, scientific, commercial, political, or financial) to declare.

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