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## EDITED BY

Melissa Miller,  
University of Florida, United States

## REVIEWED BY

Joel Strong,  
Barker Central School District, United States  
Jeff Goessling,  
Eckerd College, United States

## \*CORRESPONDENCE

Jordan Donini  
✉ jtdonini@fsw.edu

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# Florida Box Turtles (*Terrapene carolina bauri*) as a potential seed dispersal agent for invasive Beach Naupaka (*Scaevola taccada*)

Jordan Rios and Jordan Donini\*

Department of Pure and Applied Science, Florida SouthWestern State College, Naples, FL, United States

Vertebrates are often associated with the dispersal of plant seeds in ecosystems. Although megafauna are often the focus of seed dispersal studies, reptiles, particularly herbivorous and omnivorous turtles, have also been recognized as important dispersal vectors. Specifically, North American Box Turtles (*Terrapene* sp.) have been investigated as seed dispersal agents; however, findings vary from study to study and even based on plant species. The Florida Box Turtle (*Terrapene carolina bauri*) has been documented serving as a vector of seed dispersal for several native plant species in southern Florida. In this study we sought to investigate the potential of *Terrapene carolina bauri* as seed dispersal agents of the invasive Beach Naupaka (*Scaevola taccada*). We collected ingested *S. taccada* seeds from box turtle fecal samples and from fruiting trees from August through November 2023 and planted them in an outdoor growing plot to document both success and time to germination. Germination largely occurred within a 3–6 week time frame but continued until week 10. Germination success (%) did not significantly differ between the two study groups with final germination percentages of 52% for ingested seeds and 58% for non-ingested seeds. These results suggest that while ingestion does not significantly impact germination likelihood, seeds consumed by box turtles can still successfully germinate, indicating their potential role in the dispersal of this invasive species across habitats.

## KEYWORDS

box turtles, Beach Naupaka, seed dispersal, germination, chelonochory

## 1 Introduction

Seed dispersal in many species of plants is facilitated heavily through zoochory, which refers to the dispersal of seeds through animals. Among the different forms of zoochory, endozoochory, or ingestion and defecation of viable seeds, is one of the most well studied forms and has been associated with numerous plant and animal species interactions

(Traveset et al., 2007). A wide variety of vertebrates, including avians and mammals are recognized as seed dispersers, notably in both frugivorous and omnivorous species (Cypher and Cypher, 1999; Chen et al., 2018; Martín-Vélez et al., 2021).

Although research on seed dispersal by reptiles, or saurochory, has increased in recent decades, it remains limited compared to that of avian and mammalian systems. However, it is largely recognized that early reptiles played a major role in selection for the evolution of food plants (van der Pijl, 1982). Evidence regarding frugivory in lizards and crocodilians suggests the possibility of their function as effective dispersal agents (Braun and Brooks, 1987; Platt et al., 2013; Valido and Olesen, 2019). Additionally, a recent literature review by Falcón et al. (2019) assessed the known breadth of chelonian frugivory and seed dispersal (chelonochory), with many species identified as potential seed dispersal agents (Rick and Bowman, 1961; Moolna, 2008; Elbers and Moll, 2011; Johnston et al., 2015).

Specifically a number of studies indicate North American Box Turtles (*Terrapene* sp.) as potential seed dispersal agents for a number of fleshy-fruited plants (Braun and Brooks, 1987). The Florida Box Turtle (*Terrapene carolina bauri*), in particular, has been subject to investigations regarding diet and seed dispersal potential (Liu et al., 2004; Platt et al., 2009; Loredó et al., 2022). *Terrapene carolina bauri* is a generalist species occurring across peninsular Florida and south into the Florida Keys, inhabiting a wide variety of ecosystems and habitats and feeding on a diverse range of plant and animal matter (Dodd et al., 1994; Liu et al., 2009; Donini et al., 2024). Because of its broad diet and habitat use, *T. carolina bauri* is known to seek out and consume fruit shrubs in dune and coastal ecosystems including invasive species like Beach Naupaka (*Scaevola taccada*) (Loredó et al., 2022).

*Scaevola taccada* is an evergreen shrub that forms large mounds up to 3.5m tall endemic to the tropic-to-subtropic Indo-Pacific (Yang and Kuo, 2018). *Scaevola taccada* grows close to the sea and is exposed to high salinity, generally found growing in sand with a preference for open sun and high temperatures (Plant Atlas, n.d; University of Florida IFAS, n.d; Yang and Kuo, 2018). In its native distribution, it has been documented in the diet of a number of bird species (Emura et al., 2012; 2014), along with Aldabra Giant Tortoises (*Aldabrachelys gigantea*) (Falcón et al., 2019). *Scaevola taccada* is highly invasive in the Caribbean and Florida, and competes with its native relative, Inkberry (*Scaevola plumieri*), which is endemic to Florida and the Caribbean basin (Swenson et al., 2024). *Scaevola taccada* is now listed as a Category I invasive species in Florida while the native *S. plumieri* is listed as a threatened species (Swenson et al., 2024). Both *S. plumieri* and *S. taccada* are a food source for *T. carolina bauri* in a coastal ecosystem (Loredó et al., 2022), however, *S. taccada* was observed in fecal samples at a much higher frequency. At this coastal site (further described by Donini et al., 2024) in southwestern Florida, *S. taccada* dominates in comparison to *S. plumieri* which is seen at much lower densities (Figure 1). Visual observations during transect walks at this site show a ratio greater than 30:1 of mature *S. taccada* to *S. plumieri* in the primary 60 ha survey region (Rios and Donini Personal Observation).



**FIGURE 1**  
Native Ink Berry (*Scaevola plumieri*) in the left foreground next to higher density patch of Invasive Beach Naupaka (*Scaevola taccada*) in the background of the field site.

In general, there are few studies on the seeds of *S. taccada* (Liang et al., 2020; Yang and Kuo, 2018) and even fewer regarding its relationships with fauna native to American territories (Swenson et al., 2024). We sought to test if *T. carolina bauri* are effective seed dispersers of *S. taccada* by collecting seeds from the feces of turtles and from plants and growing them in controlled conditions. We hypothesized that seeds from turtles would effectively germinate, and that germination rates in seeds collected from turtles would be higher than seeds directly harvested from plants.

## 2 Materials and methods

### 2.1 Site description

We studied the same site and population described by Loredó et al. (2022) and Donini et al. (2024). Exact location details are left undisclosed due to concerns about illegal collection for the pet trade. The area of survey was approximately 60 ha, consisting primarily of coastal prairie and mangrove (*Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*) forest habitat. The predominant vegetation includes Muhly Grass (*Muhlenbergia capillaris*) Bluestem (*Andropogon* sp.) and various other low-lying grasses. Additionally, Sea Grape (*Coccoloba uvifera*), Cocoplum (*Chrysobalanus icaco*), Brazilian Pepper (*Schinus terebinthifolii*), *S. taccada* and *S. plumieri* and are all present and utilized as food and shelter by *T. carolina bauri* (Dodd et al., 1994; Platt et al., 2009; Loredó et al., 2022; Donini et al., 2024).

### 2.2 Sample collection and processing

We collected all *S. taccada* seeds from the feces of turtles found in coastal prairie and dune habitats during the months of September and October. We found turtles through meandering, visual surveys (Currylow et al., 2010) and detected individuals under vegetation by

use of wooden stick or random visual observations. Once detected, we placed individuals in two or five-gallon buckets filled with water high enough to cover the bottom of their carapace and soaked them in the shade, until there was evidence of defecation (Loredo et al., 2022). If there was no evidence of defecation, turtles were retained in their bath overnight (12–18 hours) in the lab. Feces were also opportunistically collected from other turtles that defecated while being handled during processing. We seined feces through a small kitchen colander to collect seeds or collected seeds directly from samples when easily accessible. *Scaevola taccada* seeds are round with multiple protruding edges and are approximately 4 mm in diameter (Yang and Kuo, 2018) and may have a protuberance or concavity at the peak (Emura et al., 2014), making them easy to identify and separate from other seed species. Florida SouthWestern State College does not have an IACUC committee, thus all handling of animals followed the protocols outlined in the Herpetological Animal Care and Use Committee Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory research Herpetological Care and Use Committee (2004). All turtle sampling was conducted under FWC Permit # LSSC-21-00003A.

For collection from plants, we took only mature white fruits (Yang and Kuo, 2018). We manually de-pulped seeds by removing them from fruits (Liu et al., 2009) and then washed them in a bucket with tap water following the protocol described by Yang and Kuo (2018).

## 2.3 Plant and growth monitoring

We planted both the ingested and non-ingested seed samples within 24 hours of collection in a monitored section of the horticulture nursery at the Naples Botanical Garden, Collier County, Florida, U.S.A. We used 3-gallon plastic pots containing a perlite-organic soil mix to plant the seeds. This mixture was used to create a closer mimic of the natural substrate where the seeds

were collected. We spaced seeds uniformly at least 2.5 cm apart in all directions to provide ample room for growth. After placement, we covered the seeds with approximately 1 cm of the potting mixture (Liu et al., 2009). The planters received full sun for 6–8 hours per day and remained in that position for the duration of the study. The planters containing the seeds received water twice per day, as part of the irrigation system in use at the botanical garden.

We checked the samples once per week for the first 10 weeks, each time on the same day of the week and at a similar time (e.g., afternoon). During each observation, we documented any germinating seeds. Over the following 16 weeks, germination activity decreased, and we reduced observations to bi-monthly. All seedlings were destroyed after final documentation.

## 2.4 Analysis

We used a Pearson's Chi-squared test to compare germination success between ingested and non-ingested *S. taccada* seeds. We constructed a 2x2 contingency table using the total number of germinated and non-germinated seeds for each treatment (ingested vs non-ingested). We performed the test without Yates' continuity correction due to the relatively small sample size. All statistical analyses were conducted in R version 4.4.2 (R Core Team 2024) using the `chisq.test()` function.

## 3 Results

A total of 50 ingested seeds were collected from turtle feces. Approximately 20 individual turtles were used to collect samples, though the exact number isn't known due to aforementioned opportunistic sampling during processing, as individuals couldn't always be directly linked to a given fecal sample. A total of 50 seeds were collected directly from *S. taccada* for comparison. Both seeds

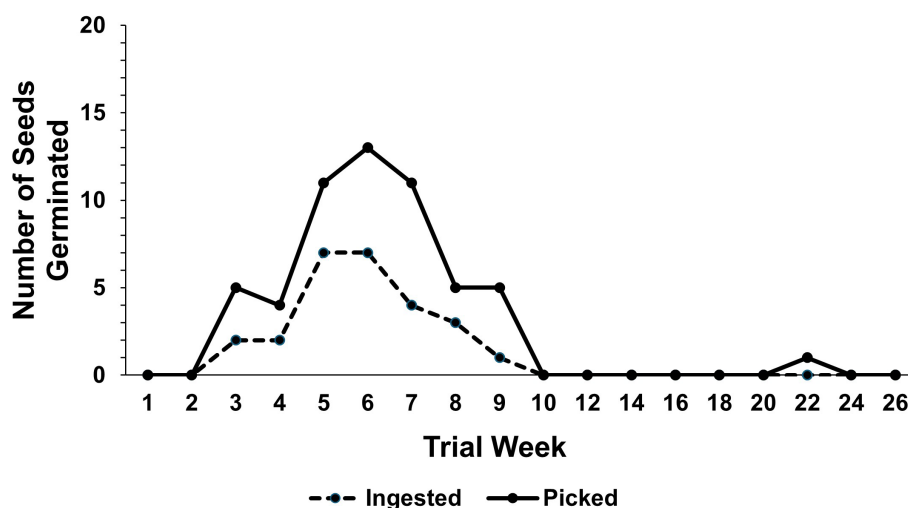


FIGURE 2  
Number of *Scaevola taccada* seeds germinated per week of trial.

ingested by *T. carolina bauri* and non-ingested seeds picked from plants germinated mainly during the 3-to-6-week period (Figure 2), but seeds continued to germinate until 10 weeks. A total of 26 out of 50 ingested seeds (52%) and 29 out of 50 non-ingested seeds (58%) germinated. The difference in germination success between treatments was not statistically significant based on Pearson's Chi-squared test ( $\chi^2 = 0.364$ ;  $p = 0.547$ ), indicating that passage through the digestive tract of *T. c bauri* did not significantly impact seed germination outcomes.

## 4 Discussion

While *T. carolina bauri*, has been subject to investigation regarding their role as seed dispersers (Platt et al., 2009; Liu et al., 2004), there have been no descriptions of potential interactions with invasive *S. taccada* outside of Loredó et al. (2022). The results of this study indicate that the seeds of *S. taccada* can successfully germinate after being ingested by *T. carolina bauri* in controlled conditions. However, there was no significant difference in germination success between the ingested and non-ingested seeds, an observation documented in many other species of turtles and ingested seeds (Moll and Jansen, 1995; Liu et al., 2004; Jerozolimski et al., 2009; Johnston et al., 2015). Despite the lack of difference in germination success, the germination of ingested seeds does indicate the *T. carolina bauri* could serve as a potential dispersal vector for seeds of *S. taccada*. A study performed by Braun and Brooks (1987) confirmed the Woodland Box Turtle (*Terrapene carolina carolina*) as a seed dispersal agent, but germination success of seeds was variable and species dependent. Similarly, Liu et al. (2004) found that germination of fleshy-fruited seed species ranged from 10–80%, after defecation by *T. carolina bauri*, further emphasizing the variability of germination between plant species. Regardless, these results support our own which confirm successful germination of *S. taccada* post ingestion by *T. carolina bauri*.

Additionally, our results were similar to the expected germination rate of fresh, mature *S. taccada* seeds as described by Yang and Kuo (2018). In the two trials, seeds emerged mainly in the 2-to-4-week period and the 2-to-5-week period, with only a small number of seeds germinating through the 13- 20-week marks. The study by Yang and Kuo (2018) was conducted during the months of August and September and showed better germination of seeds under temperature ranging from 20–30 °C with 12 hours of light for 20 weeks, similar to the conditions of our study. Yang and Kuo (2018) recorded germination percentages of the two trials were 71.0% and 75.7%, respectively. Our hypothesis was not supported, as there was no significant difference between the germination success of ingested versus non-ingested Seeds. The germination percentage of our results (52%, ingested and 58%, non-ingested) was lower than the results described by Yang and Kuo (2018), but similar to results from (Liang et al., 2020) in which the 60-day germination percentage was  $45 \pm 4\%$  in seeds that only underwent depulping. Experimental pre-germination treatments indicate the exposure to things such as saltwater may additionally increase

germination likelihood (Liang et al., 2020), and it is possible that the ingestion by Box turtles may inhibit germination success compared to submersion in saltwater or other environmental conditions. In fact, several studies indicate negative impacts on germination in some species of plant after ingestion by chelonians (See review by Falcón et al., 2019), further indicating the need for additional study. Additionally, our low sample size could be obscuring overall effects, and supplementary samples would help to verify the observed trends.

Little information on the macronutrient composition of *Scaevola taccada*, and even less so for *S. plumieri*, poses an issue for determining whether *T. carolina bauri* selects one over the other based on energetic payoff. Additionally, *S. taccada* is fast growing and blooms year-round, with potential for early reproductive maturity in favorable conditions (University of Florida IFAS, n.d; Florida Invasive Plants) while *S. plumieri* generally flowers during the summer and exhibits slower growth (Gilman et al., 2018). These life history traits, in addition to the observed abundance (~30:1 ratio described previously) of mature plants, indicate that *T. carolina bauri* may simply be making use of the more widely available food source.

While we confirmed the ability of *T. carolina bauri* to serve as seed dispersal agents for *S. taccada*, we did not detect any significant difference in germination rates between ingested and non-ingested seeds, however our sample size was lower than anticipated due to abnormally dry conditions inhibiting surveys. The results from this study bring more questions to the forefront about the interactions of invasive plant species with native fauna, and additional studies are needed to investigate the full impact of the interactions between *S. taccada* and *T. carolina bauri* among other coastal species. Questions regarding the potential impact of *S. taccada* seed dispersal into other habitats, due to *T. carolina bauri*'s use of multiple habitat types across Florida are a key area for future research, particularly in understanding how this interaction might influence plant community composition, ecosystem dynamics, and the spread of invasive species beyond coastal habitats.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements.

## Author contributions

JR: Conceptualization, Formal Analysis, Investigation, Methodology, Project administration, Writing – original draft,



Writing – review & editing. JD: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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