

PREPRINT

Author-formatted, not peer-reviewed document posted on 05/06/2023

DOI: <https://doi.org/10.3897/arphapreprints.e107200>

**Climate change and jump dispersal drive invasion of the
Rosy Wolfsnail (*Euglandina rosea*) in the United States**

 Dana Mills, Michael McKinney

1.0 Title:

Climate change and jump dispersal drive invasion of the Rosy Wolfsnail (*Euglandina rosea*) in the United States

2.0 Author Information:

Dana H. Mills¹

Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996

¹Corresponding author: dhiggi10@vols.utk.edu

(ORCID 0000-0001-9235-5885)

Michael L. McKinney

Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996

(ORCID 0000-0001-6390-1795)

Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Dana H. Mills and Michael L. McKinney. The first draft of the manuscript was written by Dana H. Mills and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

3.0 Keywords:

Invasion biology

Rosy Wolfsnail

Euglandina rosea

Niche modeling

Range expansion

Climate change

Urban Heat Island

Satellite population

Jump dispersal

4.0 Abstract:

The rosy wolfsnail (*E. rosea*) is a carnivorous, highly detrimental invader in many parts of the world. While its negative impact on endemic island mollusk populations has been well documented, little is known about its range expansion in North America, where populations are not constrained by oceanic barriers. In this study, we present three compelling lines of evidence indicating significant ongoing and projected geographic range expansion of *E. rosea*: 1) we analyze the current range using data from iNaturalist, 2) we report on the demographics and persistence of an isolated extra-limital satellite population in Nashville, Tennessee since its discovery in 2006 and 3) we employ a predictive ecological model that incorporates environmental variables indicating that the range expansion will continue into the central US well beyond its present range limits. The findings of this study shed light on the underlying mechanisms behind the invasion of this species. First, the invasion is frequently associated with jump dispersal events, which are often linked to horticultural and landscaping activities. Second, the establishment and proliferation of satellite populations are facilitated by common landscape management practices, such as irrigation, as well as the urban heat island effect (UHI). Third, there is a synergistic interplay between the UHI effect and climate change which accelerates the range expansion via global warming.

5.0 Introduction:

Global temperature isotherms are migrating toward both poles at an approximate rate of 27.5 kilometers per decade (Burrows et al. 2011). This poleward migration has created conditions favorable for many species, leading to the expansion of their geographic range (Lenoir and Svenning 2015). According to one estimate, the leading edge of terrestrial species' poleward migration has moved at an average rate of 6.1 kilometers per decade (Parmesan et al. 2003), but this is likely to accelerate as the rate of global warming increases. These poleward shifts, caused by global climate change, now play a major role in the ongoing spread of invasive species, documented across many taxa, as temperature barriers to a diversity of thermophilic species are removed (Robinet and Roques 2010, Pauchard et al. 2016). This has led to the increasing use of ecological niche models (ENM) to delineate the expansions of species under current and future climate change scenarios.

Here we report on the potential range expansion of the predatory invasive snail, *Euglandina rosea*, commonly known as the "rosy wolfsnail", as a consequence of climate change. This is a topic of great significance due to the destructive impact *E. rosea*, which has been widespread through misguided biological control introductions around the world (Gerlach 1994, Lowe et al. 2004). *E. rosea* is a voracious predator that mainly feeds on other mollusk species, particularly terrestrial snails (Cook 1989). In comparison to most gastropod species, *E. rosea* is remarkably fast and can rapidly capture its prey once a slime trail has been identified (Gerlach 1994). These traits make *E. rosea* a uniquely effective and aggressive predator. Between the 1950s and 1970s, scientists and policymakers thought those qualities could make it a valuable biological control agent.

For example, in 1936, the giant African land snail (*Lissachatina fulica*), an invasive species, was introduced to the Hawaiian Islands (Davis and Butler 1964), perhaps from Japan or Taiwan as a food source (Lv et al. 2008). *L. fulica* soon became established (Davis and Butler 1964), consuming a wide variety of plants, including beans, peas, cucumbers, and melons (USDA 2022). Consequently, the Hawaiian Territorial Department of Agriculture (HTDA) launched a widespread campaign to eradicate them (Ezzell 1992). Between 1950 and 1959, HTDA introduced 19 different snail species and 11 different insect species (Davis and Butler 1964). A comparable invasion was unfolding elsewhere in the Pacific and Indian Oceans, with government agencies in French Polynesia, Samoa, Mauritius, and Micronesia (Lowe et al. 2004). Out of the 30 species that HTDA introduced, none of them were effective in controlling *L. fulica*. Importantly, only one introduced species, *E. rosea*, became established on the islands (Davis and Butler 1964, Solem 1990).

As often happens, the introduction of *E. rosea* has led to major unintended ecological consequences (Hadfield et al. 1993). Rather than acting as a biological control agent for the giant African snail, *E. rosea* has become a predator of native snails, many of which were already endangered or threatened (Meyer and Cowie 2010, Holland et al. 2012). The Hawaiian Islands are home to a large number of native terrestrial snail species (Holland and Hadfield 2004), with

Cowie (1995) estimating 752 species, the majority of which are endemic (99.5%) (Lydeard et al. 2004). *E. rosea* has had a particularly negative impact on the Oahu tree snails (*Achatinella spp.*) in Hawaii, resulting in significant declines (Solem 1990). This has led to the extinction of several Oahu tree snail species, with others now classified as endangered (Hadfield 1986).

Unfortunately, *E. rosea* populations can now be found in many other parts of the world, often from its introduction as an unsuccessful biological control agent (Simberloff and Stiling 1996, Mack et al 2000). Moreover, there is evidence that *E. rosea* is expanding its range in the United States, facilitated by modern horticultural practices and climate change (Irwin et al. 2016). While the impact of *E. rosea* on endemic mollusk populations in island environments has been extensively researched by invasion biologists, little is known about the expansion of its native range in North America, where populations are not restricted by oceanic barriers. Previous studies have indicated that *E. rosea* is native to several states in the southeastern United States, including Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and southeastern Texas (Auffenberg and Stange 2021). However, since 2006, a persistent population of *E. rosea* has been observed outside of this assumed range, just south of Nashville, TN (Irwin et al. 2016). The stability of this population implies a type of range expansion for *E. rosea* which is facilitated by factors such as climate change, the urban heat island effect (UHI), and modern horticultural commerce. Our paper examines this pattern of range expansion using publicly available data sets provided by the Global Biodiversity Information Facility (GBIF). We document the persistence of and provide demographic data (abundance, age, size of individuals) about an extra-limital satellite population of *E. rosea* since its discovery in 2006. Finally, we apply a predictive ecological model that incorporates environmental variables to delineate where potential habitats exist that are suitable for *E. rosea* habitation.

6.0 Materials and Methods:

6.1 Current Geographical Range

We utilized GBIF to assess the current distribution of *E. rosea* in the United States. GBIF is an international organization that aims to make biodiversity data easily available and accessible. It is a network of organizations that collect and share data on species distribution, abundance, and other characteristics (Ivanova and Shashkov 2021). These data were processed and only include research grade observations obtained from iNaturalist (iNaturalist 2023). Such research grade observations are those where a species identification has been reviewed, the community is in agreement, and where the upload contains valid data, location, photograph and is not a captive/cultivated organism (Cox 2019). These occurrence records have been checked for accuracy and quality and are considered reliable observations in the large majority of cases (Maldonado et al. 2015).

6.2 Satellite Population Persistence in Nashville, TN

In summer of 2006, a Nashville homeowner contacted the Tennessee Department of Environment and Conservation (TDEC) to report the presence of several large unidentified land snails in the yard, apparently introduced with recently installed landscaping materials (plants and mulch). The snails were determined to be *E. rosea*. TDEC expected that population would soon become extirpated by the upcoming winter temperatures as the population was far above the native range of this relatively thermophilic species. However, the homeowner continued to observe these snails each year from 2006 to 2010. In 2010 the area experienced a relatively cold winter, and no live snails were observed. It was inferred that the population had indeed become extirpated. But in 2014, following a relatively warm winter, another live snail was found, indicating a continuously reproducing population.

In 2015, coauthor Michael McKinney was contacted by TDEC to conduct more thorough and systematic surveys of the area to collect on this apparently persistent satellite population. These investigations were conducted at the homeowner's residence, in Hill Place Neighborhood, located in southwest Nashville. Properties in this neighborhood have expansive yards and well-maintained landscaping features. There are few physical barriers such as privacy fences, roads, or waterways. Two surveys of the homeowner's yard, and adjacent yards, were carried out in April 2015, and September 2015. These two surveys were extensive at 30 person-hours and 14 person-hours respectively using methods described in Irwin et al. (Irwin et al. 2016). These surveys found no living *E. rosea* but did find 25 shells of individuals dead for some time, indicated by the absence of fresh tissue. The presence of juvenile shells among the dead implied that reproduction had occurred. As the exhaustive surveys turned up no live individuals on the property or surrounding properties, it was concluded that the population may have become extirpated after 2013, possibly due to two exceptionally cold winters in 2014 and 2015 (Irwin et al. 2016). However, in March 2022, nine years after the last live sighting, the same Nashville homeowner discovered a single adult living specimen of *E. rosea*. This prompted two more additional surveys led by coauthor Dana Mills on April 2022, and November 2022, to observe and collect any additional living or dead *E. rosea* individuals.

6.2.1 Search Methods:

In April 2022, the Nashville property, covering more than 13,000 square feet, was searched for 2.5 hours by five people. Thus, the total search effort was 12.5 person-hours. In November 2022, the search was carried out by 6 people for 2.5 hours for a total of 15 person-hours. In both cases, we searched the entire area for living or dead *E. rosea*. In addition to the large yard, smaller microhabitats were searched, which included: the vertical exterior walls of the home, under loose mulch, inside potted vegetation, and underneath leaves of vegetation. We also searched adjacent nearby yards that immediately surrounded the homeowner's property.

Observed *E. rosea* were collected and placed into individual containers for transportation and observation. The location and microhabitat of the collection site were recorded. Using digital calipers, the shells of all collected *E. rosea* were measured for length to the nearest 0.01 millimeter at the longest point of central axis. To examine

population data in the context of temperature changes, monthly temperature data for 2000-2022 for this area were collected from NOAA Centers for Environmental Information (NOAA 2023)

6.3 Ecological Niche Modeling

6.3.1 Data Collection

E. rosea observational data were obtained from GBIF. This dataset contained presence-only records derived from human observations submitted to iNaturalist (iNaturalist 2023). This study's aims to define *E. rosea*'s current range and the potential range expansion of its endemic range in the. Therefore, only records from the contiguous United States, where oceanic boundaries are absent, were considered. The GBIF query yielded 1,075 occurrence records in total and covered a period from 2011 to 2023 (GBIF.Org 2023).

Current and projected climate data were acquired from the AdaptWest West Project (AdaptWest Project 2022), comprising 33 parameters evaluated for their relevance in predicting *E. rosea* presence. Our ecological niche model utilized an ensembled mean of 13 projected climate simulations, CMIP6 AOGCMs (Mahony et al. 2022). Three bioclimatic layers were selected: degree-days below 0° Celsius, temperature annual range, and average precipitation (mm) in Autumn. These variables represent climatic extremes that typically constrain species distributions. These layers were deemed most suitable as many other bioclimatic layers either depend on various combinations of these variables or have high correlation with them, as noted by Root (1988). Climate data were downloaded at a 1-kilometer resolution and covered the period from 2000 to 2100 in 20-year increments (Mahony et al. 2022).

6.3.2 Data processing

Using the default settings in the MaxEnt 3.4.3 program (Phillips et al. 2006), we created potential distributions of *E. rosea*, while also eliminating duplicate species records from the same grid square. We plotted all points in ArcGIS Pro 3.0.2 and excluded any points falling far outside the assumed distribution. The recorded coordinates of a data point may not necessarily correspond to its exact collection location due to differences in specificity levels. To ensure consistency, we removed all data points with coordinate specificity greater than 1000 meters (Feng et al. 2019). In order to mitigate the impact of sampling bias, we applied a spatial filter to the occurrence dataset to ensure that no two locations were within a 10 km radius of each other (Boria et al. 2014). After these steps had been implemented, 362 occurrence records remained.

6.3.3 Model Calibration

We employed the maximum entropy approach to perform ecological niche modeling (ENM) using MaxEnt 3.4.3 (Phillips et al. 2006). MaxEnt is a modeling algorithm that estimates the likelihood of a species' presence based on observed values within a raster. This algorithm calculates the probability and assigns each point a value

representing the highest and lowest likelihood of species presence. MaxEnt then extrapolates from areas with similar conditions in the study region, using those calculations.

We developed a correlative niche model that related environmental conditions with 362 *E. rosea* presence records. We executed the model by randomly sampling 10,000 background points within the study area. To optimize the model's complexity and predictive power, we employed ENMeval, an R package that implements MaxEnt across a range of settings and provides evaluation metrics to assist in selecting settings that balance model fit and predictive ability. We used a jackknife approach for each species presence record and assessed models with linear, quadratic, threshold, and hinge feature classes, along with regularization multiplier values ranging from 0.5 to 3.0, increasing by 0.5.

The final model utilized the combination of regularization multiplier and bioclimatic variables that had the lowest AIC and all 362 *E. rosea* occurrence records in MaxEnt, using 10 subsampled replicates. We evaluated the omission rate and test AUC to ensure that the model was optimized. The logistic output format was used with a random test percentage of 25%. We repeated the procedure 10 times for each algorithm with no clamping and applied the fixed cumulative value 10 threshold rule (Radosavljevic and Anderson 2014) to transform each map into binary. The resulting ENM for *E. rosea* was projected in ArcGIS.

7.0 Results:

7.1 Current Geographical Range

The current geographical range of *E. rosea* is primarily the coastal regions of the Southeastern United States (Figure 1). Observations become sparser farther away from coastal areas, implying lower abundance of species populations. In areas where the average minimum temperature of the coldest month is less than 25 degrees, instances of *E. rosea* observations are sparse. Our satellite colony discovered in 2006 is both the farthest reproducing population from the coast and the only recorded reproducing population north of the 36th parallel. It is also approximately 125 miles from the next nearest *E. rosea* observation (Figure 1).

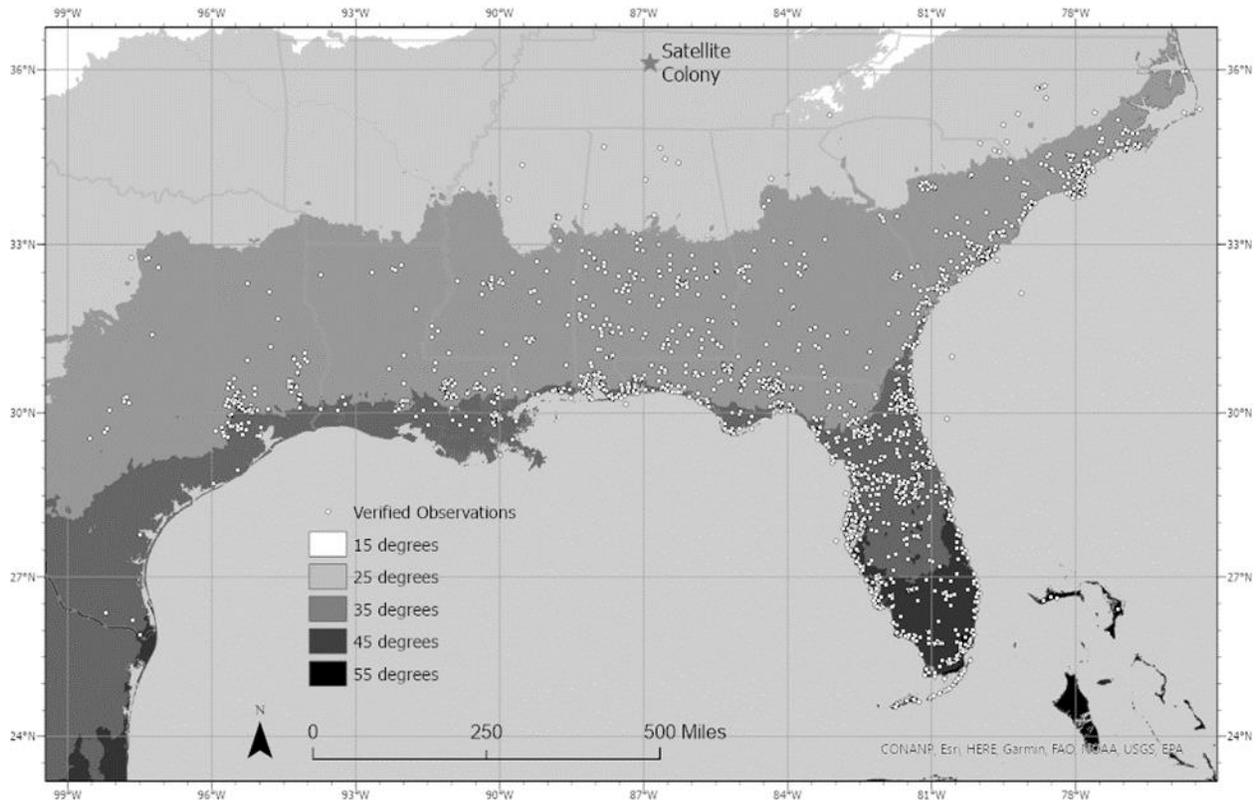


Figure 1. States encompassing the home range and verified observations of *E. rosea*, including satellite colony in Nashville, TN (GBIF.Org 2023) and the average temperature during the coldest months of the year (NOAA 2023)

7.2 Satellite Population Persistence

Based on our surveys, a self-sustaining reproducing *E. rosea* population has been observed in Nashville, TN periodically since 2006 when it was first discovered (Irwin et al. 2016). Since then, it was assumed that the population had been extirpated both in winter 2011 and 2014 because no individual specimens were sighted for one or more years due to freezing winter temperatures which are not suitable for *E. rosea* survival. In 2014, for example, the local minimum temperature fell to 2°F (-17°C). However, our investigation shows that this population has indeed persisted despite these inhospitable conditions. Specifically, 9 years after the last sighting, on April 24, 2022, two additional adult *E. rosea* specimens were captured in the yard of the Nashville residence and placed in separate artificial habitats for observation. These specimens measured 44.86 mm and 48.82 mm respectively. This suggests that these individuals were greater than 460 days old, according to growth tables produced by Gerlach (1994), and they had likely survived two winters prior to collection (Table 1). Furthermore, both of the individuals were sexually mature and produced viable eggs in captivity approximately 21 days after capture, suggesting a fertilization event had occurred prior to our investigation. These two specimens produced 45 offspring.

In November 2022, one more, very small live *E. rosea* individual was captured in the yard of the same Nashville, TN residence. Importantly, this specimen was small at 14.99 mm in length. It was estimated to be a juvenile between 100 and 150 days old (Gerlach 1994), indicating that a recent reproductive event had occurred sometime in

early 2022. This is a significant finding because it implies that the satellite colony in Nashville, TN is stable and able to reproduce.

We note that observations of *E. rosea* tend to occur after periods of warm winters where the temperature does not measure below 11°F (-12°C) for an extended period. Observations become less frequent after periods where the temperature measures below 5°F (-15°C) (Figure 2). This may be due to a reduced population size, and therefore less opportunity for observation, during colder years. Because we observed a reemergence of *E. rosea* even after long periods of absence, we infer that some of the population can withstand these temperatures and remain in aestivation until conditions become more suitable.

Table 1. Relative size and age categories based on shell length, measured from the apex of the shell to the base of the aperture. Relative categories were assigned using growth rate data from “The ecology of the carnivorous snail *Euglandina rosea*” by Gerlach (1994).

Relative Age Category	Approximate Age	Shell Length
Hatchling (prior to shell thickening)	0-41 days	<10mm
Juvenile (thickened shell, immature)	42-311 days	10-30mm
Subadult (sexually mature, not full grown)	312-460 days	31-40mm
Adult (full grown)	>460 days	>40mm

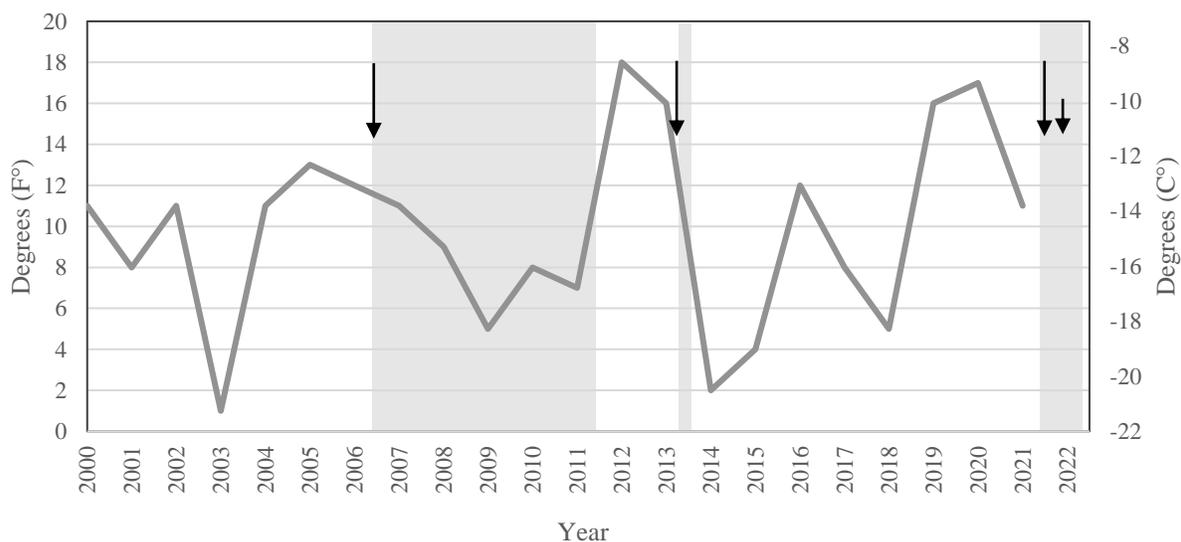


Figure 2. Lowest recorded temperature in Davidson County, Tennessee for years 2000 to 2022 (NOAA 2023). Shaded areas indicate a continuous occurrence of living *E. rosea* individuals. Vertical arrows indicate documented instances where living *E. rosea* were observed after periods of assumed extirpation (short arrow = young newly hatched specimen).

7.3 Ecological Niche Modeling

MaxEnt generated two geostatistical maps that predicted the suitable habitat and niche for *E. rosea*. At 10% training presence, the training omission rate was 0.099 and the test omission rate was 0.124. The average test AUC for the replicate runs was 0.954, and the standard deviation was 0.007. The continuous habitat suitability map suggests

that *E. rosea* are more likely to be found in coastal regions and areas where there are regular precipitation events and warmer temperatures (Figure 3). The binary map indicates areas that are suitable for *E. rosea* and describes this species' fundamental niche with a 10% threshold (Figure 4).

MaxEnt determined that the number of days below 0°C had the greatest contribution to the model with 59.4% contribution. Precipitation in autumn and the temperature annual range were the next largest contributors to the model with 22.1% and 18.5% respectively (Table 2). These three variables are consistent with what is known about most terrestrial mollusks and survival limits. They are not able to tolerate long periods of drought and low temperatures.

Table 2. Estimates of relative contributions of the environmental variables to the MaxEnt model.

<i>Variable</i>	<i>Description</i>	<i>Percent Contribution</i>
BIO6	Degree-days below 0°C	59.4%
BIO14	Autumn Precipitation (mm)	22.1%
BIO7	Temperature annual range (max – min)	18.5%

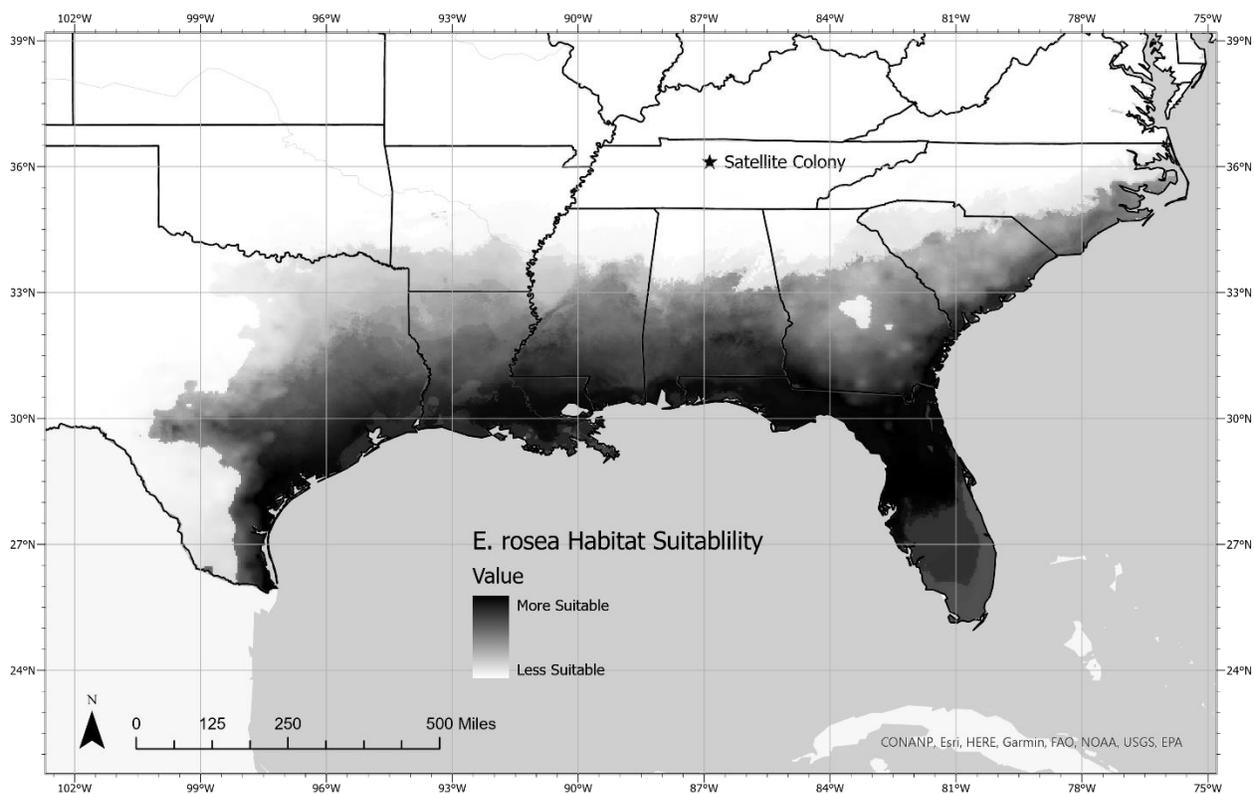


Figure 3. Continuous map of predicted suitable habitat for *E. rosea* in the southeastern United States, raw maximum entropy output. Dark areas indicate regions of higher habitat suitability and light areas indicate regions of lower predicted suitability.

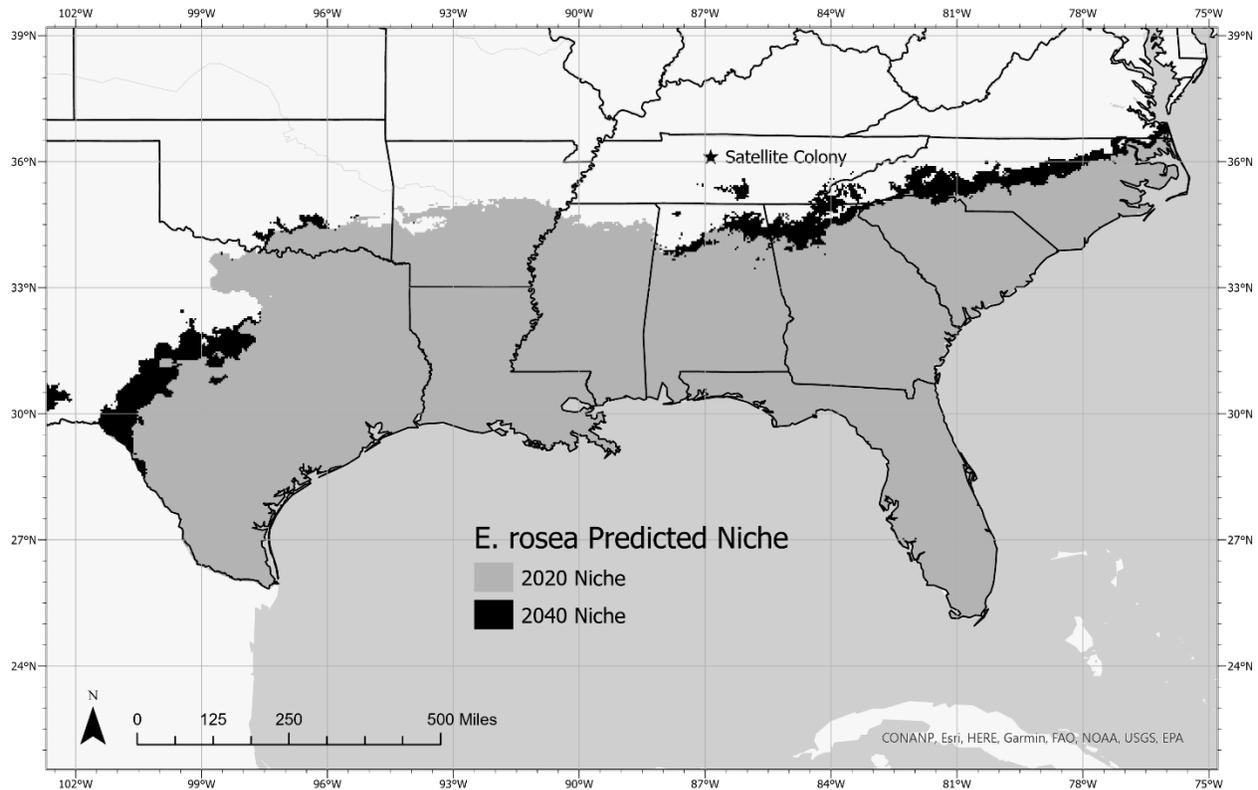


Figure 4. Binary map of predicted potential suitable habitat based on 10% cumulative threshold. Grey indicates the predicted niche for *E. rosea* between the period 2000-2020. Black indicates the predicted niche for *E. rosea* between the period 2021-2040.

8.0 Discussion:

An invasive species is considered established if it has a self-sustaining population that is reproducing and spreading in a new ecosystem (Lockwood et al. 2013, Simberloff 2013). Our results indicate that the colony population in Nashville Tennessee has indeed been successfully established for at least 16 years. Furthermore, our most recent collecting trip indicates that this satellite population continues to reproduce. The *E. rosea* specimens captured in our most recent 2022 collection found two adults that laid viable eggs 21 days after capture and one additional juvenile *E. rosea* have a gestation period of about 30 days from fertilization to the laying of the first egg (Gerlach 1994). *E. rosea* are cross-fertilizing hermaphrodites, with both male and female reproductive organs, but they require a partner for sexual reproduction (Auffenberg and Stange 2021). These animals typically lay between 25 and 40 eggs a year. The two adult specimens that were captured in 2022 laid 27 and 25 viable eggs, respectively. Because the two adult specimens were separated after collection, we estimate that a fertilization event occurred approximately one week prior to our 2022 sampling event.

Our results also indicate a strong likelihood that *E. rosea* has significant potential for continued geographic spread. There are several regions where our model indicated that the habitat and environmental condition are suitable for *E. rosea* outside of its current realized niche. Specifically, it seems likely expansion will occur well beyond its current

range which is centered on southern and coastal states of the US (Figure 1) and will begin to penetrate more deeply into Tennessee, Ohio and several other states in the central USA (Figures 3 and 4).

Regarding mechanisms of spread, there are several ways that alien species can disperse and spread to new areas. Natural dispersal occurs when an organism can spread on its own through means such as wind, water, or animal vectors (Reynolds et al. 2015, Planchuelo et al. 2016). Ecological displacement occurs when an alien species outcompetes native species for resources, leading to decline and then displacement of the native species. Human-mediated dispersal occurs when humans intentionally or unintentionally transport organisms to new areas, such as through the movement of goods, ships, or vehicles (Buck and Marshall 2009). Dispersal can also be facilitated through climate change, where changes in the environment, such as rising temperatures or changes in precipitation patterns, allow organisms to colonize new areas (Perkins et al. 2013).

In the case of the wolfsnail, we suspect that the introduction of *E. rosea* in Nashville was a human-mediated dispersal event, caused by a “hitchhiker” on mulch or plants purchased for the homeowner’s garden in conjunction with climate change. Here we use “hitchhiker” to define organisms that are dispersed by unintended anthropogenic pathways (Coulson and Witter 1984). This is a common way that invasive species are distributed to new habitats (Lockwood et al. 2013, Simberloff 2013). For land snails, it is well documented that horticultural and landscaping activities are a major mechanism of non-native species introductions (Bergey et al. 2014). In the USA, the extent, scale, and volume of such introductions must be enormous given the quantity of landscaping materials purchased in both commercially and non-commercial quantities at large home supply distribution centers across the United States (Dyer et al. 2017). Following such long-distance “jump” dispersal events via home supply distribution centers in cities in many parts of the USA, these nonnative snails often survive and become established, as is well documented by Bergey and Figueroa (2016) in residential yards. Because residential and other urban green space habitats are generally moist, nutrient-rich, and generally hospitable to land snails (Bergey and Figueroa 2016), this can lead to the establishment of isolated satellite populations of nonnative snails that are far removed from the source or other populations. Once established in residential and other urban green space habitats, these nonnative snails can spread on their own. A long-term study by Bergey (2019) showed that the invasive common garden snail, *Cornu aspersum*, spread across 16 residential yards (up to 110 m) in Norman, Oklahoma over a period of 6 years, moving outward in a generally diffusive pattern.

A critical observation about this satellite population is that there are very likely many more nonnative land snail populations in residential areas throughout the USA but they are undetected. The homeowner in this study who found the reported population is a physician who has a strong avocational interest in invertebrates and it is very likely that the average homeowner would not have noticed the unusual nature of this snail and contacted TDEC. And in general, land snails are greatly understudied relative to many other groups. This is exemplified by a recent inventory of land snails of Knox County, Tennessee: of the 151 species found in Knox County, nearly half (70 species) had never been reported from the County and 15 of those had never been recorded in the entire state. Most importantly, 11 of these

15 unreported state species were nonnatives (Dinkins and Dinkins 2018). Most of these nonnatives were found in urban habitats and many were found in vegetation adjacent to plant nurseries and landscaping businesses (Dinkins and Dinkins 2018), as predicted by previous studies (Bergey et al. 2014).

Our study also sheds light on the importance of the urban heat island (UHI) effect, which allows the establishment of populations far outside their normal temperature range (Borden and Flory 2021). The UHI occurs because the temperature in urban areas is higher than the temperature in surrounding rural areas, caused by heat-absorbing surfaces such as buildings, roads, and other infrastructure (Gallo et al. 1995). This produces higher temperatures, particularly during the summer months (Yang et al. 2016) and promotes the establishment of invasive species that could not otherwise survive at higher latitudes (Frank and Just 2020). As a result, invasive species in cities are now experiencing temperatures not predicted to occur for another 50-100 years in outlying non-urban areas (Frank and Just 2020). In this case, the long distance and isolation of the established satellite Nashville population from the general distribution of known wolfsnail observations (Figure 1) may be attributed to the higher temperatures of the UHI in their urban environment. This is reflected in our ecological niche modeling of *E. rosea* (Figure 4) which indicates that the majority of the Cumberland Plateau in Tennessee is not suitable habitat for this snail species. However, there is a small area surrounding Nashville that appears to have a better combination of environmental factors required for survival, primarily temperature (Figure 3). This may be attributed the UHI effect (Gallo et al. 1995) of the densely populated greater metropolitan areas of Nashville.

The importance of satellite populations in invasive species range expansions has been noted elsewhere, such as in the well documented cane toad invasion of Australia. In this case, they are expanding not only as a continuous front but also by human translocation of a few individuals far from this front, to create satellite populations (Greenlees et al. 2018). The practical application of this observation is that finding and eradicating such satellite populations are essential to mitigating the invasion process (Greenlees et al. 2018).

In summary, our results indicate the persistence of a satellite population of a very understudied group, invasive land snails. We also provide insights into the specific processes driving this ecologically impactful invasion. One, it is often characterized by jump dispersal events typically related to horticultural and landscaping activities. Two, establishment (persistence) and expansion of these satellite populations are aided by landscape management practices including irrigation as well as the urban heat island effect (UHI). Three, there is a synergistic interaction between climate change (global warming) and the UHI effect whereby the latter accelerates isothermal range expansion by allowing “sleeper” populations to persist far outside their normal isothermal limits in the cooler nonurban countryside (Frank and Just 2020).

9.0 Availability of data and materials

The *E. rosea* occurrence datasets analyzed during the study are available in the Global Biodiversity Information Facility repository and can be accessed using the following link: [<https://doi.org/10.15468/dl.bfxtvg>]

Current and predicted climate data analyzed during this study are made available by AdaptWest -A Climate Adaptation Conservation Planning Database for North America and can be accessed using the following link: [<https://adaptwest.databasin.org/pages/adaptwest-climatena>]

10.0 Acknowledgments

We thank Dr. Howard Rosenblum for taking a keen interest in the biodiversity of his backyard and giving us full site access. Without his curiosity, this *E. rosea* colony would not have been discovered. We also thank David Withers, with the Tennessee Natural Heritage Program, Department of Environment and Conservation, for investigating the initial *E. rosea* sightings.

11.0 Statements and Declarations

Funding

No funding was received for conducting this study or preparation of this manuscript.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

12.0 Bibliography

- AdaptWest Project (2022) Gridded current and projected climate data for North America at 1km resolution, generated using the ClimateNA v7.30 software (T. Wang et al., 2022). A Climate Adaptation Conservation Planning Database for North America. Available from: adaptwest.databasin.org (May 24, 2023).
- Auffenberg K, Stange LA (2021a) Snail-Eating Snails of Florida, Gastropoda. Gainesville Available from: <http://entnemdept.ifas.ufl.edu/creatures/>.
- Bergey EA (2019) Dispersal of a non-native land snail across a residential area is modified by yard management and movement barriers. *Urban Ecosystems* 22: 325–334. <https://doi.org/10.1007/s11252-018-0815-1>
- Bergey EA, Figueroa LL (2016) Residential yards as designer ecosystems: Effects of yard management on land snail species composition. *Ecological Applications* 26: 2536–2545. <https://doi.org/10.1002/eap.1378>
- Bergey EA, Figueroa LL, Mather CM, Martin RJ, Ray EJ, Kurien JT, Westrop DR, Suriyawong P (2014) Trading in snails: Plant nurseries as transport hubs for non-native species. *Biological Invasions* 16: 1441–1451. <https://doi.org/10.1007/s10530-013-0581-1>
- Borden JB, Flory SI (2021) Urban evolution of invasive species. *Frontiers in Ecology and the Environment* 19: 184–191. <https://doi.org/10.1002/fee.2295>
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* 275: 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>
- Buck JH, Marshall JM (2009) Hitchhiking as a secondary dispersal pathway for adult emerald ash borer, *Agrilus planipennis*. *Great Lakes Entomol* 41: 197–199.
- Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel C v., Keissling Wolfgang, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334: 652–655. <https://doi.org/10.1021/nl202318u>
- Cook A (1989) 55 Moll. Stud Factors affecting prey choice and feeding technique in the carnivorous snail *Euglandina rosea ferussac*. The Malacological Society
- Coulson RN, Witter JA (1984) *Forest Entomology: Ecology and Management*. John Wiley & Sons, Inc., 191–253 pp.
- Cowie RH (1995) Variation in Species Diversity and Shell Shape in Hawaiian Land Snails: In Situ Speciation and Ecological Relationships. *Evolution* 49: 1191–1202.

- Cox G (2019) What is a 'Verifiable Observation' and how does it reach 'Research Grade'? iNaturalist.org. Available from: <https://www.inaturalist.org/posts/26549-what-is-a-verifiable-observation-and-how-does-it-reach-research-grade> (May 24, 2023).
- Davis CJ, Butler GD (1964) XVIII Introduced Enemies of the Giant African Snail, *Achatina fulica* Bowdich, in Hawaii (Pulmonata: Achatinidae).
- Dinkins BJ, Dinkins GR (2018) An Inventory of the Land Snails and Slugs (Gastropoda: Caenogastropoda and Pulmonata) of Knox County, Tennessee. *American Malacological Bulletin* 36: 1–22. <https://doi.org/10.4003/006.036.0101>
- Dyer AR, Cochran JE, Phillips JM, Layne KI, Berry ME, Kule AK (2017) Bagged Commercial Soils are an Avenue for Regional Dispersal of Weedy Plant Species. *American Midland Naturalist* 178: 275–283. <https://doi.org/10.1674/0003-0031-178.2.275>
- Ezzell C (1992) Strangers in paradise: alien species disrupt the ecology of Hawaii. *Science News* 149: 314–316. Available from: <https://www.thefreelibrary.com/Strangers+in+paradise%3a+alien+species+disrupt+the+ecology+of+Hawaii.-a012868447> (July 2, 2022).
- Feng X, Park DS, Walker C, Peterson AT, Merow C, Papeş M (2019) A checklist for maximizing reproducibility of ecological niche models. *Nature Ecology and Evolution* 3: 1382–1395. <https://doi.org/10.1038/s41559-019-0972-5>
- Frank SD, Just MG (2020) Can cities activate sleeper species and predict future forest pests? A case study of scale insects. *Insects* 11. <https://doi.org/10.3390/insects11030142>
- Gallo KP, Tarpley JD, McNab AL, Karl TR (1995a) 37 Atmospheric Research Assessment of urban heat islands: a satellite perspective.
- GBIF.Org (2023) Occurrence Download. The Global Biodiversity Information Facility. Available from: <https://doi.org/10.15468/dl.bfxtvg> (May 8, 2023).
- Gerlach J (1994) The ecology of the carnivorous snail *Euglandina rosea*. Dissertation. Wadham College Available from: <https://www.researchgate.net/publication/35233512>.
- Greenlees MJ, Harris S, White AW, Shine R (2018) The establishment and eradication of an extra-limital population of invasive cane toads. *Biological Invasions* 20: 2077–2089. <https://doi.org/10.1007/s10530-018-1681-8>
- Hadfield MG (1986) Extinction in Hawaiian Achatinelline Snails. *Malacologia* 27: 67–81.
- Hadfield MG, Miller SE, Carwile AH (1993) The Decimation of Endemic Hawaiian Tree Snails by Alien Predators'. *American Zoologist* 33: 610–622. Available from: <https://academic.oup.com/icb/article/33/6/610/2107211>.
- Holland BS, Hadfield MG (2004) Origin and diversification of the endemic Hawaiian tree snails (Achatinellidae: Achatinellinae) based on molecular evidence. *Molecular Phylogenetics and Evolution* 32: 588–600. <https://doi.org/10.1016/j.ympev.2004.01.003>
- Holland BS, Chock T, Lee A, Sugiura S (2012) Tracking behavior in the snail *Euglandina rosea*: First evidence of preference for endemic vs. Biocontrol Target pest species in Hawaii. *American Malacological Bulletin* 30: 153–157. <https://doi.org/10.4003/006.030.0113>
- iNaturalist (2023) Observations of *Euglandina rosea* from the United States. Available from: <https://www.inaturalist.org> (May 7, 2023).
- Ivanova N v., Shashkov MP (2021) The Possibilities of GBIF Data Use in Ecological Research. *Russian Journal of Ecology* 52. <https://doi.org/10.1134/S1067413621010069>
- Lenoir J, Svenning JC (2015) Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography* 38: 15–28. <https://doi.org/10.1111/ecog.00967>
- Lockwood JL, Hoopes MF, Marchetti MP (2013) *Invasion Ecology*. 2nd ed. John Wiley & Sons.
- Lowe S, Browne M, Boujelas S, De Poorter M (2004) 100 OF THE WORLD'S WORST INVASIVE ALIEN SPECIES. Available from: www.issg.org/booklet.pdf.
- Lv S, Zhang Y, Steinmann P, Zhou X-N (2008) Emerging Angiostrongyliasis in Mainland China. Available from: www.cdc.gov/eid.
- Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) Global Decline of Nonmarine Mollusks. *BioScience* 54: 321–330.
- Mahony CR, Wang T, Hamann A, Cannon AJ (2022) A global climate model ensemble for downscaled monthly climate normals over North America. *International Journal of Climatology* 42: 5871–5891. <https://doi.org/10.1002/joc.7566>

- Maldonado C, Molina CI, Zizka A, Persson C, Taylor CM, Albán J, Chilquillo E, Rønsted N, Antonelli A (2015) Estimating species diversity and distribution in the era of Big Data: To what extent can we trust public databases? *Global Ecology and Biogeography* 24: 973–984. <https://doi.org/10.1111/geb.12326>
- Irwin KL, McKinney ML, Womble S, Irwin KL (2016) First Reported Occurrence of the Invasive Land Snail *Euglandia rosea* in Tennessee: Implications for Global Warming. Knoxville Available from: <https://www.researchgate.net/publication/333759921>.
- Meyer WM, Cowie RH (2010) Feeding preferences of two predatory snails introduced to Hawaii and their conservation implications. *Malacologia* 53: 135–144. <https://doi.org/10.4002/040.053.0106>
- NOAA (2023) Global summary of the year. National Centers for Environmental Information. Available from: <https://www.ncei.noaa.gov/data/gsoy/> (May 24, 2023).
- Parmesan C, Yohe G, Andrus JE (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42. Available from: www.nature.com/nature.
- Pauchard A, Milbau A, Albiñá A, Alexander J, Burgess T, Daehler C, Englund G, Essl F, Evengård B, Greenwood GB, Haider S, Lenoir J, McDougall K, Muths E, Nuñez MA, Olofsson J, Pellissier L, Rabitsch W, Rew LJ, Robertson M, Sanders N, Kueffer C (2016) Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. *Biological Invasions* 18: 345–353. <https://doi.org/10.1007/s10530-015-1025-x>
- Perkins AT, Phillips BL, Baskett ML, Hastings A (2013) Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecology Letters* 16: 1079–1087. <https://doi.org/10.1111/ele.12136>
- Phillips SB, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259. <https://doi.org/10.1016/J.ECOLMODEL.2005.03.026>
- Planchuelo G, Catalán P, Delgado JA (2016) Gone with the wind and the stream: Dispersal in the invasive species *Ailanthus altissima*. *Acta Oecologica* 73: 31–37. <https://doi.org/10.1016/j.actao.2016.02.006>
- Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography* 41: 629–643. <https://doi.org/10.1111/jbi.12227>
- Reynolds C, Miranda NAF, Cumming GS (2015) The role of waterbirds in the dispersal of aquatic alien and invasive species. *Diversity and Distributions* 21: 744–754. <https://doi.org/10.1111/ddi.12334>
- Robinet C, Roques A (2010) Direct impacts of recent climate warming on insect populations. *Integrative Zoology* 5: 132–142. <https://doi.org/10.1111/j.1749-4877.2010.00196.x>
- Root T (1988) Environmental Factors Associated with Avian Distributional Boundaries. *Journal of Biogeography* 15: 489–505.
- Simberloff D (2013) *Invasive Species*. Oxford University Press. <https://doi.org/10.1093/wentk/9780199922017.001.0001>
- Simberloff D, Stiling P (1996) How Risky is Biological Control? *Ecology* 77: 1965–1974.
- Solem A (1990) How Many Hawaiian Land Snail Species Are Left? and What We Can Do for Them. *Bishop Museum Occasional Papers* 30: 27–40.
- USDA (2022) *Lissachatina fulica*. Available from: https://www.aphis.usda.gov/plant_health/plant_pest_info/gas/lissachatina-fulica.pdf (March 26, 2023).
- Yang L, Qian F, Song DX, Zheng KJ (2016) Research on Urban Heat-Island Effect. In: *Procedia Engineering*. Elsevier Ltd, 11–18. <https://doi.org/10.1016/j.proeng.2016.10.002>