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

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1.0 Title:

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

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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.

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4.0 Abstract:

The rosy wolfsnail (*Euglandina 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. 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 possible 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). These warmer aggregate temperatures have 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 climate-change-driven poleward shifts 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). The increasing need to predict distributional shifts and their potential impacts has therefore precipitated the use of tools such as 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 of *E. rosea*, which has become 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 detected (Gerlach 1994). These traits make *E. rosea* a uniquely effective predator.

Between the 1950s and 1970s, scientists and policymakers thought *E.* rosea's proficiency in hunting combined with their unique diet could make them a valuable biological control agent. In 1936, the giant African land snail (*Lissachatina fulica*), another 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 as potential biological control agents (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). At the same time, similar *E. rosea* invasions were unfolding elsewhere in the Pacific and Indian Oceans, facilitated by government agencies in French Polynesia, Samoa, Mauritius, and Micronesia (Lowe et al. 2004).

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 have not been intentionally introduced and 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, Tennessee (Irwin et al. 2016). The stability of this population suggests that a type of range expansion of *E. rosea* which may be facilitated by factors such as climate change, the urban heat island effect (UHI), and modern horticultural commerce. Our paper examines this potential range expansion using publicly available data sets provided by the Global Biodiversity Information Facility (GBIF). Furthermore, we document the persistence of and provide demographic data (abundance, age, size of individuals) of the 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 potential suitable habitats for *E. rosea*. We predict that *E. rosea* is expanding its range northward in the United States.

6.0 Materials and Methods:

6.1 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 found much further north than the presumed native range of this relatively thermophilic species. However, the homeowner continued to observe these snails each year from 2006 to 2009. In 2009 and 2010 the area experienced a relatively cold winter where temperatures dropped to -13 and -15 degrees Celsius respectively, and no live snails were observed thereafter. It was then inferred that the population had indeed become extirpated. However, in 2014, following a relatively warm winter where temperatures remained above -9 degrees Celsius, another live snail was found. The homeowner reported that no foreign landscaping materials had been installed on his or any adjoining property in that timeframe, which suggests that this population was able to tolerate several years of colder minimum temperatures

In 2015, coauthor Michael McKinney was contacted by TDEC to conduct more thorough and systematic surveys of the area. 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. This property is characterized by mature oak trees that shade the entire backyard, short ornamental shrubs, full-shade groundcover (e.g., English Ivy), and fescue grass. Much of the vegetation on this property is not endemic. They require more water than vegetation native to central Tennessee. A permanent irrigation system provides water to the vegetation and maintains a high level of humidity throughout the year. 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. (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 may have 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.

6.1.1 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, trees up to head height, 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).

6.2 Current Endemic Range in North America and Ecological Niche Modeling

6.2.1 Obtaining Data

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 included mostly research grade observations obtained from iNaturalist (iNaturalist.org). 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 the subject is not a captive/cultivated organism (Cox 2019). Unlike other terrestrial snails, *E. rosea* can usually be accurately identified due to their large size and distinct morphology. This study is interested in the current endemic range of *E.* rosea in the contiguous United States and potential range expansion due to predicted climate change scenarios. Historical and other curated archival records made up a negligible portion (less than 0.1%) of total downloaded records from GBIF. These records were checked for accuracy and quality and are considered reliable observations in the large majority of cases (Maldonado et al. 2015). In total, 1,879 *E. rosea* occurrence records were downloaded for use in this study on November 12th, 2023 (GBIF.org, 2023).

Current and projected climate data were acquired from the Adapt West Project (AdaptWest Project 2022), comprising 33 parameters evaluated for their relevance in predicting *E. rosea* presence on November 11th, 2023. Our ecological niche model utilized an ensembled mean of 13 projected climate simulations, CMIP6 AOGCMs SSP3-7.0, where human influence on climate is moderate (Mahony et al. 2022). This dataset used a predicted emissions scenario that is considered “middle of the road” (Mahony et al. 2022). Climate data were downloaded at a 1-kilometer resolution and covered the period from 2000 to 2040 in two 20-year increments (Mahony et al. 2022).

6.2.2 Data processing

To clean and process our *E. rosea* occurrence records, we first eliminated all duplicate records. These were records where the latitude and longitude of the record were identical. In total, 447 duplicate records were removed. Next, we plotted all points in ArcGIS Pro (version 3.0.2), investigated suspicious records by searching those locations on iNaturalist, and removed any points that were deemed unreliable. Records deemed unreliable were those misidentified or originally observed at commercial garden retailers. We assumed that *E. rosea* records observed at commercial garden retailers were likely hitchhikers. In total, only three occurrence outliers were removed due to unreliability. To ensure consistency in spatial accuracy, we then removed all data points with coordinate specificity greater than 1000 meters (Feng et al. 2019). The recorded coordinates of a data point may not necessarily correspond to its exact collection location due to differences in specificity levels. In total, 383 occurrence records were removed due to their coordinate uncertainty. Lastly, our data was spatially thinned to mitigate observation bias and account for over representation in areas of high human population. Occurrence records were thinned to 10km where no two observations could be reported withing the same area (Boria et al 2014). In total, 473 localities shared the same 10 km gridcell. After these steps had been implemented, 574 occurrence records remained for use in our ecological niche model.

All bioclimatic layers were processed in ArcGIS Pro (version 3.0.2) and R (version 4.3.2). Bioclimatic layers were projected in ArcGIS Pro to ensure that the spatial resolution and map extent was identical for all environmental variables. The layers were exported as ASCII (.asc) files with 1km resolution and map extent that includes all of North America for additional processing in R. All 33 bioclimatic layers were analyzed for their relatedness using the R-package “ENMeval” and a correlation matrix was generated using the function “raster.cor.matrix” (Kass et al. 2021). The results of this matrix allowed us to determine which variables could be disregarded because they contributed mostly redundant data to our model and could lead to overfitting. Bioclimatic variables with a correlation index greater than 0.4 were not considered for our final niche model. In total, four bioclimatic variables remained after evaluation: winter mean temperature (December – February), summer mean temperature (June – August), winter precipitation (December – February), and summer precipitation (June – August). These remaining variables were deemed most suitable as many other bioclimatic layers either depended on various combinations of other variables and were highly inter-correlated (i.e. yearly precipitation and precipitation in wettest quarter), as noted by Root (1988). We asked the model to perform a ‘jackknife’ assessment of the variables to determine variable importance. The variable ‘mean summer temperature’ was removed from the model because it had less than 2% contribution to the model.

6.2.3 Model Calibration

We employed the maximum entropy approach to perform ecological niche modeling (ENM) using MaxEnt 3.4.4 (Phillips 2006, Phillips 2017). 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 574 *E. rosea* presence records. To optimize the model's complexity and predictive power, we employed the function ‘ENMevaluate’ in the R -package ‘ENMeval’ that implemented MaxEnt across a range of settings and provided evaluation metrics to assist in selecting settings that balance model fit and predictive ability (Kass et al. 2021). To generate our final models for *E. rosea*, we used the following settings. the combination of regularization multiplier and bioclimatic variables that had the lowest omission rate and AICc. Our final model uses the following features for parameterization: linear, quadratic, product, and hinge (LPQH).

To generate the final model for *E. rosea* in current and future climate scenarios, we used the following settings. The number of iterations was set to the default (500); the number of background points was set to 10,000, replicate run type was set to 'crossvalidate'; the output type was set to 'logistic'; the feature selected was LQPH. The model was replicated 10 times for each run. Variable importance was measured using 'jackknife' test to determine dominant climatic factors. We employed a regularization multiplier of 1. By selecting 'random seed', a different random background sample was used for validating the model with each iteration. Each procedure was done with no clamping and applied the '10-percentile training presence' rule (Radosavljevic and Anderson 2014) to transform each map into binary. The resulting ENM for *E. rosea* was projected in ArcGIS. A step-by-step detailed description of our ecological niche modeling process is available in the supplemental materials.

6.2.4 Model Validation

We assessed the optimization of the model by examining the Receiver Operating Characteristic curve (AUC) and Boyce index. The AUC evaluates the model's ability to correctly rank a random background point and a random presence point, with values ranging from 0.0 to 1.0. An ideal model would have an AUC of 1.0, but relying solely on this measure is problematic because the overall extent of model application significantly impacts well-predicted absences and AUC scores (Lobo 2008). The Boyce index compares the predicted and expected number of occupied sites based on habitat suitability. Boyce index values range from -1 to 1, where positive values indicate a model consistent with the presence distribution, values near zero suggest predictions close to random, and negative values indicate predictions contrary to presence distributions (Boyce et al. 2002). Additionally, Boyce indices generate predicted-to-expected ratio curves, offering further insights into the model's quality, including robustness, habitat suitability resolution, and deviation from randomness (Herzel et al. 2006).

7.0 Results:

7.1 Current Geographical Range

The current geographical range of *E. rosea* is primarily the Southeastern United States (Figure 1). In areas where the average minimum temperature of the coldest month is less than 25 degrees, instances of *E. rosea* observations are sparser. 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).

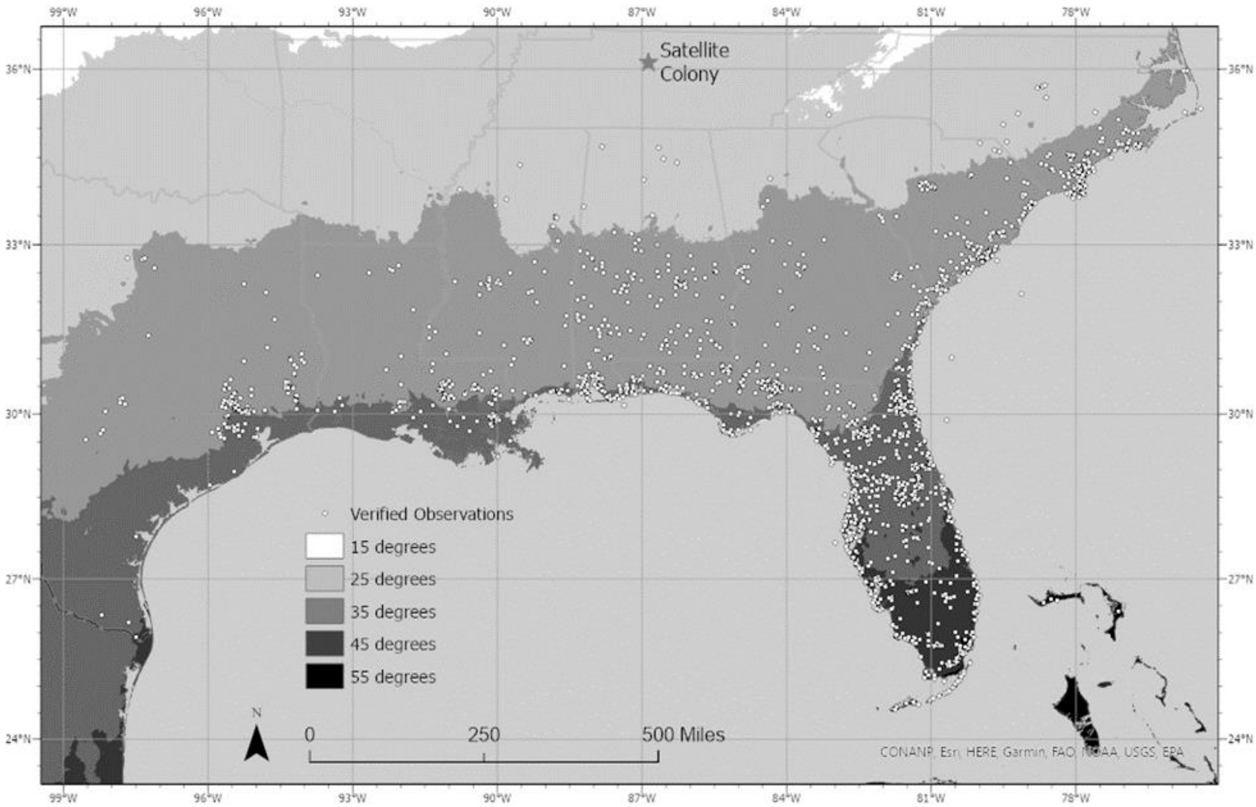

Figure 1. States encompassing the home range and verified observations of *E. rosea*, including satellite colony in Nashville, TN (GBIF.org 2023) and the average temperature during the coldest months of the year (NOAA 2023)

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, small live *E. rosea* individual was captured in the yard of the same Nashville, Tennessee 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

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early 2022. This is a significant finding because it implies that the satellite colony in Nashville, Tennessee 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. To date, no studies have investigated the thermal limits of *E. rosea*. 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 may be overwintering in smaller microhabitats where they are able to endure temperatures in regions that are below their documented tolerance levels. This is feasible due to their avoidance of direct exposure to these colder temperatures. In residential areas, potential warm microhabitats might include areas adjacent to houses emitting heat or well-insulated sites, like beneath logs, within stacks of wood, or burrowing underground. It may be possible 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

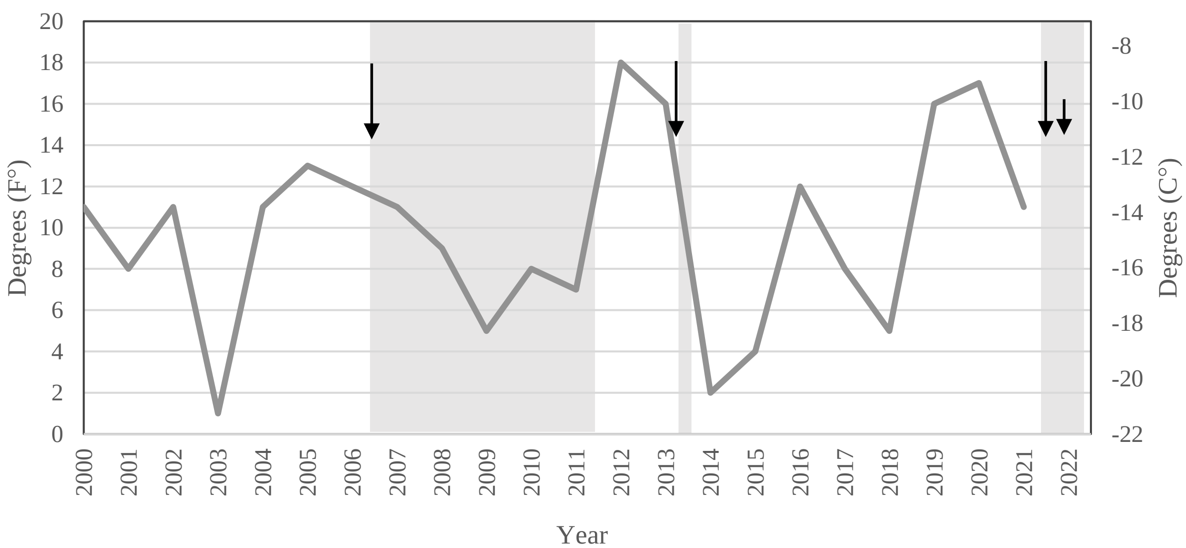

Figure 2. Lowest recorded temperature in Davidson County, Tennessee for years 2000 to 2022 (NOAA 2023). Shaded areas indicate a continuous occurrence of living *E. rosea* individuals. Vertical arrows indicate documented instances where living *E. rosea* were observed after periods of assumed extirpation (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 25% training presence, the training omission rate was 0.098 and the test omission rate was 0.105. The average test AUC for the replicate runs was 0.924, and the standard deviation was 0.008. The Boyce index value was 0.949. The omission rate, AUC, and Boyce index values all indicate that our model is calibrated well and should be considered reliable for predicting the niche of *E. rosea*. 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 mean winter temperature had the greatest contribution to the model with 49.0% contribution. Precipitation in winter and the precipitation in summer were the next largest contributors to the model with 26.1% and 25.0% respectively (Table 2).

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

Variable	*Description*	*Percent Contribution*
BIO33	Mean Winter Temperature (C°) (Dec – Feb)	49.0%
BIO27	Winter Precipitation (mm) (Dec – Feb)	26.1%
BIO26	Summer Precipitation (mm) (Jun – Aug)	25.0%

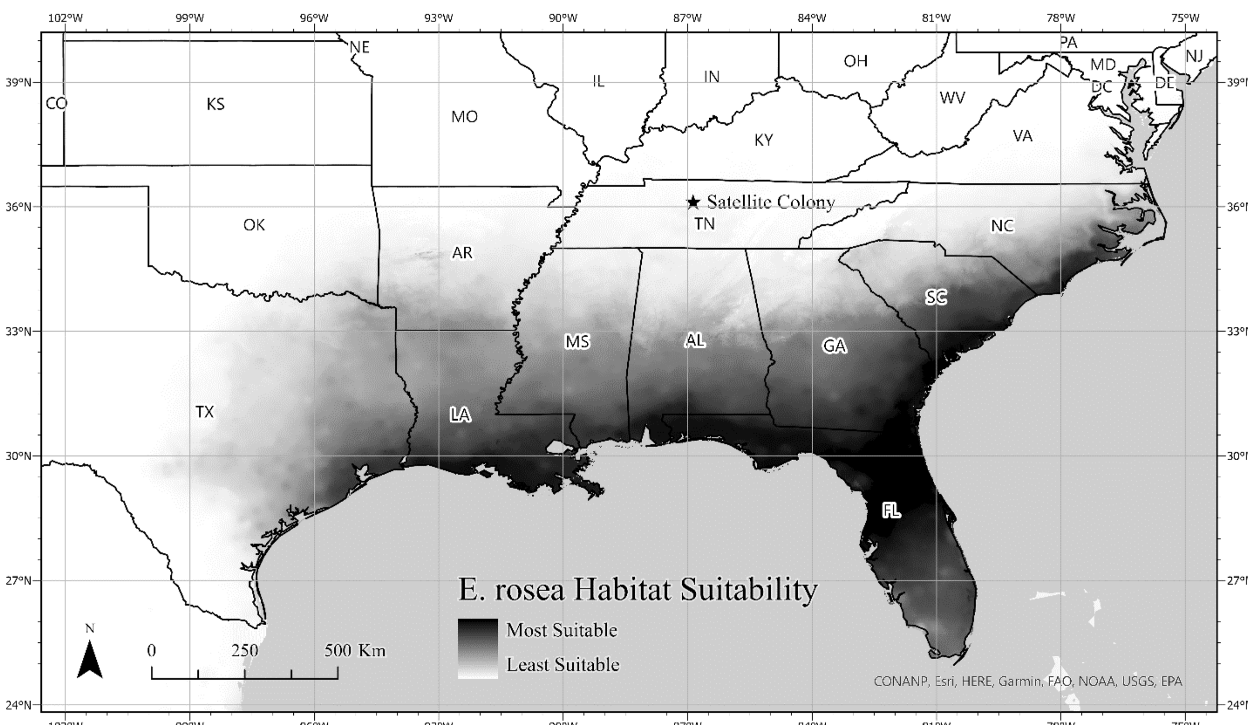

Figure 3. Current continuous map of predicted suitable habitat for *E. rosea* in the southeastern United States, raw maximum entropy output. Dark areas indicate regions of higher habitat suitability and light areas indicate regions of lower predicted suitability.

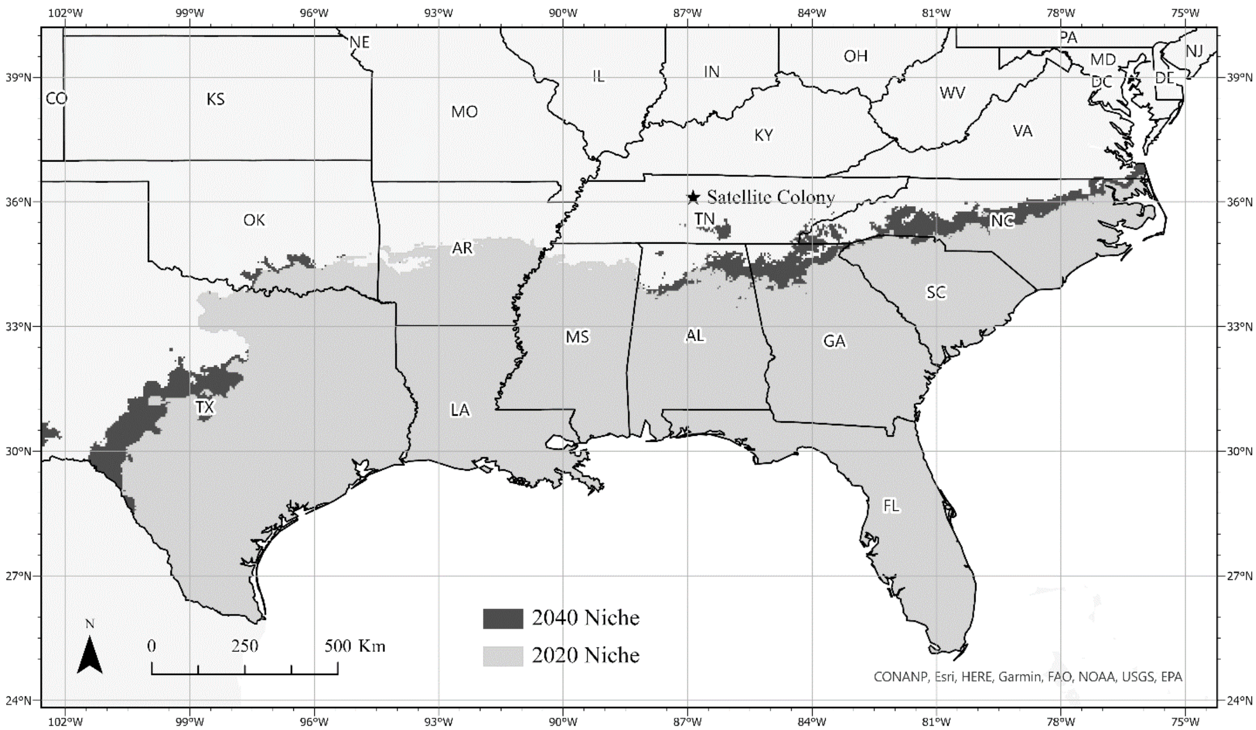

Figure 4. Binary map of predicted potential suitable habitat based on 10th percentile presence threshold. Grey indicates the predicted niche for *E. rosea* between the period 2000-2020. Black indicates the predicted niche for *E. rosea* between the period 2021-2040.

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 sampling events indicate 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. However, the region where our satellite population has become established does not appear to be one of them. We suspect that this unique satellite population in Nashville, TN will not persist indefinitely without anthropogenic influence. Meaning, human interventions such as supplemental irrigation during dryer seasons and poor home insulation may be artificially sustaining this satellite population. However, 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 beyond its current range in the next two decades which is centered on southern and coastal states of the US (Figure 1) and will begin to penetrate more deeply into Texas, Alabama, Georgia, and Virginia and isolated regions in central Tennessee (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 by its own locomotion or through natural processes such as wind, water, or carried by other animal vectors (Reynolds et al. 2015, Planchuelo et al. 2016). 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). This was especially apparent when we identified the three outliers in our occurrence records that were observed in commercial garden retailers. One was located in Lancaster Ohio, Florence Kentucky, and St. Louis Missouri. All three of these *E. rosea* specimens were likely hitchhikers.

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 findings may also be relevant to the urban heat island (UHI) effect, which allows the establishment of populations 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 the suburban environment located near a heavily commercialized part of Nashville. This is reflected in our ecological niche modeling of *E. rosea* (Figure 4) which indicates that areas within the Cumberland Plateau in Tennessee are not suitable habitats for this snail species. However, pockets of isolated populations may persist within anthropogenic microhabitats cause by human land management behaviors (Gallo et al. 1995).

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 9 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 *E. Rosea* outside of its range. 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 and possibly the urban heat island effect (UHI). Three, there may be 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 outside their normal isothermal limits in the cooler nonurban countryside where specific niche requirements are met (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]

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Competing interests

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

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