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ORIGINAL ARTICLE

Personality differences between native and invasive populations of the eastern gray squirrel

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Abstract

Invasive alien species are a major threat to global biodiversity, thus recent work has aimed to identify traits of successful invaders to better inform management efforts and predictions of future invasions. Personality and intraspecific behavioral variation are important characteristics that may mediate individuals' and species' invasion success. However, to the best of our knowledge, no study to date has looked at the personality differences between an invasive species in its native and invasive ranges. Here, we filled this gap by studying the sociality and self-grooming behavior of eastern gray squirrels (*Sciurus carolinensis*) in their native range in Northeastern USA and in their invasive range in Italy. We used the open field and mirror-image stimulation tests to assess the personality of 466 unique gray squirrels, including 271 individuals from the native population and 195 from the invasive population. We found that both the distribution and the median value of sociality significantly differed between populations, with a higher median value of sociality among invasive squirrels, while the distribution and median of self-grooming, a proxy for stress-coping ability, did not significantly differ between populations. Overall, we demonstrate that certain personality traits differ between native and invasive populations, highlighting the importance of considering intraspecific behavioral diversity for the prediction and management of invasive alien species. We urge further work to elucidate the mechanisms behind such personality differences.

Keywords Arboreal squirrel · Biological invasion · Intraspecific variation · Invasive alien species · Self-grooming · Sociality

Introduction

Biological invasions are a major driver of global change, threatening the functioning of ecosystems and causing severe economic losses (Bellard et al. 2016; Pyšek et al. 2020; Diagne et al. 2021). Invasions by alien species, or species introduced to new regions due to human activity, are steadily increasing, with the problem being exacerbated by climate change, land-use change, and increasing global connectivity and trade networks (Pyšek et al. 2020; Seebens et al. 2020; Diagne et al. 2021). This is putting pressure on biodiversity, as invasive alien species, or alien species which have harmful impacts on the economy or environment, are one of the major threats to native biological diversity (Lowe et al. 2000). The persistence of invasive alien species in a habitat can lead to the exclusion of native species through several mechanisms, including direct and indirect competition, pathogen spillover, and predation (Mazzamuto et al. 2021; Chinchio et al. 2022). While several studies have focused on the identification of life-history traits that make

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a species more likely to be a successful invader (Capellini et al. 2015; Pili et al. 2024), we have a limited understanding of whether some individuals are particularly important in mediating invasion success. Identification of individual traits that facilitate invasion can have important consequences for conservation, as it may help prioritize management efforts and predict future invasions (Pili et al. 2024).

Behavior and personality (i.e., behavioral differences between individuals maintained across time and contexts; Réale et al. 2007; Dingemanse et al. 2010; Carter et al. 2013) may play an important role in determining species' invasion success (Fogarty et al. 2011; Wolf and Weissing 2012; Carere and Gherardi 2013; Macali et al. 2024). Indeed, an "invasion syndrome", including boldness, aggression, activity, and exploration, has been hypothesized to aid individuals in all phases of the introduction process, highlighting the role of personality in affecting invasion (Sih et al. 2004; Chapple et al. 2011, 2012). Sociality may also mediate invasion success (Weis 2010; Capelle et al. 2015), as, for example, both sociality and aggression facilitated the rapid spread of the invasive round goby (*Neogobius melanostomus*) in Canada (Capelle et al. 2015). In general, the role of intraspecific behavioral variation is crucial, as it can result in differential abilities among individuals, impacting invasion success at the individual level and promoting success at the species level (Fogarty et al. 2011). Due to the pressures placed on introduced populations, only a subset of individuals are successful through each stage of the invasion process, thus increased intraspecific behavioral variation facilitates a species' invasion success (Fogarty et al. 2011; Chapple et al. 2012). Moreover, due to the filtering effect invasion has on introduced populations, these populations may differ in personality from native populations of the same species because only certain individuals are able to invade and persist (Chapple et al. 2012; Blight et al. 2017). However, it is important to consider that trait differences between native and invasive populations may be attributed to multiple mechanisms (Nota et al. 2024). Differences may be due to founder effects, where originally introduced individuals exhibited certain personalities and reduced variation, which were maintained in the invasive range, leading to differences between populations (Nota et al. 2024; Blight et al. 2017). Another possibility, however, is that habitat conditions or different competitors in the invasive range exert selective pressures that differ from those in the native range, selecting for behaviors that provide context-related advantages in the novel environment (Nota et al. 2024).

Despite difficulties in disentangling the mechanisms involved in driving personality distributions of native and invasive populations, comparing personality traits, such as boldness, exploration, and social tendency, in a species' native and invasive ranges can enhance our understanding of factors that drive species' invasion success (Chapple et al. 2012). For example, inclusion of behavioral traits has improved predictions of establishment success among birds (Sol et al. 2002; Blackburn et al. 2009), and an understanding of a population's behavioral profile can be useful for deciding on specific management methods for personalities (Merrick and Koprowski 2017; Eccard et al. 2023). However, the number of studies that have explored this question is limited (Pintor and Sih 2009; Candler et al. 2015; Blight et al. 2017). A study on cane toads (*Rhinella marina*) in their native and invasive range found lower levels of neophobia (estimated through presenting novel feeding opportunities) in the introduced population compared with the native one, suggesting a different ability to exploit novel resources among invasive individuals (Candler et al. 2015). Among signal crayfishes (*Pacifastacus leniusculus*) and ants (*Linepithema humile*), individuals in invasive populations were more aggressive and active foragers than those in native populations (Pintor and Sih 2009; Blight et al. 2017). Past studies have compared behavioral tendencies between populations, but no study, to the best of our knowledge, has used repeated behavioral assays on individuals from native and invasive populations to investigate changes in the distribution of repeatable personality traits between populations. As a consequence, past works lack the key step (assessment of repeatability) required for considering a trait as 'personality'. Comparative studies on established populations of invasive alien species in both of their ranges are fundamental to understanding which traits are related to successful introductions, to inform predictions of future invasions and apply efficient behavior-based management (Berger-Tal et al. 2011; Goldstein et al. 2015).

Tree squirrels are highly successful invasive alien species due to their ecology and ability to adapt to different habitats (Palmer et al. 2007; Bertolino 2009). They have been introduced worldwide and show high potential to establish populations (Wood et al. 2007; Bertolino 2009; Mazzamuto et al. 2021). The eastern gray squirrel (*Sciurus carolinensis*) is registered on the "100 of the World's Worst Invasive Alien Species" list (Lowe et al. 2000) with an establishment success rate of 80% (Bertolino 2009), well over the mean of 50–60% reported for many vertebrates (Jeschke and Strayer 2005). This species, native to the eastern United States and parts of Canada (Koprowski 1994), was the object of various introductions in several regions, including Europe, South Africa, and Australia (Wauters et al. 2023). Especially in Britain and Italy, gray squirrels are expanding their invasive ranges, causing local extinctions of the native squirrel species, the Eurasian red squirrel (*Sciurus vulgaris*; Bertolino 2009; Wauters et al. 2023). The gray squirrel is also a fundamental species with potentially ecosystem-level impacts due to its role as a primary seed predator and disperser of large-seeded tree species, such as oaks (*Quercus*; Barnett 1977; Steele 2021).

In this study, we used eastern gray squirrels as a model system to fill the gap in knowledge about the potential differences in personality between native and invasive populations. We compared the distribution of repeatable personality traits within gray squirrel populations from their native North American range and from their invasive range in Italy. Although the native populations we sampled are not necessarily the ones from which the invasive Italian populations originated, we compared squirrels across multiple study sites in both their native (across four states in the USA) and invasive range. We provide a first step toward increasing our knowledge of personality in native and invasive populations and laying the foundation for future studies aimed at understanding the mechanisms behind invasive populations' personality differences. Specifically, we assessed how gray squirrels in invasive versus native populations differed in the entire distribution of their (1) behaviors towards conspecifics, including sociality and aggression in a mirror-image stimulation test, and (2) in their stress-coping ability, measured here as self-grooming behavior in an open-field test, which in rodents is often considered a measure of sensitivity to stress (Estanislau et al. 2019; Andronikashvili et al. 2024; although other meanings of this behavior have been theorized; Bursten et al. 2000). We expected to see differences in the distribution of personality between the two populations, as sociality might play a role in facilitating rapidly growing populations (Capelle et al. 2015), aggression could allow individuals to outcompete native species (Weis 2010), and stress-coping may facilitate invasive animals' reaction to novel habitats.

Materials and methods

To compare gray squirrels' personality distributions between populations in their native and invasive ranges, we used data collected as part of two separate studies (Tranquillo et al. 2024; Merz et al. 2025) with different aims, conducted in the Northeastern USA in 2020–2023 and in Italy from 2015 to 2021. These studies used similar methods for quantifying personality among gray squirrels, facilitating the comparisons and analyses we conduct here. Below, we detail methods of squirrel trapping and behavioral assessments from both studies, highlighting the similarities as well as important methodological differences, which we address.

Study areas

We trapped squirrels throughout their native range in Northeastern USA, including in the states of Rhode Island, Massachusetts, New Hampshire, and Maine (Fig. 1). Most USA sites were in suburban or urban areas, often on university or high school campuses or in urban parks, thus in wooded habitats with some open grassy areas (Table S1). One site in Maine was in a rural, fully wooded area. All sites were dominated by temperate broadleaf and mixed forests. Study sites in Italy were established in Piedmont and Lombardy in Northern Italy (Fig. 1), where the gray squirrel, first introduced in 1948, is an invasive alien species. All sites in the invasive range were in woodland or park-like habitats, including two urban parks and five more natural sites (Table S1). Italian sites were all dominated by mature seed-bearing trees.

Squirrel trapping and behavioral testing

Data from USA sites was collected from 2020 to 2023, whereas at Italian sites, it was collected from 2015 to 2021. We trapped all gray squirrels using Tomahawk live traps (models 202.5 & 102XL; Tomahawk Live Trap Co., WI, USA). We baited traps with peanut butter at the USA sites, while at the Italian sites we baited traps with walnuts and hazelnuts and conducted a pre-baiting period followed by a trapping session. Trapping was conducted between the months of June and November from 2020 to 2023 in the USA. In Italy, trapping was conducted between December 2015 and April 2016 at one site, between November 2016 and January 2017 and between October 2020 and December 2020 at another site, and between May 2020 and October 2021 at all other sites. Traps were set in the morning and checked periodically throughout the day.

The methods adopted in both study areas to quantify personality were similar, but not identical, therefore we carefully selected behavioral variables that would make the data as comparable as possible. Upon capture, all squirrels went through behavioral testing including an open field test to measure activity and stress-coping in a novel environment (Fernández-Teruel and Estanislau 2016; Mazzamuto et al. 2019; Gharnit et al. 2020; Fig. 1) and a mirror-image stimulation test to measure sociality and aggression (Svendsen and Armitage 1973; Mazzamuto et al. 2019; Fig. 1). For squirrels captured at sites in the USA, we transferred captured squirrels into a clean 79 × 79 × 90 cm white arena with a clear plexiglass top and recorded squirrel behavior from above for a 5-minute open field test. Then, we revealed a mirror by sliding back one side of the arena and we recorded animals for another 2.5-minute mirror-image stimulation test. For squirrels captured in Italy, we transferred individuals into a 51 × 51 × 51 cm white polycarbonate box for the open field test and recorded their behavior from above for 4 min with a camera fitted into a hole in the lid of the arena. We then removed a sliding panel from one wall of the arena,

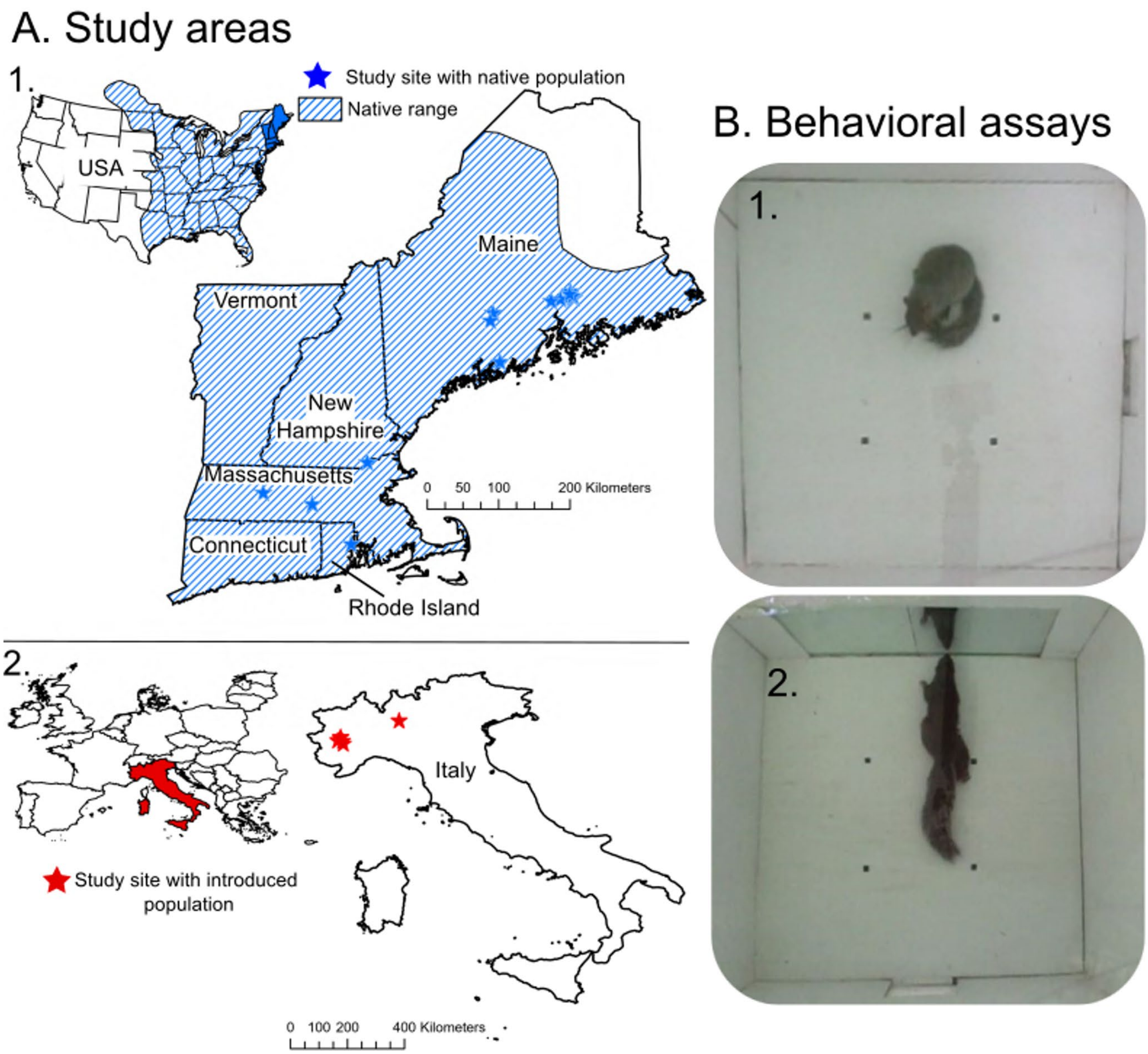

Fig. 1 We compared the distribution of personality traits between native versus invasive populations of eastern gray squirrels (*Sciurus carolinensis*). **A**.) We trapped gray squirrels (1) within their native range throughout the Northeastern USA, the inset map of the USA shows the extent of the gray squirrel native range in blue hatch (IUCN and NatureServe 2008). Blue stars represent study sites within the native range of the gray squirrel. We also trapped squirrels from (2) invasive populations in Northern Italy. Red stars represent study sites within squirrels' invasive range. **B**.) We tested the personality of gray squirrels, quantifying their (1) stress-coping ability by the proportion of time they spent grooming in the open field test and (2) their sociality by the proportion of time they spent socially interacting with the mirror in the mirror-image stimulation test. Credit for gray squirrel range map: IUCN and NatureServe 2008

revealing a mirror, and recorded a 3-minute mirror-image stimulation test. Behavioral assays were repeated during different trapping sessions to obtain multiple measures for the same individual. Invasive gray squirrels in Italy were euthanized by CO_2 inhalation during a final and separate trapping session, after personality test execution and initial release back into the wild for use in ongoing experiments, as indicated by Italian legislation on invasive alien species. Euthanasia followed EC and AVMA guidelines (Close et al. 1996; Leary et al. 2020). All squirrel capture, handling, and arena tests followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

We weighed squirrels and recorded data on sex and reproductive status of all captures. We also marked each animal with a numbered metal ear tag (National Band and Tag Co., Newport, Kentucky) for individual identification. Handling and marking was performed before personality testing at sites in Italy and after behavioral testing at USA sites. This difference presents a significant divergence between methods conducted in the two ranges with potential impacts on behavioral testing, as animals tagged before testing may have increased stress and reactivity (see the limitations section of the Discussion for a full discussion of this potential issue). This variation was unavoidable, thus while we have confidence in the overall trends we identify, our results may be biased due to these different handling procedures (see also the Discussion section).

Following data collection in the field, recordings of behavioral assays were analyzed to quantify behavioral traits. Due to the size difference between the arenas used and the different lengths of the tests at our different field sites, there were certain traits related to activity and exploration in the open field that we could not compare. We elected to utilize proportional variables, as they account for the difference in the length of the tests. We chose three behavioral traits that were most comparable between the two testing arenas, including the proportion of time a squirrel spent grooming itself in the open field test, a measure we interpreted as indicative of stress-coping ability (Fernández-Teruel and Estanislau 2016), the proportion of time a squirrel spent interacting with the mirror non-aggressively (i.e., sniffing or touching the mirror in a non-aggressive stance), a measure of sociality (Mazzamuto et al. 2019), and the proportion of time a squirrel spent attacking the mirror (i.e., lunging at the mirror) during the mirror-image stimulation test, a measure of aggressiveness (Mazzamuto et al. 2019). Accordingly, an observer recorded the amount of time squirrels spent in each behavior using the software ANY-maze© (version 5.1; Stoelting CO, USA) for videos recorded in the USA and the software CowLog 3.0.2 (Hänninen and Pastell 2009) for videos recorded in Italy.

Behavioral and statistical analysis

Among all the mirror-image stimulation tests we conducted, we only recorded two aggressive events among native squirrels and one among invasive squirrels. Therefore, aggressive behavior was not considered for further analyses. We ran a repeatability analysis to determine whether the other two behavioral traits we quantified could be considered as personality traits. We calculated the adjusted repeatability, or the amount of among-individual variance in the data (Dingemanse and Dochtermann 2013), of each trait and considered them as animal personality if the 95% confidence interval on the repeatability estimate did not overlap zero (Nakagawa and Schielzeth 2010). For the repeatability estimates, we included data from squirrels caught in all years and at all sites, including those which were only caught once as it is generally advised not to remove these individuals from analyses (Martin et al. 2011), strengthening our statistical power to detect significantly repeatable traits. We used a Box-Cox transformation (Box and Cox 1964) on the behavioral data to approach normality. We included squirrel sex (categorical variable with two levels), squirrel body mass (centered and scaled; covariate), testing month (modeled as a second-order polynomial to consider a possible nonlinear effects) to account for seasonality, site of capture (categorical variable with 19 levels; Table S1), to account for population differences within the native and invasive ranges, and a binomial variable describing whether the test was an individual's first or not, to account for habituation (Dingemanse et al. 2012), as fixed effects. Individual squirrel ID was included as a random effect. We used the 'rptR' package (Stoffel et al. 2017) in R (version 4.4.0, R Core Team 2024) to run the repeatability models.

We also calculated the mean BLUP (best linear unbiased prediction) value over 1,000 simulations using the 'arm' package (Gelman and Su 2018) for each trait. We used a linear mixed effect model including the same fixed effects we included in our repeatability models (squirrel sex, body mass, testing month, site of capture, and whether an observation was from an individual's first test or not) to obtain one personality value (BLUP) for each squirrel for each trait (Dingemanse et al. 2020; Vandal et al. 2024). It was necessary to get one behavioral measure per individual squirrel per trait to account for repeated observations of individuals in our analysis comparing the personality distributions between the two squirrel populations. Thus, we used the mean BLUP value, versus simply one calculated BLUP value, because it obtains this unique value for each squirrel necessary for further analyses while accounting for variability in the behavioral measurements of individuals and minimizing possible bias (Martin and Réale 2008; Peignier et al. 2023). This method addresses concerns that the use of BLUPs does not account for uncertainty (Hadfield et al. 2010; Houslay and Wilson 2017), as averaging across many simulations results in less precise estimates but reduces bias (Dingemanse et al. 2020). Further mentions of personality refer to this mean BLUP value.

We checked model residuals from the linear mixed effects models used to calculate our BLUPs and these residuals indicated that our data does not conform to assumptions of normality. Trying multiple types of transformations, the Box-Cox transformation most improved the distribution of our data (Box and Cox 1964), although it was not possible to fully reach normality. Thus, we moved forward using the Box-Cox transformation for the BLUP and repeatability models, but we acknowledge that this violation of the normality assumption may influence our results. Therefore, we checked correlations between calculated BLUP values and raw personality data finding high values ($r = 0.62$ for grooming and $r = 0.67$ for sociality, $p < 0.05$ in both cases), indicating the reliability of the BLUP values as measures of individual personalities. We are unable to check the reliability of our repeatability estimates in this way; thus, we discuss this limitation in the discussion. We emphasize that repeatability analyses were used only to determine whether behavioral data could be considered personality or not, and all following results and conclusions remain the same regardless of our repeatability estimates.

We used two methods to assess whether the distribution of personality traits differed between the native and the invasive populations. We conducted both analyses using the mean BLUP values per individual as personality variables, including only one observation per individual in each analysis because these tests were unable to account for repeated measurements. Additionally, since BLUP values were calculated from linear mixed effect models including fixed effects, the personality variables included in our analyses accounted for variation in these factors. First, we performed non-parametric Kruskal-Wallis tests (Brehm et al. 2019) in R, comparing the mean rank values of personality traits for each of the two populations and testing the null hypothesis that the population distributions are identical. Additionally, we calculated the phenotypic distance between the populations with the non-parametric Δp test (Brehm et al. 2019) using the MATLAB software (The MathWorks Inc. 2022). This method calculates a non-parametric distance measure based on a joint cumulative distribution function, with higher absolute Δp values corresponding to greater distance, but values may be either positive or negative depending on which population has the larger median for the trait of interest (Safran et al. 2012).

Results

Behavioral analysis

We caught and measured the behavior of 466 unique gray squirrels, including 271 (F = 142; M = 129; 311 observations) from the native population remeasured an average of 1.15 times (range: 1–5) and 195 (F = 103; M = 92; 312 observations) from the invasive population remeasured an average of 1.6 times (range: 1–4). Squirrels in the native range were from 12 populations with an average of 23 squirrels tested per population (range: 1–129) and squirrels in the invasive range were from 7 populations with an average of 28 squirrels tested per population (range: 15–52).

Both stress-coping ability, or proportion of time spent grooming ($R = 0.314$ [0.17, 0.44]), and sociality, or proportion of time spent socially interacting with the mirror ($R = 0.414$ [0.28, 0.53]), were significantly repeatable (Table 1). For the grooming variable, 30% of the variance was explained by squirrel ID and 29% by the fixed effects, while for sociality, 41% of the variance was explained by squirrel ID and 8% was explained by the fixed effects.

Personality distributions

The mean rank value for stress-coping ability (i.e., grooming) was not significantly different between the two populations (Kruskal-Wallis $\chi^2 = 0.07$, $p = 0.80$). In contrast, the mean rank value of sociality did significantly differ between native and invasive gray squirrel populations (Kruskal-Wallis $\chi^2 = 9.67$, $p = 0.002$), with a higher median value of sociality among invasive squirrels.

Additionally, the distribution of stress-coping ability did not differ between the two populations (Δp = -4.97, $p = 0.29$; Fig. 2), but distributions of sociality among native squirrels versus among invasive squirrels were significantly different (Δp = -15.20, $p < 0.001$; Fig. 2).

Discussion

Through a large-scale field experiment conducted in both the USA and Italy, we highlight personality differences between native and invasive populations of the eastern gray squirrel. Specifically, there was a different distribution of sociality values among invasive squirrels compared to the distribution among native squirrels, and there was a higher

Table 1 Adjusted repeatability estimates for two personality traits and 95% confidence intervals (CI) calculated for gray squirrels from all years and sites, including both native and invasive populations. The mean proportion of time squirrels spent in each behavior are displayed, as well as the range of proportions of time spent in each behavior across all squirrels

Behavioral Variable	Behavioral test	Mean	Range	Repeatability (standard error)	95% CI	Observations	Individuals
Proportion time grooming	Open field test	0.028	0–0.56	Random effect: 0.30 (0.074)	[0.16, 0.45]	613	459
				Fixed effects: 0.29 (0.052)	[0.23, 0.44]		
Proportion time social	Mirror-image stimulation test	0.02	0–0.995	Random effect: 0.41 (0.067)	[0.27, 0.53]	613	459
				Fixed effects: 0.085 (0.03)	[0.08, 0.19]		

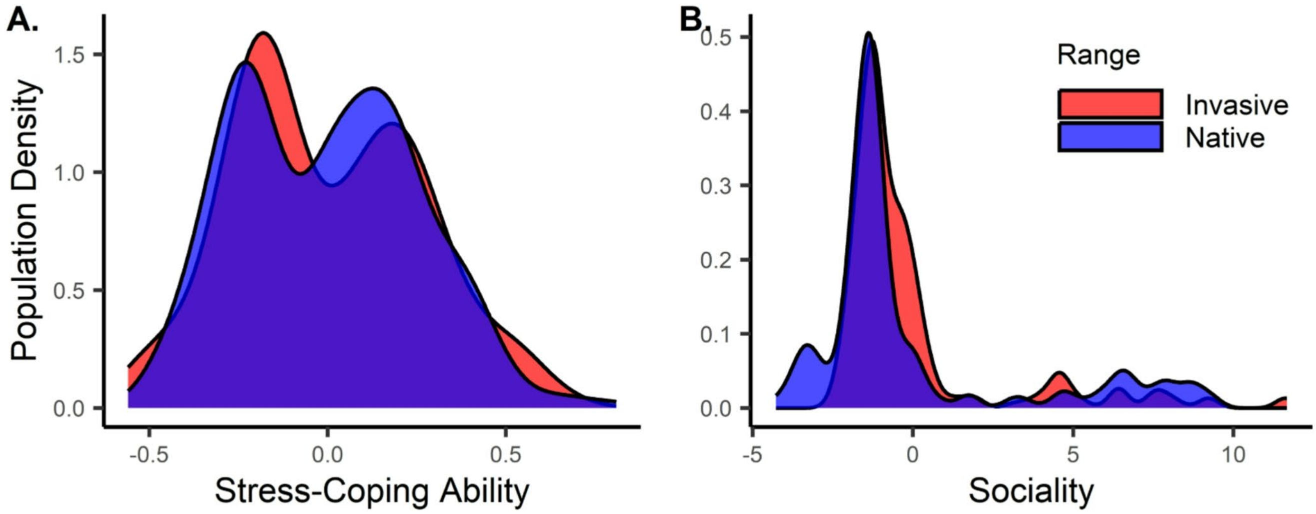

Fig. 2 Probability density plots of (**A**) stress-coping ability and (**B**) sociality of gray squirrels in native and invasive populations. Best linear unbiased predictions (BLUPs; Dingemanse et al. 2020) are plotted on the x-axis as our personality variables. The distribution of stress-coping ability is not significantly different between the two populations, but the distribution of sociality significantly differed, and the median value of sociality is higher among invasive squirrels

median value of sociality, indicating that there were more squirrels that behaved more socially with the mirror in the invasive than in the native populations. However, the distribution of stress-coping ability, or time spent self-grooming in the open-field test, did not differ between populations. We emphasize the need to consider intraspecific variation when making predictions about the invasion risk and potential impacts of a species in new environments.

Differences in sociality between native and invasive populations

The median value for sociality, scored as the proportion of time squirrels spent interacting socially with a mirror, was higher among invasive squirrels (Fig. 2). Gray squirrels have a complex social system, often exhibiting extensive home range overlap and minimal territoriality, but with individuals able to exhibit dominance over others (Koprowski 1994; Gurnell et al. 2001). Here, we interpret social interactions with the mirror in the mirror-image stimulation test as indicating sociality towards conspecifics (Mazzamuto et al. 2019; Wauters et al. 2019), but further research is needed to validate how measures of sociality in this test correlate with social behavior and tendency in free-living squirrels.

Evidence indicates that sociality may be an important trait mediating squirrels' success in novel habitats. Specifically, gray squirrels in urban environments are more social than those in suburban areas (measured in a mirror-image stimulation test; Tranquillo et al. 2024). Thus, squirrels in both introduced ranges and novel urban environments show enhanced sociality, suggesting the importance of this trait for squirrels' persistence in novel habitats. Additionally, due to parasite release (Romeo et al. 2014) and the tendency of invasive populations to spread, invasive populations grow quickly and often face high densities which may favor social individuals (Chapple et al. 2012; Capelle et al. 2015). Invasive gray squirrels' capacity to spread was indicated by a study in Northern Italy which found a slightly higher fecundity in the invasive population than in native populations (Santicchia et al. 2015) and by a study in central Italy (Umbria), which found high reproductive success among invasive squirrels (Maranesi et al. 2020). Although gray squirrel aggressiveness increases with competition (Parker and Nilon 2008), it is unknown how sociality may correlate with competition. High competition and reproduction may contribute to the increased sociality of invasive populations, but more research should investigate the link between sociality and competition.

Squirrel sociality also mediates their selection and consumption of food, with social squirrels (measured in a mirror-image stimulation test) more likely to eat novel seeds (Merz et al. 2025). Since sociality varies among introduced and native populations and has consequences for squirrel novel seed consumption, squirrel's role in the seed dispersal process in introduced regions may be different than in their native range. To predict the impact of this invasive species in their introduced regions, we must consider both the impacts of invasion on the personality composition of the population and the consequences of personality on individuals' roles in the ecosystem. Overall, sociality is a complex trait which may mediate squirrels' reaction to novelty, enhancing their success in novel habitats. Consequently, we emphasize the need to consider individual differences and traits such as sociality when predicting invasive species' success and impacts in new regions.

Consistency in stress-coping ability across populations

In contrast to sociality, gray squirrels' time spent grooming did not vary between native and invasive populations (Fig. 2). Here, we interpreted self-grooming as an indication of stress-coping ability (Fernández-Teruel and Estanislau 2016; Estanislau et al. 2019; Andronikashvili et al. 2024). However, other interpretations of self-grooming have been suggested (Bursten et al. 2000) and the role of self-grooming in rodents remains debated. Future work determining the role of self-grooming among gray squirrels would allow for further and more specific interpretations of our results.

Gray squirrels are highly successful invaders, well-adapted to thrive in a variety of habitats (Palmer et al. 2007; Bertolino 2009), suggesting that invasive populations may not need to adapt their stress-coping ability to be successful. Similarly, gray squirrels in rural and urban habitats in both native and non-native environments had overall comparable cognitive performances, suggesting a preadaptation that allows squirrels to perform well in different environments (Chow et al. 2021). Thus, gray squirrels may be preadapted to cope with the challenges of novel environments. In fact, gray squirrels in the same invasive population as we studied here exhibited no difference in fecal glucocorticoid metabolite levels, an integrated measure of individuals' stress, along an urbanization gradient (Santicchia et al. 2024). Our results complement those findings, with both suggesting that gray squirrels have a preadaptation for an enhanced ability to cope with stress and novel environmental challenges (Hufbauer et al. 2012; Santicchia et al. 2024). Additionally or alternatively, various personality traits may be advantageous at different stages of the invasion process, thus our results from a long-established invasive population (> 10 years) does not mean that there was no variation in stress-coping ability at earlier invasion stages (e.g., transportation or establishment stages; Chapple et al. 2012; Nota et al. 2024).

In summary, our results suggest that certain personality traits vary between native and invasive populations while others do not, highlighting the need for further research to understand the mechanisms behind such differences (Nota et al. 2024).

Mechanisms of personality variation among populations

We provide evidence that invasive and native populations vary in their degree of sociality, but we cannot differentiate between potential mechanisms for this variation. Individuals originally introduced into the invasive range may have exhibited higher levels of sociality and reduced variation, indicating a founder effect, or habitat and environmental pressures in the invasive range may have selected for sociality if it provides a context-related advantage in the novel environment (Blight et al. 2017). Hence, we advocate studies measuring both fitness components (e.g. survival, reproductive success) and personality traits, and investigating their correlations to elucidate whether differences in personality are conveying fitness advantages within specific habitats (e.g. Santicchia et al. 2018; Wauters et al. 2019). Furthermore, comparing the personality distributions of squirrels across other invasive populations in distinct habitats and at different stages of the invasion process would help elucidate the mechanisms behind our results and test the adaptive flexibility hypothesis, which states that behavioral diversity is high during the initial stages of introduction and then declines during establishment due to social learning of successful behaviors (Wright et al. 2010). Overall, we encourage further work into the drivers of behavioral variation among invasive and native squirrel populations.

Limitations

Although this work was the result of combining data from two different studies (Tranquillo et al. 2024; Merz et al. 2025), and thus some methods were not the same, we strived to focus on the most comparable traits. Some differences were unavoidable, however, such as the fact that squirrels in our two study sites underwent a different order of handling and marking versus behavioral testing, with squirrels in the invasive population being handled before behavioral assays. However, steps were taken to reduce the stress of handling invasive individuals, including using a cloth handling bag to weigh and mark them, not directly handling them, and ensuring that all manipulation lasted less than five minutes. Additionally, squirrels in both populations experienced some degree of manipulation before testing, as trapping and transporting squirrels in traps necessitates human interaction and stress. Thus, we are confident that squirrels underwent similar enough experiences prior to and during open field tests, reducing potential bias in behavioral measures due to different handling procedures. This is also supported by the fact that we did not observe any significant difference in self-grooming between populations (Fig. 2). Squirrels in the two populations were also tested in arenas of different sizes, and although we eliminated behavioral traits that are directly affected by arena size (i.e., mean speed, distance travelled), it is possible that stress-coping behaviors may be affected by arena size. Further research is needed to determine if arena size impacts stress-coping behaviors in gray squirrels, but the arenas used here were both sufficiently large to allow squirrel movement and exploration and were similar in novelty to squirrels, thus they both served as efficient open-field test arenas and allowed comparison among behaviors such as stress-coping (Savazza et al. 2025).

Additionally, the behavioral data we collected on both grooming and sociality of gray squirrels were not normally distributed and we were unable to reach normality even after data transformations. Thus, we suggest caution when interpreting our repeatability estimates as those models rely on the assumption of normality. We used the significant repeatability estimates as evidence that grooming and sociality behaviors could be considered personality traits. However, since these repeatability estimates may be influenced by the violation of the normality assumption, we acknowledge that those behaviors may not be true personality traits. Even if this were the case, however, grooming and sociality would still be important behavioral traits, and our results still indicate that the amount of social behavior exhibited among squirrels in invasive populations versus those in the native population differs.

Lastly, some unmeasured factors of the habitats in which squirrels were living in this study, such as predation pressure, population density, or food availability, could have potential confounding effects (Mortelliti and Brehm 2020; Bucklaew and Dochtermann 2021; Tranquillo et al. 2023). We accounted for site differences within populations by including site of capture as a fixed effect in our repeatability and BLUP calculations. However, there is still the potential that our native and invasive sites varied in some factor we did not measure, which may have affected personality.

Implications and conclusions

We contributed to current research identifying traits of successful invaders to better inform predictions of biological invasions and their impacts. We show that sociality distributions differed between native and invasive populations of eastern gray squirrels and that median values of sociality were higher among invasive squirrels. This is timely and important work because changing climate conditions are expected to promote further spread of gray squirrels (Di Febbraro et al. 2013). Additionally, increasing urbanization (United Nations, 2022) may facilitate their invasion, in part because urban squirrels tend to be more social (Tranquillo et al. 2024), and we found that successful invasive populations also tend to be more social. We add to research recording changes in personality distributions following anthropogenic disturbances such as urbanization (Miranda et al. 2013; Dammhahn et al. 2020) and forest management (Brehm et al. 2019) by documenting the difference in personality after a human-caused biological invasion. We highlight the need to consider the consequences of behavioral compositional changes on ecosystem services to predict invasive species' impacts. Personality has consequences for individuals' roles in ecosystem functioning (Hunter et al. 2022; Mortelliti 2023), specifically altering gray squirrel's seed caching behavior (Merz et al. 2025). Hence, to fully predict invasive alien species' impacts in introduced regions, we must integrate the altered personality distribution of invasive populations with the impact of those personality traits on individuals' roles in the ecosystem. Overall, we urge continued research looking at the mechanisms behind personality differences between invasive and native populations and the incorporation of intraspecific behavioral variation in predictions and management of invasive alien species.

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Author contributions All authors contributed to the study conception, design, and data collection. Analyses were performed by Margaret R. Merz. The first draft of the manuscript was written by Margaret R. Merz and Claudia Tranquillo. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability All data and code needed to replicate analyses are deposited on Figshare: https://figshare.com/s/74ed90647f9dd27e6bd1.

Declarations

Ethical approval USA-based research was approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC numbers A2015_11_02, A2018_11_01 and A2021-12-01). Legal requirements according to the Italian Wildlife Protection and Hunting Law (L.N. 157 from 1992) and fieldwork was approved by authorization decrees n. 294-34626 of 12 September 2014 from the Provincia di Torino and authorizations n. 62-3025 of 20 March 2017, n. 1015 of 20 March 2020 from Città Metropolitana di Torino, and by authorization decrees n. 1938 of 18 February 2020 from Direzione Generale Agricoltura, Alimentazione E Sistemi Verdi, Regione Lombardia.

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

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