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RESEARCH ARTICLE

Assessing the context-dependence of invasiveness in the Italian wall lizard (*Podarcis siculus*)

Roberto Sacchi[1] | Stefano Scali[2] | Marco Mangiacotti[1] | Federico Storniolo[1] | Martino Flego[1] | Marco A. L. Zuffi[3]

[1]Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, via Taramelli 24, 27100 Pavia, Italy

[2]Museo di Storia Naturale di Milano, Corso Venezia 55, 20121, Milano, Italy

[3]Museo di Storia Naturale, Università di Pisa, Via Roma 79, Calci, 56011, Italy

Correspondence
Roberto Sacchi, Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia via Taramelli 24, 27100 Pavia, Italy.
Email: roberto.sacchi@unipv.it

Abstract

The number of alien species has increased significantly in recent decades, but only a few become invasive, posing threats to biodiversity and human activities. However, the invasive potential of alien species might depend on environmental compatibility and local conditions. The Italian wall lizard (*Podarcis siculus*) has been introduced across Europe, North Africa, and North America, and its actual invasiveness varies by location. Detrimental impacts have been observed mainly on congeneric species, often due to competition or habitat overlap. Nevertheless, in some regions, including the United States, no evidence for spread and impact has been reported. On Gorgona Island, Italy, the Italian wall lizard was likely introduced accidentally around 2000 and has rapidly expanded. This study examined the colonization of the Italian wall lizard on Gorgona Island and its interaction with the native common wall lizard (*P. muralis*). Findings indicate the Italian wall lizard thrives in human-altered habitats, while the common wall lizard persists in natural areas. The spread of the Italian wall lizard appears to be driven by environmental conditions rather than inherent aggressiveness, aligning with patterns observed on other Mediterranean islands. Its expansion stalled between 2021 and 2024, suggesting habitat saturation, not competition, limits spread. The study warns against labeling the Italian wall lizard as uniformly invasive, advocating context-specific assessments to avoid misdirecting conservation resources.

KEYWORDS

alien species, interaction with native species, invasive species, multispecies modeling, *Podarcis siculus*

The number of alien species has grown rapidly during the last 2 decades and is expected to continue to do so in the near future (Seebens et al. 2018). However, only a small fraction of these species establishes, becomes widespread, and eventually has a significant impact on local biodiversity and human activities (Kolar and Lodge 2001, Keller et al. 2011). It is therefore crucial to understand the patterns of colonization and the factors promoting the transition of alien species towards the invasive level, possibly under a common framework (Blackburn et al. 2011). According to the categorization scheme for invasive species proposed by Blackburn et al. (2011), established alien species may either be able to survive and reproduce without significantly spreading far from the original point of introduction (category D), or they may become a fully invasive species, capable of surviving and reproducing "at multiple sites across a greater or lesser spectrum of habitats" (category E).

The 2-level classification of non-native species as fully invasive (E) versus established and non-invasive (D) is overly simplistic, as alien species might behave differently based on the physical and ecological characteristics of their introduction sites. For example, species might have a long establishment phase before rapid spreading, which does not necessarily occur equally in all introduced populations (Crooks 2005, Falaschi et al. 2018, Oskyrko et al. 2022*a*). Indeed, it is possible that only a small portion of alien species can be considered invasive *per se*, where the transition from category D to E is highly probable anytime the alien species establishes in a new area and occurs irrespective of the local conditions. Rather, most alien species that become invasive do so thanks to the compatibility between their own ecological characteristics (life-history traits) and those of the introduction sites. Still referring to the Blackburn et al. (2011) framework, 2 alternative scenarios should be acknowledged within category E: E1 would represent alien species that are fully invasive depending on the local context, and E2 would represent alien species that are fully invasive and able to spread irrespective of the local context.

The challenge of categorizing invasive species is deeply intertwined with practical management protocols and established risk assessment tools (e.g., the Generic Non-indigenous Risk Assessment Guidelines [GNRAG] or the Environmental Impact Classification for Alien Taxa [EICAT]; World Organisation for Animal Health 2012, Hawkins et al. 2015). While these protocols inherently attempt to integrate site-specific considerations to produce actionable information for wildlife managers, the binary nature of high-risk versus low-risk outputs often necessitates further empirical data, especially for species that display variable invasiveness across their introduced range.

Labeling an alien species as fully invasive (or established) is not just a theoretical matter, but it immediately influences the management of the usually limited resources available for biodiversity conservation. Considering an alien species as fully invasive may lead stakeholders to allocate part of such resources to its management and containment, thereby diverting them from other important conservation actions or from the management of more impactful invasive species.

The Italian wall lizard (*Podarcis siculus*) is a small-bodied (snout-vent length up to 90 mm), diurnal, heliothermic lacertid, endemic to the Italian peninsula, Sicily, and the east coast of the Adriatic Sea (Corti et al. 2011). The species has several established populations within and outside of its native range in Italy (i.e., Northern Italy, Sardinia, Corsica, and the Tuscan, Aeolian, and Dalmatian Archipelagos; Corti et al. 2011, Ficetola et al. 2021, Zuffi et al. 2022). It is also present in other European countries (Spain, Portugal, France, United Kingdom, Switzerland, Romania, Croatia, Greece, Turkey, Russian Federation, Azerbaijan; Corti et al. 2011, Schulte and Gebhart 2011, Schulte et al. 2012, Sillero et al. 2014, Oskyrko et al. 2022*b*), North Africa (Libya and Tunisia; Arnold and Ovenden 2002), and North America (United States and Canada; Silva-Rocha et al. 2012, Kolbe et al. 2013, Clemens and Allain 2021). Introduction pathways are multiple, ranging from the transportation of materials and goods (Zuffi et al. 2022), including olive trees for gardening (Valdeón et al. 2010, Schulte and Gebhart 2011, Tuniyev et al. 2020), to the pet trade industry from which individuals escaped or were released (Ferner 2004, Kolbe et al. 2013), to involuntary (Briggler et al. 2015) or voluntary releases (Burke 2010) that probably started many years ago, thanks to commerce and human migrations.

The Italian wall lizard is often labeled as invasive and commonly reported as a notorious example of a successful colonizer that has invaded numerous habitats outside its natural distribution range (Herrel et al. 2008, Silva-Rocha et al. 2012, Kapsalas et al. 2016, D'Amico et al. 2018, Damas-Moreira et al. 2019, Tuniyev et al. 2020). Indeed, thanks to its spread across 4 continents, it has been used as a model organism for several eco-physiological and behavioral tests, even in relation to invasiveness (Burke et al. 2002, Downes and Bauwens 2002, Burke and Ner 2005, Vervust et al. 2007, 2010, Kapsalas et al. 2016, Tomé et al. 2021).

Detrimental effects on native species have been reported, especially on congeneric native species. For example, direct behavioral interference by Italian wall lizards has been hypothesized to be the main driver of competitive exclusion of native congeneric species (Nevo et al. 1972, Downes and Bauwens 2002, Herrel et al. 2008, Ficetola et al. 2024). Other authors have explained the ability to disperse to the detriment of native congeneric species with greater efficiency in physiological performances, including thermoregulation, parasitic resistance, or exploratory behavior, which would make the alien species more competitively efficient compared to the native species (Kapsalas et al. 2016, Damas-Moreira et al. 2019, Tomé et al. 2021). Molecular analyses have also suggested that the Italian wall lizard can hybridize with native *Podarcis* species (Capula et al. 1993, Capula 2002, Ficetola et al. 2021), but hybridization itself does not probably represent a major threat (Paris et al. 2024).

There are also studies in which native congeneric species seem unaffected by the presence of the Italian wall lizard, despite its higher aggressiveness in controlled experimental conditions, and species coexist by using different microhabitats (Vanhooydonck et al. 2000, Mangiacotti et al. 2013). These studies highlight the role of habitat structure in the spread of Italian wall lizard range, especially its higher adaptability to human-related landscapes (Mangiacotti et al. 2013). Nonetheless, evidence on invasiveness of the Italian wall lizard is basically weak in the United States, as introduced populations did not significantly spread out from their first settlements (Burke 2010, Deichsel et al. 2010, Goldfarb et al. 2016, Hollingsworth and Thompson 2016, Lambert et al. 2016), and no cases of detrimental effects on native species in the United States have been documented to date.

Despite the widespread tendency to consider the Italian wall lizard an invasive species, it is our opinion that there is not enough experimental evidence to consider this species as invasive as other particularly impactful invasive species, for which public and private biodiversity protection institutions have promoted regulations and management actions aimed at containing their spread. On the other hand, the invasiveness of the Italian wall lizard seems to be conditioned by local circumstances, and its introduction might result in detrimental effects on native congeneric species only in specific conditions. This does not imply an underestimation of the risk of introducing the Italian wall lizard outside of its natural range but emphasizes the importance of understanding if and when the species can become a real threat to native species, and what factors may establish competition with native species significant enough to cause a substantial contraction of their distribution. Without this type of information, and given the ever-increasing number of alien species, it becomes nearly impossible to optimize the already scarce resources available for containing invasive species.

In this paper, we use the recent introduction of the Italian wall lizard on Gorgona Island (Tuscan Archipelago, Central Italy; Zuffi et al. 2022) as a high-resolution case study to highlight the risk of misallocating scarce resources because of the overestimation of a species' invasiveness. Our primary question was whether the species actively excludes the native species owing to its intrinsic level of competitiveness (i.e., truly invasive), or whether the exclusion mechanism is more dependent on the specific context of inter-species competition. After the sampling carried out in 2020, we conducted systematic monitoring in 2021 and 2024 on the same network of transects to assess the progress of colonization by the Italian wall lizard and the possible effects on the distribution of the native congeneric common wall lizard. We report the results of these 2 surveys and apply multispecies occupancy models to investigate potential species interactions in space and habitat use.

STUDY AREA

Gorgona Island (43.42° N, 9.90° E) is the northernmost island of the Tuscan Archipelago, located about 34 km west of the mainland (Figure 1). It is a rocky island with an area of only 2.1 km^2 and a perimeter of about 7 km. The island hosts a state prison (established in 1869), and access to the island is restricted only to police officers and a few visitors, who can only stay in the small town near the harbor. Prisoners are employed in some activities, such as farming and agriculture in the town neighborhood; therefore, habitat structure can be simplified into 3 main categories (Figure 1): urban areas (with buildings, harbor, streets, etc.), agricultural areas (mainly vineyards and olive trees), and natural areas (herbaceous, woody, and shrubby vegetation). Since 1996, the island has been entirely included in the Tuscan Archipelago National Park, with approximately 40% designated as a strict nature reserve (corresponding to the northwestern portion of the island), with strict restrictions on human activities for environmental protection.

The only native lizard potentially interacting with the Italian wall lizard is the common wall lizard (*Podarcis muralis*), which on Gorgona Island exhibits an eco-phenotype and was previously assigned to an insular subspecies (*P. m. vinciguerrai*), no longer supported by genetic analyses (Bellati et al. 2011). The occurrence of the Italian wall lizard on the island was reported for the first time in 2020 (Zuffi et al. 2022), but it was probably introduced by accident a few years earlier, as the species was already widespread on the island. The last survey on the island was carried out at the beginning of 2000 (C. Corti, University of Florence, personal communication), and no evidence of the species was reported, confirming the species' absence reported in the Atlas of amphibians and reptiles of Tuscany (Vanni and Nistri 2006). Genetic analyses revealed multiple origins of the Gorgona lizards from different populations on the Tuscan coasts facing the island (Zuffi et al. 2022). Therefore, passive transport, probably within fodder for cattle via boats from the harbor on the mainland, is the most probable way of introduction (Zuffi et al. 2022). Considering the very restricted access to Gorgona, other sources of lizard introduction are unlikely.

METHODS

Data sampling

During summer 2021, we conducted field work from 23–27 July. We defined 37 linear transects, approximately 200 m long, within the spatial sampling already designed in 2020 (Zuffi et al. 2022). Two people traversed the transects at a constant speed and counted all lizards observed within 10 m of the transect. We recorded individual location using a global positioning system (GPS) unit, and recorded the starting hour, track, and time spent for each survey. We repeated each transect 3 times on 3 different days, between 0900 and 1700, with constant meteorological conditions (similar temperature, no rain, low or absent wind).

Between 29 July and 1 May 2024, we carried out opportunistic surveys to map the 2 species all over the island. The survey period was restricted by prison authorities, combined with unfavorable weather conditions (very high temperatures). We checked all localities where Italian wall lizards were previously detected, as well as natural portions of Gorgona where the species was not previously observed. We recorded the location of individuals of both species using a GPS. During the opportunistic survey, we gathered 36 records (12 for Italian wall lizard and 24 for common wall lizard), which we used for a visual comparison against occupancy predictions from the 2021 data.

Data analysis

We analyzed data systematically collected in 2021 with multispecies occupancy models (Devarajan et al. 2020). We applied the multispecies occupancy model for 2 or more interacting species proposed by Rota et al. (2016), a generalization of the single-species occupancy model (MacKenzie et al. 2002), which assumes the latent occupancy

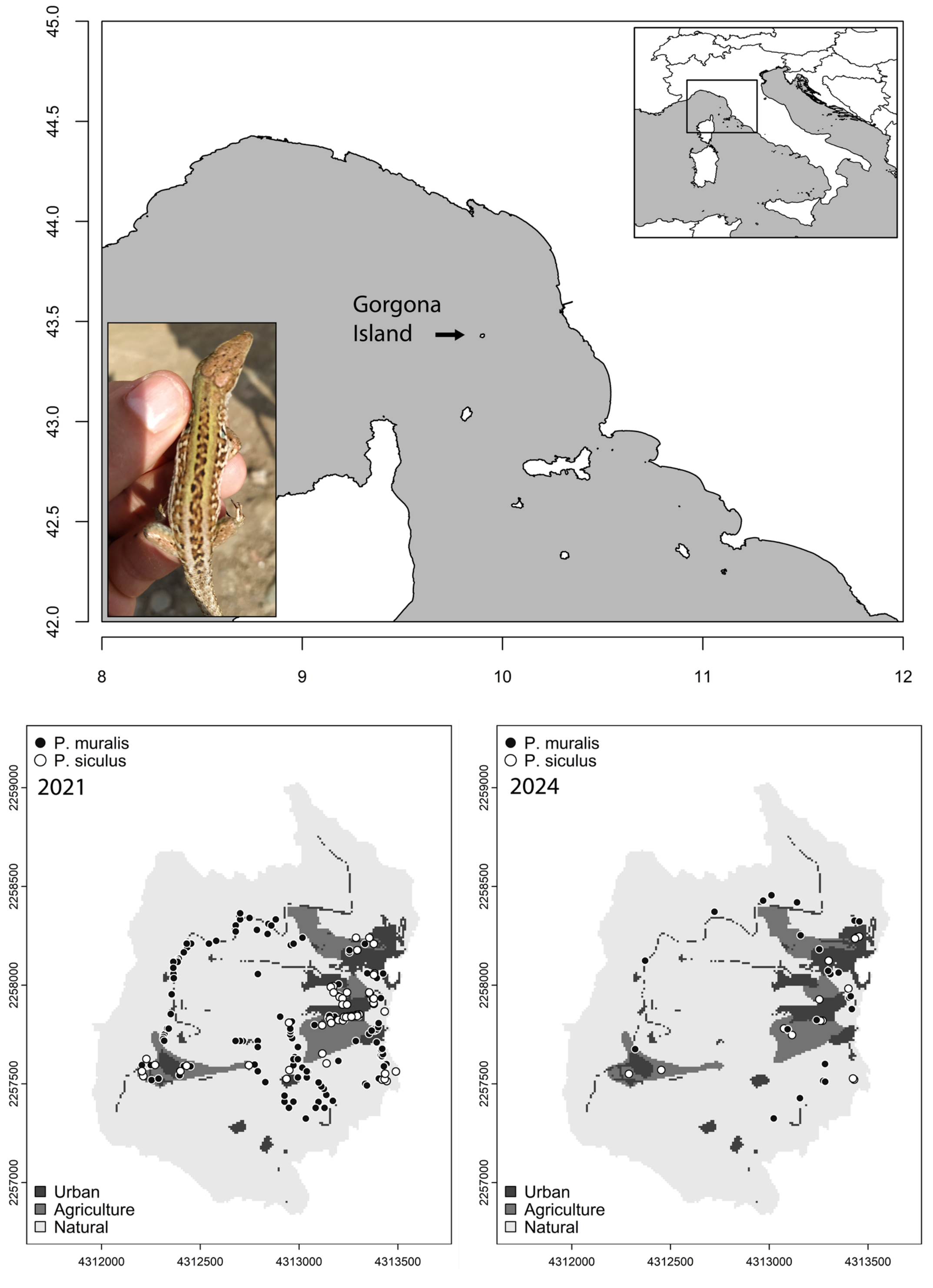

FIGURE 1 Gorgona Island, Italy, with the 3 main land use classes and the records of Italian wall lizard (*P. siculus*) and common wall lizard (*P. muralis*) collected during 2021 (n = 154) and 2024 (n = 36). The image represents a male Italian wall lizard (collected on the island).

state is a multivariate Bernoulli random variable (Dai et al. 2013). This approach allows estimation of pairwise co-occurrence probability and tests of the effects of covariates on the occupancy of individual species, accounting for imperfect detection (Rota et al. 2016). Specifically, we were interested in testing the interaction between the 2 species, especially looking for any negative effects of Italian wall lizards on common wall lizard occupancy. We included covariates to model the effect of land use class on the 2 *Podarcis* species occurrence probability. We derived land use variables from the Land Use Map 2022 provided by ISPRA, the Italian Institute for Environmental Protection and Research (https://groupware.sinanet.isprambiente.it/uso-copertura-e-consumo-di-suolo/library/copertura-del-suolo/carta-di-copertura-del-suolo/uso-del-suolo-2022, accessed 7 Feb 2025). The land use classes represented on the island are mainly non-economic use (natural areas), urban and assimilated areas, and agricultural use, ascribable to fodder crops, gardens, and olive groves or vineyards. After controlling for correlation among variables, we selected as predictors urban areas and agricultural areas. We calculated percent cover in a buffer of 50 m around each linear transect and then standardized the variable. We conducted all spatial analyses using the package terra (Hijmans 2020) in R (R Core Team 2022). We fitted the model in JAGS (Plummer 2003) accessed through the R environment via the packages rjags (Plummer 2022) and R2jags (Su and Yajima 2015). We adapted the code provided by Ken Kellner (https://www.mbr-pwrc.usgs.gov/workshops/ahm2023/04_Multispecies%20_occupancy/multispecies-occupancy.html, accessed 7 Feb 2025) to our data. Notably, we allowed environmental covariates to affect occupancy, but we kept separate but constant detectability for the 2 species. We sampled the posterior distribution with 3 Markov chain Monte Carlo (MCMC) chains, with 2,000,000 iterations each, from which we discarded the first 600,000 and thinned the remaining ones with an interval of 100. We evaluated convergence of the MCMC chains both by visual inspection and with the convergence statistic R-hat (Gelman and Rubin 1992). We used the model to make predictions on the occupancy of the 2 species in the 37 sampling transects. We calculated the maximum *a posteriori* probability estimate (MAP) and the associated 95% highest density interval (HDI; Meredith and Kruschke 2018) for each of the 4 possible states (presence of Italian wall lizard without common wall lizard, presence of both species, presence of common wall lizard without Italian wall lizard, absence of both species).

RESULTS

During 2021 we collected 154 records (44 for Italian wall lizard and 110 for common wall lizard), and the average records per transect ranged from 0.3 to 5.7 (Table 1). Species co-occurred in 15 transects (40.5%), while the common wall lizard was the only species observed in 17 transects, and the Italian wall lizard was the only species in 3 transects (Table 1).

The fitted model showed a good convergence, both at visual inspections of the chains and according to the R-hat statistic (equal to 1.001 for all parameters). The median estimate of detection probability was 0.59 (95% CI = 0.49–0.68) for common wall lizard and 0.33 (95% CI = 0.22–0.45) for Italian wall lizard. Site occupancy by Italian wall lizard was greater in agriculture (MAP = 20.19, HDI = 0.46, 49.75; $Pr_{\beta>0}$ = 0.996) and urban use (MAP = 20.71, HDI = 3.05, 57.76; $Pr_{\beta>0}$ = 0.995; Figure 2), with 95% credible intervals not containing zero. In contrast, site occupancy by common wall lizard was lower for agricultural use (MAP = −21.10, HDI = −52.77, −2.37; $Pr_{\beta<0}$ = 0.972) and positive for urban use ($Pr_{\beta>0}$ = 0.958; Figure 2). We failed to detect a negative interaction between the species (MAP = 13.68, HDI = −18.28, 62.45, $Pr_{a<0}$ = 0.169; Figure 2).

The model predicted presence of at least one species of *Podarcis* is almost certain in each transect (Figure 3), with a MAP value equal to zero for the double absence state in all sites (Table S1). In 24 cases the probability estimates of a single state had a 95% credible interval not overlapping that of other states, which occurred on 6 transects for the presence of only common wall lizard (mostly in the southeastern part of the island), on 17 transects for the presence of both species (near the main urban center and the built-up area in the southwest), and on only one transect for the presence of Italian wall lizard alone (a transect running almost entirely through an olive

TABLE 1 Records *of* common wall lizard (*P. muralis*; Pm) *and* Italian wall lizard (*P. siculus*; Ps) observed for each transect (data from the 3 replicates cumulated), with the percentage of habitat cover in a 50-m buffer around the transect on Gorgona Island, Italy, in 2021.

Transect	Pm	Ps	Urban areas	Natural areas	Agriculture areas	Transect	Pm	Ps	Urban areas	Natural areas	Agriculture areas
1	4	2	0.424	0.529	0.047	20	17	0	0.104	0.896	0.000
2	1	2	0.214	0.771	0.015	21	3	0	0.062	0.938	0.000
3	9	0	0.359	0.520	0.121	22	2	0	0.043	0.957	0.000
4	14	4	0.072	0.928	0.000	23	3	0	0.009	0.756	0.235
5	2	0	0.000	1.000	0.000	24	6	0	0.069	0.931	0.000
6	1	1	0.000	0.828	0.172	25	8	0	0.079	0.921	0.000
7	0	1	0.004	0.137	0.859	26	0	0	0.040	0.311	0.648
8	2	4	0.351	0.019	0.630	27	2	4	0.313	0.240	0.447
9	2	10	0.650	0.016	0.333	28	2	1	0.679	0.011	0.310
10	0	0	0.524	0.359	0.117	29	2	0	0.011	0.801	0.188
11	0	1	0.171	0.829	0.000	30	4	0	0.030	0.822	0.148
12	2	0	0.022	0.978	0.000	31	4	0	0.004	0.996	0.000
13	2	1	0.087	0.895	0.018	32	3	0	0.000	0.725	0.071
14	7	2	0.090	0.903	0.007	33	6	0	0.018	0.982	0.000
15	3	0	0.015	0.952	0.033	34	3	0	0.030	0.970	0.000
16	4	5	0.201	0.380	0.405	35	1	5	0.454	0.275	0.271
17	12	2	0.180	0.462	0.346	36	3	6	0.352	0.292	0.356
18	5	1	0.197	0.453	0.350	37	0	1	0.495	0.281	0.224
19	6	0	0.119	0.853	0.028						

grove). In the remaining 13 cases, credible intervals overlapped for >1 state (Figure 3). Plotting the locations acquired in 2024 against the 2021 model showed distributions to be apparently unchanged (Figure 1).

DISCUSSION

The aim of this study was to analyze the potential displacement of the native common wall lizard by the introduced Italian wall lizard on Gorgona Island. Italian wall lizard colonization of Gorgona Island, a small and isolated island, occurred between 2000 and 2020 (Zuffi et al. 2022). We showed that by 2021, the Italian wall lizard had become widespread across the island but appears to be confined to human-related environments, namely urban and agricultural lands. In contrast, the native species has remained well established in the natural areas of the island, which are included within the strict nature reserve. Our occupancy analysis supported the hypothesis that the spread of the Italian wall lizard was facilitated by human activities, as its occupancy was positively influenced by human land use. However, we did not observe the anticipated interference of the Italian wall lizard with the native common wall lizard. Human-related environments, such as agricultural use, negatively affected site occupancy by the native species and, consequently, the species persisted in the natural areas. These results support the

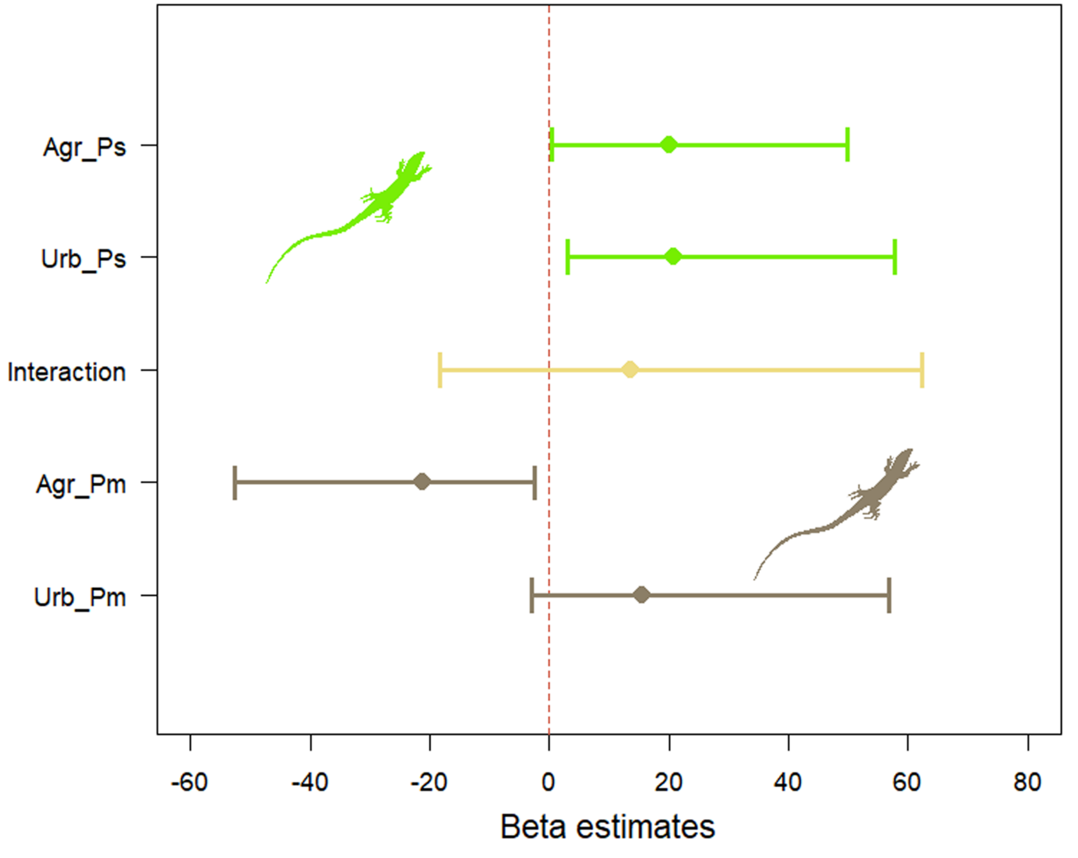

FIGURE 2 Median estimates (dot) and the 95% credible intervals of the betas of multispecies occupancy models in green for Italian wall lizard (*Podarcis siculus*; Ps) and in brown for common wall lizard (*Podarcis muralis*; Pm). The estimates of species co-occurrence are shown in the middle in yellow. Land cover variables include the percentage of agriculture (Agr) and urban (Urb) cover in a 50-m buffer around the transects surveyed on Gorgona Island, Italy, in 2021.

hypothesis that the invasiveness of the Italian wall lizard depends on environmental context, rather than an intrinsic propensity to outcompete the native species because of its greater aggressiveness (Ficetola et al. 2024). In other words, our data suggest that the Italian wall lizard becomes invasive when the environment allows it, particularly in human-related land cover types, where it appears to be better adapted than other congeneric species. This interpretation differs from the concept of habitat-dependent competitive ability, which assumes that behavioral mechanisms, including aggressiveness and direct exclusion, vary according to the environmental context. Instead, our hypothesis posits that the segregation between species is determined solely by the environmental setting itself, without the involvement of direct competition or aggressive interactions.

By proposing the environmental context as the primary filter, we suggest that the success of the Italian wall lizard is driven by its superior fit to the unique physical and structural characteristics of human-related environments (urban and agricultural areas). This conclusion is consistent with previous research on the interaction between the Italian wall lizard and the congeneric Tyrrhenian wall lizard (*P. tiliguerta*), a Corso-Sardinian endemic, where the 2 species responded differently to habitat alteration caused by human activities, with the introduced lizard appearing to be much more tolerant than the endemic one. This difference was likely one of the main factors influencing their spatial distribution on Sardinia (Mangiacotti et al. 2013). The higher tolerance of the Italian wall

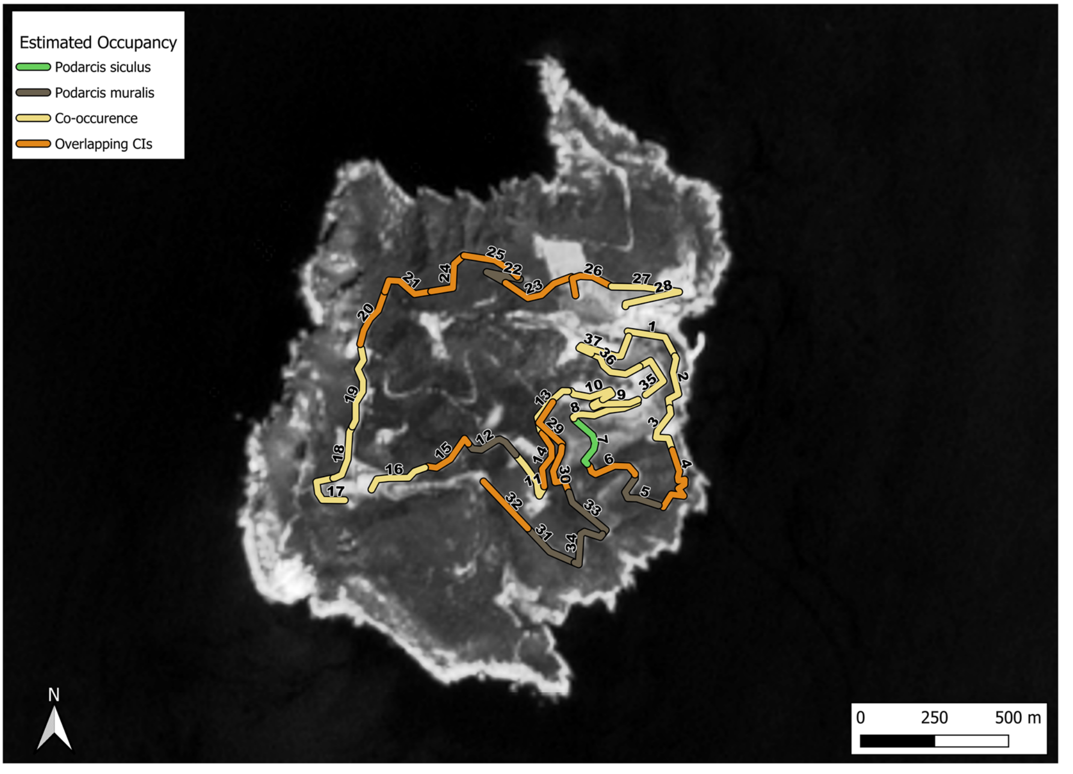

FIGURE 3 Gorgona Island, Italy, with the sampling transects surveyed in 2021. The transect colors depend on the estimated probability of occupancy. Occupancy states are indicated when the 95% credible interval for a state does not overlap the credible interval of other states: presence of only Italian wall lizard (*P. siculus*), presence of only common wall lizard (*P. muralis*), or co-occurrence of the species. The base image is from the European Space Agency mission Sentinel-2 and was obtained by the Copernicus Browser (https://browser.dataspace.copernicus.eu/, accessed 11 Mar 2025).

lizard to human-altered landscapes, combined with greater locomotor endurance (Vanhooydonck et al. 2000) and more efficient thermoregulation under changing environmental temperatures (Van Damme et al. 1990), makes it a better disperser across altered landscapes and, consequently, a better colonizer (Mangiacotti et al. 2013). On Corsica, species microhabitat choice did not appear to be constrained by intraspecific competition, meaning that lizards were not forced out of their preferred microhabitats through direct interactions despite Italian wall lizard repeatedly outcompeting the native Tyrrhenian wall lizard in terrarium tests (Vanhooydonck et al. 2000). Both case studies suggest that the decline of native *Podarcis* species in the presence of the alien Italian wall lizard may be driven by habitat alteration rather than direct competitive exclusion. In contrast, the introduced species can thrive in an altered landscape without necessarily displacing native species through direct interaction.

Further support for this conclusion comes from the observation that between 2021 and 2024, the distribution pattern of the Italian wall lizard on Gorgona Island has essentially not changed, as if the invasive species had halted its spread on the island, and a final equilibrium between introduced and native species was reached. This pattern would not be expected if interference competition was the primary driver of the spread of the alien species, as the outcome of the interference should not be affected by the habitat where it is actually occurring (Nevo et al. 1972, Downes and Bauwens 2002, Ficetola et al. 2024). On the other hand, a slowdown, and even ceasing, of the invasion process is the type of pattern one would expect if the driver of the invasion was environmental suitability, with spread halting once suitable habitat becomes saturated. In the case of Gorgona, we can also rule out that the slowdown of the invasion might be due to depletion of the founding population capacity, as it is highly likely that the population of Italian wall lizards is repeatedly supplied with involuntary novel introductions from the mainland owing to transportation of provisions for the prison. Genetic analyses conducted to determine the origin of the introduced lizards have indeed revealed multiple source origins from Tuscany, even in a relatively small number of samples (Zuffi et al. 2022).

Therefore, human-altered environments could promote the settlement of newly introduced Italian wall lizards, and their spread might be constrained by natural landscapes. When natural areas are lost, we will likely observe a simultaneous regression of endemic lizards and an expansion of the introduced Italian wall lizard. These arguments may also apply to another system of interaction between Italian wall lizard and a native congeneric species, specifically, the native Aeolian wall lizard (*P. raffonei*) in the Aeolian Archipelago in Southern Italy (Sicily; D'Amico et al. 2018, Ficetola et al. 2024). As on Gorgona Island, human activities have profoundly altered the natural environments of the Aeolian Archipelago, negatively affecting native species and leading to the rapid replacement process we observe today. More generally, the dependence of the Italian wall lizard on human-mediated environmental changes for successful establishment in newly colonized areas may also explain why most introductions in North America did not become invasive. In these cases, the Italian wall lizard has only persisted in urban areas and gardens (Brown et al. 1995), despite suitable climatic conditions that could have allowed its survival in other regions (Burke et al. 2002, Burke and Ner 2005).

Therefore, our data suggest that considering the Italian wall lizard a fully invasive species, on the same level as the red swamp crayfish (*Procambarus clarkii*) or the common slider (*Trachemys scripta*), to name some, might be inaccurate. The invasiveness of the Italian wall lizard appears to be context-dependent and is seemingly linked to the extent of human-induced alterations of natural areas, along with the sensitivity of native species to these environmental changes. More generally, our data suggest that the definition of invasive might be too simplistic, or at least valid only for the (few) alien species that consistently cause detrimental effects on native biodiversity once established. However, it is likely that the majority of newly introduced, potentially invasive species become fully invasive depending on the specific conditions of the invaded locality.

An additional and important consideration emerging from this study concerns the reliability of extrapolating laboratory experiment data to natural conditions in the attempt to assess competitive interactions between native and introduced species. In the case of the Italian wall lizard, all studies conducted under such controlled conditions have consistently identified a higher competitive ability compared to congeneric native species (Tyrrhenian wall lizard, Vanhooydonck et al. 2002; common wall lizard, Sacchi et al. 2024; Aeolian wall lizard, Ficetola et al. 2024; Dalmatian wall lizard (*P. melisellensis*), Downes and Bauwens 2002). While these results provide valuable insights into species characteristics, they may not accurately reflect how interactions occur in nature. For example, in terrarium-based experiments, the setting inevitably forces individuals into direct and aggressive interactions, without offering the same opportunities for escape or coexistence that otherwise would be available in nature. Therefore, the extrapolation of these results to natural systems must be done cautiously, keeping in mind that the displacement occurring in laboratory experiments may not necessarily occur in nature, as seen in the cases of the Tyrrhenian wall lizard in Corsica (Vanhooydonck et al. 2000) and of common wall lizard on Gorgona Island.

MANAGEMENT IMPLICATIONS

Understanding the invasive potential of a species and its mediators has direct practical consequences in terms of the management of invasive species. Indeed, identifying an increasing number of species as invasive, but perhaps not directly affecting native species, could divert some of the already limited resources available for biodiversity conservation toward less critical situations. For example, we believe that the threat posed by the Italian wall lizard as an invasive species may be overestimated. In light of our results, requesting significant resources to eradicate or merely contain Italian wall lizards on Gorgona Island would be drastic and unnecessary when, instead, careful monitoring and protection of the strict natural reserve might suffice to preserve the native common wall lizard. We consider the invasiveness of this species to be context-dependent and argue that it is crucial to evaluate, on a case-by-case basis, the potential for the species to expand at the expense of native species before implementing management actions that require significant financial resources from the relevant conservation authorities. More generally, our study highlights the importance for managers dealing with introduced species in protected areas to carefully evaluate the role of habitat structure, notably the human-related habitats, in promoting the spread of introduced species. Indeed, management actions can be fundamentally different if spread is driven by habitat rather than by the alien species itself.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Zenodo from https://zenodo.org/uploads/17678895.

ETHICS STATEMENT

Capture and handling permissions were issued by Ministero Ambiente (prot. 0008139, 9 April 2019, for the 2019-2021 period, to MAL Zuffi) and for allochthonous species eradication, as in the Decreto Legislativo 15 December 2017 n. 230.

ORCID

Roberto Sacchi https://orcid.org/0000-0002-6199-0074
Stefano Scali https://orcid.org/0000-0002-4318-751X
Marco Mangiacotti https://orcid.org/0000-0001-7144-3851
Federico Storniolo https://orcid.org/0000-0002-3303-4464
Martino Flego https://orcid.org/0009-0000-8368-9330
Marco A. L. Zuffi https://orcid.org/0000-0003-1710-9929

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SUPPORTING INFORMATION

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