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Response of structure and temporal dynamics of ant communities to spatial characteristics and habitats on small Mediterranean islands

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Résumé

L'objectif de cette thèse est d'évaluer les effets des caractéristiques spatiales des îles sur la structure des communautés de fourmis et leur dynamique temporelle, avec un intérêt particulier pour les effets de l'habitat et de ses changements. Les îles suscitent un grand intérêt pour la recherche en raison de leurs enjeux de conservation, mais, considérées comme les laboratoires de la nature, elles sont aussi utilisées pour l'avancement de théories fondamentales. La Théorie de l'Équilibre de Biogéographie Insulaire (TEBI) a offert un cadre de recherche en biogéographie insulaire et en écologie pour comprendre la structure et la dynamique des communautés, considérées comme les résultats d'événements stochastiques de colonisation et d'extinction, en lien avec la taille et l'isolement des îles. Cependant, les petites îles sont considérées comme une anomalie de la TEBI de par leur absence de relation aire-espèce : c'est l'Effet Petites Îles (Small Island Effect ou SIE). En effet, elles seraient en proie à des événements stochastiques d'extinction plus fréquents mais aussi intrinsèquement moins diversifiées, notamment en termes d'habitats. Bien que la TEBI ait été largement étudiée, comprendre les effets des caractéristiques spatiales et écologiques des îles sur la structure et la dynamique des communautés reste un défi.

En utilisant 207 petites îles méditerranéennes de moins de 10 km², nos résultats montrent que la superficie des îles est un prédicteur clé de la richesse en espèces de fourmis. Cependant, en utilisant un sous-ensemble de 36 petites îles corses, nous constatons qu'elle n'affecte pas le turnover temporel. L'impact de l'isolement est moins évident, surtout lorsqu'il est mesuré par la distance au continent, car les îles étudiées sont peu isolées et font souvent partie de chapelets d'îles. Ainsi, la proportion de masse terrestre autour d'une île semble être un meilleur prédicteur de sa richesse en espèces. Comme un faible isolement réduit la β-diversité, les dynamiques de colonisation et d'extinction maintiendraient un pool d'espèces limité expliquant pourquoi le turnover n'y répond pas. L'étude de la relation aire-espèce des fourmis montre l'existence d'un seuil de taille des îles en dessous duquel la richesse en espèces augmente très lentement avec la taille, ce qui corrobore le SIE. Étant donné que la richesse en espèces et le turnover répondent respectivement positivement à la proportion d'habitat et négativement à la diversité de l'habitat, cela confirme l'importance de considérer des facteurs autres que spatiaux pour les petites îles. En accord avec l'hypothèse de l'hétérogénéité de l'habitat, l'importance des habitats peut s'expliquer par l'augmentation des ressources et des sites de nidification. La réponse positive des fourmis au changement d'habitat et à la diversification de la végétation après l'éradication de la griffe de sorcière sur une seule île met également en lumière l'importance des habitats. Il semble que les communautés de fourmis soient relativement plus stables sur des sites bien diversifiés avec une végétation non perturbée. Néanmoins, même si la dynamique des communautés de fourmis est faible, nous observons que, même sur des îles relativement bien préservées, la composition tend à s'homogénéiser dans le temps, avec l'expansion d'espèces généralistes, ce qui pourrait être attribué aux changements climatiques.

La diversité de fourmis sur les îles semble être le produit de la combinaison de multiples facteurs, tels que la superficie, l'isolement et la disponibilité de l'habitat. La réponse rapide et claire des fourmis au changement d'habitat souligne l'importance de ce facteur sur les petites îles, mais aussi l'importance des fourmis en tant qu'espèces indicatrices.

Mots-clés : Fourmis, Biogéographie, Petites Iles, Diversité d'habitats, Restauration écologique, SIE

Abstract

The objective of this PhD thesis is to assess the effects of island spatial characteristics on ant community structure and its temporal dynamics, with a particular focus on the effects of habitat and habitat change. If islands draw high research interest due to conservation concerns, they are also valued as nature's laboratories, ideal for the advancement of fundamental theories. The Equilibrium Theory of Island Biogeography (ETIB) has indeed offered a great framework in island biogeography and ecology to understand community structure and dynamics as results of stochastics events of colonization and extinction in relation to size and isolation of islands. However, small islands are considered as an anomaly of the ETIB and the Island's Species-Area Relationship (ISAR), which is called the Small Island Effect (SIE). Indeed, they may be more prone to stochastic events of extinction and they may be inherently less diversified, including in habitats. Despite the fact that the ETIB has been extensively studied, understanding the effects of spatial and ecological characteristics on community structure and dynamics is still at stake.

Using 207 small Mediterranean islands of less than 10km², our results show that island area is a key determinant of ant species richness. However, while using a subset of 36 small Corsican islands, we find that it does not affect temporal turnover. The impact of isolation is less evident, especially when measured by distance to the mainland, as the studied islands are poorly isolated and often part of island chains. Thus, the proportion of landmass around the focal islands seems to be a better predictor of species richness. As low isolation reduces beta diversity it may explain why turnover is unaffected, as colonization and extinction dynamics maintain a limited pool of species. The study of ant ISAR shows evidence of an island size threshold below which the increase in species richness is particularly low, corroborating with the SIE. As species richness and turnover respond respectively positively to habitat proportion and negatively to habitat diversity, it confirms the importance to consider other deterministic factors than area on small islands. In line with the habitat heterogeneity hypothesis, the importance of habitats can be explained by increased resources and nesting sites. Ant positive response to habitat change and vegetation diversification after iceplant removal on a single island further highlights the importance of habitats. It seems that ant communities are relatively more stable on sites that are well-diversified with non-disturbed vegetation. Nevertheless, if ant community dynamics has a low bio-dynamism, we also observe that, even on relatively well-preserved islands, composition tend to homogenize, with generalist species expanding their range, which may be attributed to climate change.

Eventually, species richness is a product of the combination of multiple factors, such as area, isolation and habitat availability. The quick and clear response of ants to habitat change emphasizes the importance of habitats on small islands, but also the importance of ants as indicator species.

Keywords: Ants, Biogeography, Small Islands, Habitat diversity, Ecological restoration, SIE

Acknowledgement

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General Introduction

Islands have fascinated naturalists for centuries (Darwin, 1891; Wallace, 1857), considering them as nature's laboratories (Whittaker et al., 2017). Research on islands led to the definition of many processes and major theories in ecology, such as the assembly rules or the equilibrium theory, and also contributed to the understanding of ecological succession, metapopulation dynamics or the species-area relationship (Santos et al., 2016). They display a range of features that facilitate experimentation and make them good model systems (Vitousek, 2002). Thanks to their restricted geographical limits, that create discrete isolated units, inherently smaller than the continents, they can be used as natural ecological replicates, offering optimal conditions for testing and observing ecological processes (Warren et al., 2015). Despite having been studied for decades, they remain an ideal ground to address a range of ongoing research questions, and notably those on the effects of spatial and ecological factors on communities and their dynamics (Santos et al., 2016; Warren et al., 2015).

1. Insular Biogeography

1.1. Equilibrium Theory of Island Biogeography

Research in insular biogeography, and the fields of community ecology in general, have been marked by the publication of MacArthur & Wilson's Equilibrium Theory of Island Biogeography (ETIB) (1963, 1967). The apparent simplicity of their theory (Warren et al., 2015) has provided an ideal framework for decades of active research on ecological processes and patterns (Losos & Ricklefs, 2009; Whittaker et al., 2023; Whittaker & Fernandez-Palacios, 2007). MacArthur & Wilson stated that geographical factors influence the fundamental processes of immigration and extinction. Area and isolation represent opposite forces that drives gain and loss of species and can therefore be used to predict island species richness (Figure I.1). Considering stochastic events of colonization and extinction, there are higher probabilities for a propagule to reach and settle on a larger landmass area, closer to the source pool of species, than small and more isolated patches.

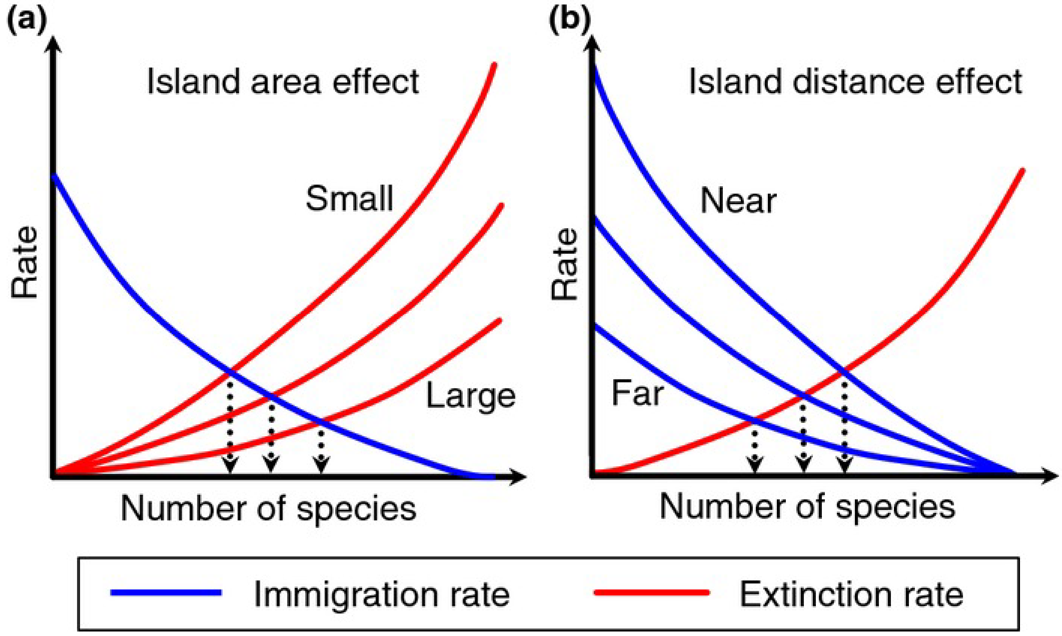

Figure I.1: The Core Island Biogeography Theory model (a) the effect of island area on extinction rate, and (b) the effect of distance from the mainland on immigration rate. Predicted species numbers appear on the x-axis, with dotted arrows marking equilibria between immigration and extinction rates. Figure and caption from Warren et al., 2015

Another fundamental aspect of the theory deals with the temporal dynamics of biodiversity on islands: the dynamic equilibrium. They stated that colonization and extinction should compensate themselves, resulting in a stable species richness but a turnover in the composition of the community. The turnover is thus based on stochastic events as well, with equivalent species following the neutral theory (Hubbell, 2005). In contrast to species richness, turnover rates should be negatively affected by area and isolation (Whittaker, 2000).

If the dynamic equilibrium was proved experimentally by Simberloff & Wilson (1969), most of the studies showed contrasted results, with few cases of equilibrium (Manne et al., 1998;

Valente et al., 2017) and many cases of non-equilibrium (Lynch & Johnson, 1974; Morrison, 2010a, 2010b; Nuvoloni et al., 2016). The existence of an equilibrium stage on islands could be frequently interrupted by non-equilibrium phases (McCollin, 2015; Valente et al., 2015), sometimes caused by disturbance, such as extreme events like hurricanes (Morrison, 2010b, 2010a; Nuvoloni et al., 2016). If the equilibrium is rarely observed, islands could still be sorted in a continuum between non-equilibrium and approximated equilibrium and on a range of magnitude of turnover, from low to high-biodynamism (Figure I.2). This theory has been extensively studied but sometimes criticized as well, notably for considering species as equivalent, and interchangeable, and for omitting differences in immigrations filters between islands (Lomolino, 2000). Nevertheless, the influence of geographical factors on island diversity, its patterns and its temporal dynamics, remain among the fundamental and priority research questions (Patiño et al., 2017).

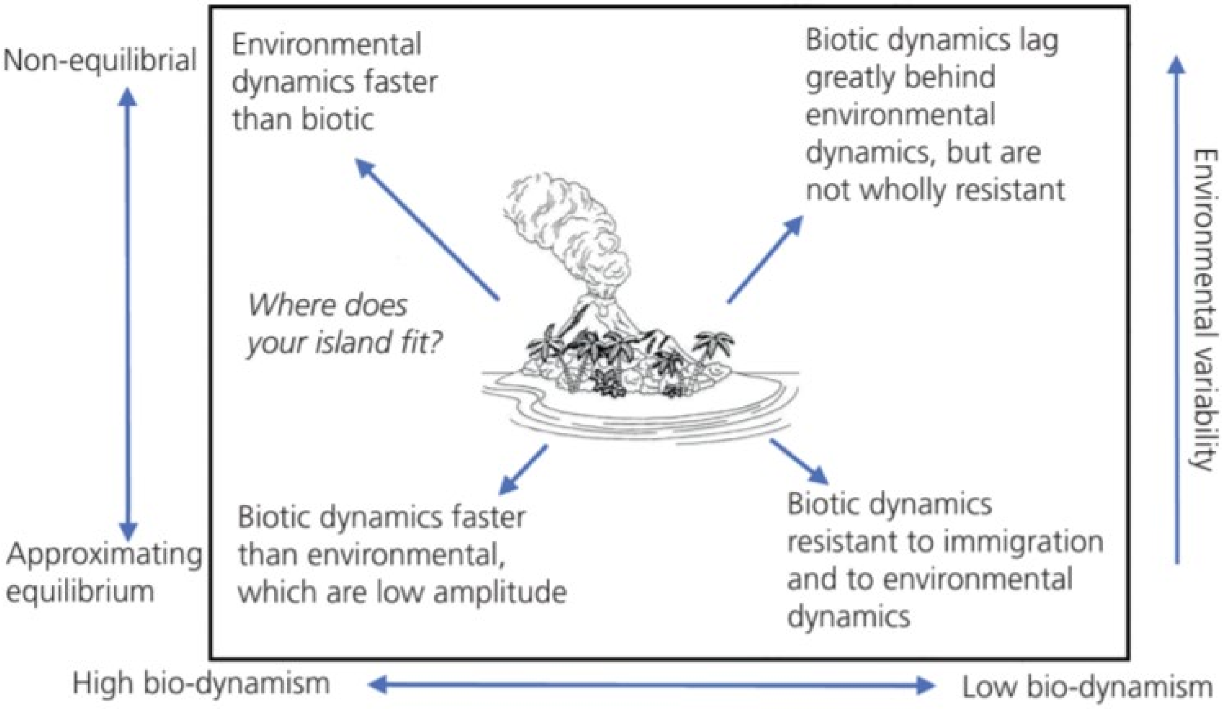

Figure I.2: Representation of the conceptual extremes of island species turnover. Figure from Whittaker et al. 2023

1.2. Island’s Species-Area Relationship (ISAR)

The Species-Area Relationship (SAR) is considered as one of the few ecology law (Schoener, 1976), in which the number of species increases with the surface area sampled. This species richness increase should be rapid initially, then slowing down for larger fragments as it approaches the mainland pool of species (Figure I.3) (Lomolino, 2001). The SAR can be divided in two classes, the Species Accumulation Curves (SAC) which involve nested fragments and the Island Species-Area Relationship (ISAR) which involves distinct fragments (Figure I.4). If this pattern was described a long time ago (Watson, 1847), it was also central point for the formulation of the Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1963, 1967).

The mathematical formulation of the ISAR has taken time (Arrhenius, 1921; Gleason, 1922), and its modelling has provoked an ongoing debate (Dengler, 2010; Tjørve & Tjørve, 2021; Triantis et al., 2012). The most popular and simple equation of the ISAR is the power model: $S = cA^z$ with S being the species richness, A the area and c and the z the parameters respectively corresponding to the initial trajectory and the rate at which the slope changes (Arrhenius, 1921). However, it is argued that the parameters of the power model can be difficult to interpret (Connor & McCoy, 2001). To simplify the relationship and the interpretation of its parameters, studies include the log-log model defined by its parameters, c, the intercept, and z, the slope, and eventually the semi-log models as well. They respectively correspond to a model with either both species richness and area log-transformed, to linearize the power model (Figure I.3), either only the area being log-transformed. Advantages of the semi-log

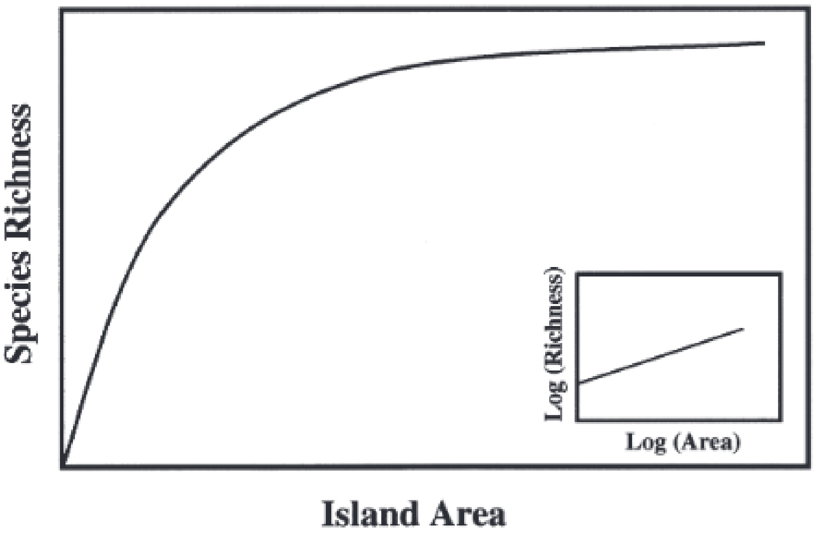

Figure I.3: General form of the Species-Area Relationship illustrating its two phases in its raw form: a rapid increase followed by a slower phase f increase on larger islands.The log-transformed relationship its linear, often used for interpretation. Figure from Lomolino 2001

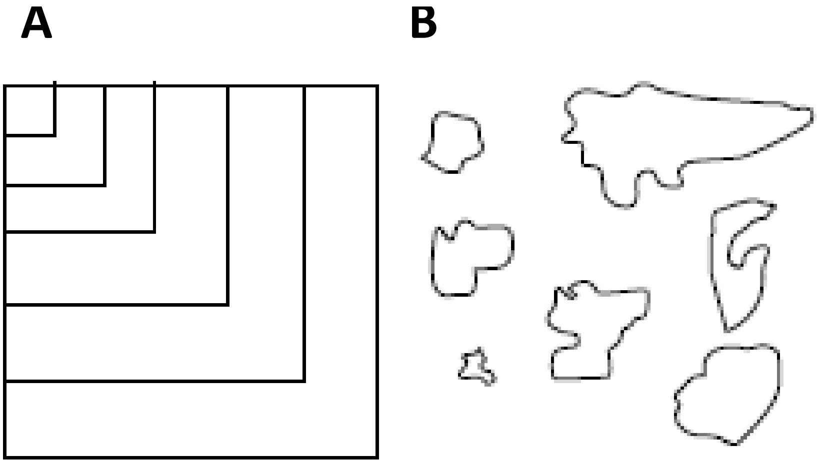

Figure I.4: The two extreme contexts commonly used while studying the Species-Area Relationship (SAR). The (A) shows the nested pattern suitable for the Species Accumulation Curves (SAC) and the (B) shows the fragmented system suitable for the Island SAR (ISAR). Figure from Whittaker et al. 2023

model, as Gleason (1922) presented it, is that it includes an intercept, corresponding to a minimum island size for the taxon studied to maintain its population (Lomolino, 2001). While studying the ISAR, discussions often focus on the slope of the log-log model. Yet, interpretations over the z-value should be done with care, notably because of data transformation (Tjørve et al., 2021). Moreover, the z-value is a scale dependent parameter, which can vary with latitude or the island context (Matthews et al., 2016; Triantis et al., 2012).

Research on the ISAR tend to consider more complex models, such as path analysis, taking into account other parameters than island area and eventually quantifying its direct and indirect effects (Matthews et al., 2019; Triantis et al., 2003) (e.g. Figure I.5). Indeed, the ISAR is generally discussed through two aspects: the direct effects of area, i.e. the area *per se*, or its indirect effects (Gentile et al., 2022; Matthews et al., 2019; Triantis et al., 2003). The area *per se* affects species richness through colonization and extinction probabilities (MacArthur & Wilson, 1967). Indeed, as the size of the island increase, propagules have higher chances to reach the target, and larger population sizes can be supported, with higher chances of survival. Moreover, larger islands may be more protected against disturbances and extreme events, such as hurricanes or volcanic eruptions (Whittaker, 1995).

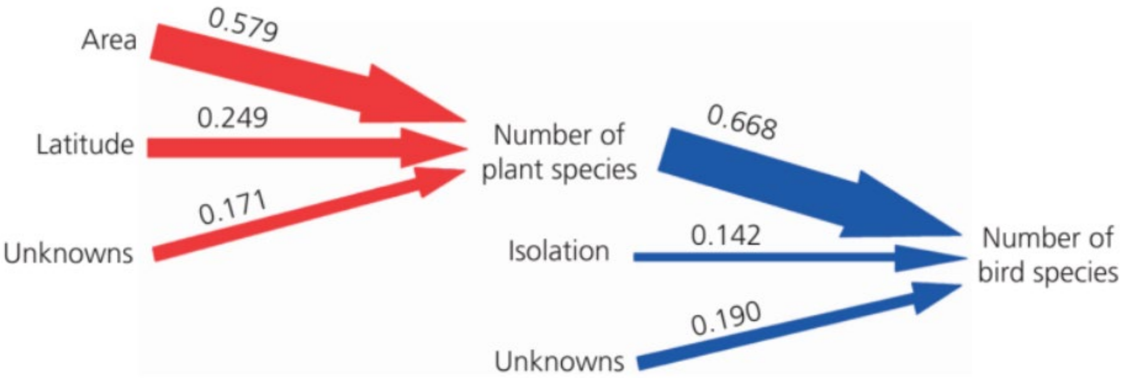

Figure I.5: Example of a path diagram showing direct and indirect relationships between spatial and ecological variables and species richness, with the particular case of birds from the study of Power (1972). The coefficient above the arrows is the proportion of variation at the end of the path explained by the variable at the beginning of the path. Their results suggest that near-coastal islands with richer and more complex floras tended to support more bird species. Figure from Whittaker et al. 2023.

Nevertheless, the area affects a range of other factors that can in turn influence the species richness. The main discussed factor is habitat diversity, which is usually positively correlated with the area as it promotes topographic and geological diversity (Kohn & Walsh, 1994; Simberloff, 1974). According to the habitat hypothesis (Williams, 1964), species richness responds well to the diversity of habitat, thanks to a greater availability of niches and feeding resources (Bazzaz, 1975; Lack, 1969; Tews et al., 2004). On islands, species richness usually responds positively to habitat diversity (Hortal et al., 2009). It can either be a better predictor than area (Triantis et al., 2003) or the opposite (Kohn & Walsh, 1994; Schrader et al., 2019), but their combination often provides good fits (Panitsa et al., 2006). The relative effect of habitat heterogeneity versus the area *per se* could be dependent on the taxon and its degree of habitat specialization (Ricklefs & Lovette, 1999), but also on the scale of the study (Schrader et al., 2019).

The choice of the measured parameters to reflect habitat diversity can be difficult and needs to be adapted to the biological model (Hannus & Von Numers, 2008; Panitsa et al., 2006; Triantis et al., 2003). It is also argued that the expression “habitat diversity” should be replaced by “environmental heterogeneity” because studies usually refer to biotopes and not specific exigences of resources relative to a species or a group of species (Fattorini et al., 2015). Nevertheless, “habitat diversity” is still widely used in literature (Panitsa et al., 2006). Similarly, there are some issues with in the estimation of other predictors, such as isolation (Itescu et al., 2020), which is another principal determinant of species richness on islands (MacArthur & Wilson, 1963, 1967). The most common isolation parameter used is the distance to mainland. However, this often poorly reflects the true degree of isolation (Whittaker et al., 2023), providing weak support for patterns of species richness on islands (Matthews et al., 2019). Alternative measures were proposed to consider non solely the distance of an island from the main source of species, the continent, but also the surrounding islands as well, that can act as stepping stones or alternative sources of propagules (Itescu et al., 2020; Weigelt et al., 2013). Overall, the ISAR and other predictors of species richness should be taken into perspective with the temporal and spatial scale of the study in order to study their relative significance (Whittaker, 2000).

1.3. Matter of scale & the Small-Island Effect

The equilibrium theory of island biogeography (ETIB) is best suited to specific temporal or spatial scales (Lomolino, 2000), notably at the population dynamic or the ecological scale (Whittaker, 2000). Considering long-term evolutionary and geological time scales, speciation or phylogenesis events should promote disequilibrium (Heaney, 2000). Its concerns notably the very large islands, included in remote archipelagos, for which the SAR should have an increased slope due to the prevalence of evolutionary dynamics and events of speciation (Whittaker et al., 2017) (Figure I.6). The effects of geological processes on evolution are studied specifically for oceanic islands, notably using the general dynamic model (Whittaker et al., 2008). However, the origin of the majority of the islands of the world is not oceanic but rather continental or past land-bridges (Meiri, 2017). Continental islands were mostly connected to mainland during the Last Glacial Maximum and became separated islands after the rise of the sea-level (Whittaker et al., 2023). Their particularity is that most of them have always harbored life (Meiri, 2017) and are generally not very distant from continent (Whittaker et al., 2023) which influences the community assembly (Santos et al., 2016). As the island systems become smaller and less isolated, the slopes of the ISAR decrease and intercepts increase, until the “rescue effects” can be observed on the less isolated islands (Figure I.7). Extinctions are then very quickly compensated by recolonization, ensuring high levels of species richness even on small islands (Whittaker et al., 2017) (Figure I.6).

The smallest islands could be also responsible of an anomaly in the ISAR, known as the Small Island Effect (SIE) (Lomolino & Weiser, 2001; Triantis et al., 2006) (Figure I.6). It was already suggested by MacArthur & Wilson (1967), blaming the instability of the communities under a threshold of size. The thresholds can vary depending on the biological model studied and the

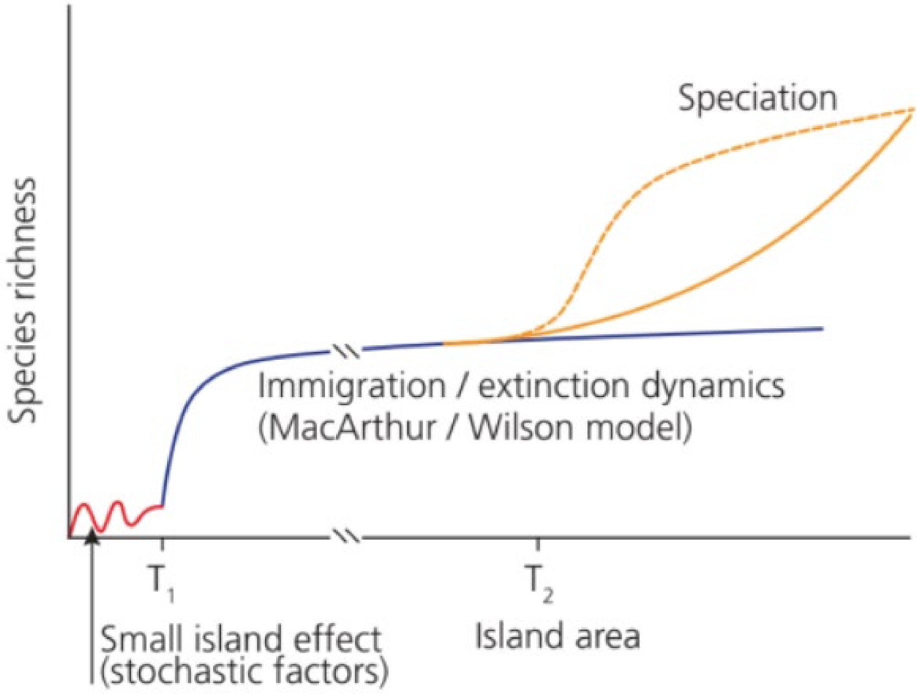

Figure I.6: The ISAR extension proposed by Lomolino (2001) with its three distinct phases. On the left, in red, the smallest island should have stochastic fluctuation of species richness, without relationship with the area; in the middle the classic convex ISAR resulting from the colonization-extinction dynamics of McArthur & Wilson (1963, 1967); during the third phase species richness should have a second phase of increase due to speciation either towards a asymptote (dashed orange line) or an upward rising curve (solid orange line). Figure from Whittaker 2023.

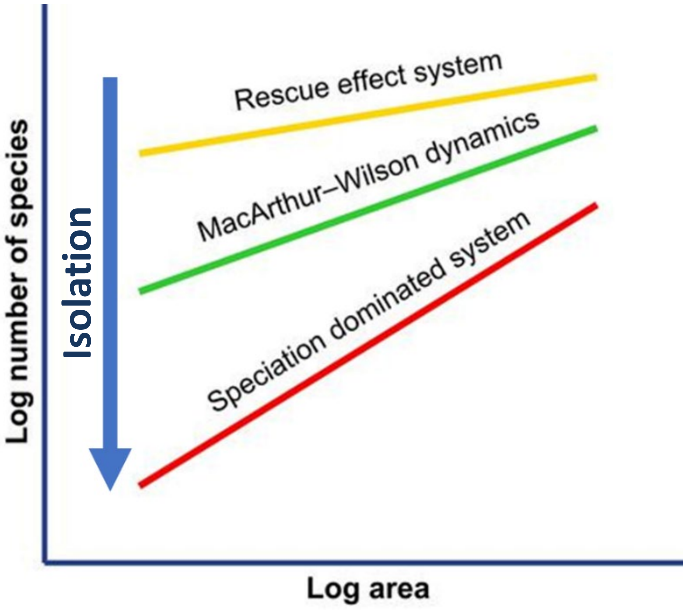

Figure I.7: Variation of the slope of the ISAR upon the island context and its isolation. ISAR slope should decrease with isolation of the system. Figure from Whittaker et al. 2023 island context, reaching lower values when the dispersal abilities of the taxon are higher (Lomolino & Weiser, 2001) and on less isolated islands with higher immigration rates (Schrader et al., 2020). The reasons to this effect may be that smallest islands are more prone to stochastic events and climatic disturbances (Lomolino & Weiser, 2001). Secondly, small islands that are inherently less diverse in terms of habitats and species richness, can increase in complexity with area beyond a certain threshold (Whitehead & Jones, 1969). Moreover, habitat distribution might be more heterogenous on small islands (Sfenthourakis & Triantis, 2009), thus becoming the main driver of species richness (Chen et al., 2020; Triantis et al., 2006). Studying the Small Island Effect (SIE) can also benefit conservation actors as a tool for reserve management or the identification of critical thresholds before drastic increase in invasives (Li et al., 2024; Lomolino & Weiser, 2001).

2. Conservation on islands

If biodiversity loss at the world's scale is alarming (Ripple et al., 2017), islands are no exception and are even among the priority for conservation (Bellard et al., 2014; Russell & Kueffer, 2019). Indeed, islands host a disproportionate part of world's biodiversity (Fernández-Palacios et al., 2021). Despite representing less than 7% of the world's landmasses, they host 20% of the biodiversity. Island biodiversity is considered particularly vulnerable (Whittaker et al., 2017), due to its high rates of endemicity, small population sizes and its naturally fragmented distribution (Frankham et al., 2002).Current knowledge indicates that 75% of extinctions occurred on islands; moreover they host half of the endangered species, which are mainly threatened by global change components, i.e. habitat loss, resource overexploitation, Invasive Alien Species (IAS) and climate change (Fernández-Palacios et al., 2021). Conservation concerns are often targeted to large oceanic islands, that can be considered as museums of biodiversity notably for being diversification cradles (Fernández-Palacios et al., 2021). However, the vast majority of islands are less than 1km² (Sayre et al., 2019), and they are mostly continental (Meiri, 2017). These islands represent important systems for conservation, notably for their contribution to the recolonization and connection of mainland regions, and thus to long-term dynamics of communities (Bellemain & Ricklefs, 2008).

2.1. Small Mediterranean Islands

The Mediterranean basin is one of the world's regions with the largest number of islands (>10,000), consisting primarily of small islands and islets, respectively under 1000 ha and under 1 ha (Médail, 2017a). This region is considered as a biodiversity hotspot (Myers et al., 2000; Perret et al., 2023), with a great plant diversity extensively supported by its islands (Médail & Quézel, 1997; Weigelt et al., 2013). Often, small islands and islets host an original and disproportionate part of the biodiversity. With their wide range of biogeographical contexts and their high sensitivity to environmental changes, the Mediterranean islands - particularly small islands- are ideal for ecological studies (Médail, 2017a) especially within the framework of conservation. If anthropogenic pressures are particularly strong and ancient in the Mediterranean basin (Blondel & Aronson, 1999), the small islands and islets, compared to the largest, are relatively less threatened by direct human disturbances (Médail, 2017a). In this context, small islands offer valuable opportunities for monitoring to better understand fundamental ecological processes.

2.2. Global changes

Small Mediterranean Islands are relatively preserved from direct anthropogenic disturbances nowadays, but there are traces of past uses. Some islands, including the small ones, were used for agriculture and grazing, sometimes since Antiquity (Brun, 1996; Vigne, 1992). They also bear other signs of human presence, sometimes through urbanization with either prisons, lighthouses, churches or military buildings (Pretto et al., 2012; Vogiatzakis et al., 2008). Nowadays, the smallest islands and islets are mostly uninhabited and often placed under protection (Vogiatzakis et al., 2008). Nevertheless, even without direct anthropogenic pressure, they are still subject to indirect disturbances caused by human activities. First of all, the Mediterranean basin could be particularly affected by climate change in the future, with increased temperatures and decreased precipitations (Giorgi & Lionello, 2008). These changes will affect community compositions and structures, as it was projected for the mammals of the region (Maiorano et al., 2011). Human pressure also indirectly affects insular community dynamics through its effect on seabird populations, as it is the case for the seagulls that fed on landfills (Mutillod et al., 2023). Seabirds bring a significant energy inflow from the sea while they nest on small islands, which strongly affects plant communities (Médail, 2017a; Vidal et al., 1998).

Island biodiversity can also be affected by biological invasions, considered as one of its main threats (Pyšek et al., 2020). By 2100, the Mediterranean basin could be among the most impacted region by IAS (Sala et al., 2000), which correspond to the species introduced outside their native range that establish and spread, causing damage to the economy, health or environment. IAS plants could particularly threaten small islands as they have limited habitat and plant diversity, whereas high diversity usually guaranty better resilience (Pretto et al., 2012). The negative impacts of plant invasions have already been demonstrated on various small Mediterranean islands (Celesti-Grapow et al., 2016). In addition to plant invasion, many islands suffer from multiple invasions, interacting together, potentially improving their own persistence and their harm to native biodiversity (Russell & Kaiser-Bunbury, 2019).

2.3. Ecological restoration

Sometimes, conservation is not enough, or not adapted, in the face of island disturbances, so restoration actions have to be taken in order to modify the trajectory of the ecosystem (e.g. Martínez-Abraín et al., 2004). In addition to restoring biodiversity or the multifunctionality of ecosystems, restoration can also provide great opportunities to understand biodiversity dynamics and response to disturbance, notably in the context of habitat modification (Palmer et al., 2006). According to the definition of the Society for Ecological Restoration the ecological restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" by addressing "biodiversity conservation and ecological integrity" (Gann et al., 2019). Among the restoration actions taken on islands, control or eradication of IAS plants or mammals are often implemented to mitigate the adverse effects on native biodiversity (Capizzi, 2020; Celesti-Grapow et al., 2016). Eradication or control programs have generally generated positive responses of native biodiversity (Bourgeois et al., 2013; Buisson et al., 2021; Jones et al., 2016). Nevertheless, restoration projects, like any management activity, should include monitoring studies to better understand the response of the wildlife (Block et al., 2001). For example, a network of "Sentinel islands" is soon to be created by the Small Mediterranean Islands Initiative (PIM) with the purpose to assess the weight of global change and conservation/restoration actions on biodiversity while using common methodologies for monitoring (Renou, 2012).

3. Ants as biological models

3.1. Indicator species and biological models for biogeography

In order to implement efficient monitoring protocols and to assess ecosystem health, it is important to consider good bioindicators (Burger & Gochfeld, 2001; Siddig et al., 2016). In the context of wildlife conservation and ecosystem restoration, the term of indicator species is usually preferred, to designate taxa associated to particular environmental conditions chosen to study changes in specific environmental attributes (Caro, 2010). Among indicator species, ants can be good candidate as they show quick responses to environmental changes (Andersen et al., 2002; De Almeida et al., 2024; Majer, 1983; Tiede et al., 2017). They are able to monopolize space and to closely interact with their environment and other organisms (Andersen, 1992). The structure of their communities is sensitive to the structure of habitats, the microclimate, resource availability and competitive interactions (Andersen, 2019). Ant diversity usually decreases with habitat simplification and resource losses (Underwood & Fisher, 2006). Moreover, ant sampling is relatively simple to implement (Agosti et al., 2000), with methods such as hand collection allowing a good estimation of diversity in the Mediterranean (Salata et al., 2020).

On top of being considered as good indicator species, ants are often studied in biogeography (e.g. Dantas & Fonseca, 2023; Gotelli & Ellison, 2002; Ohyama et al., 2021). They represent good biological models because of their high diversity, counting 14,274 described species (*Antweb*, v8.112, California Academy of Science). Ants are also particularly abundant, among the most abundant terrestrial organisms (Hölldobler & Wilson, 1990), representing 20% of the human biomass and 10% of the terrestrial arthropods (Rosenberg et al., 2023; Schultheiss et al., 2022). They have a worldwide distribution (Guenard et al., 2017), occupying a wide range of ecosystems (Economo et al., 2018; Kass et al., 2022).

The Global Ant Biodiversity Informatics (GABI, Guenard et al., 2017), gathering ant distribution data around the world, has recently been extended to islands, with more than 2,500 islands having lists of species (Liu et al., 2023). Ants are known to be ubiquitous on islands, even the smallest ones (Cole, 1983; Morrison, 2016). They may reach islands during nuptial flights (Vepsäläinen & Pisarski, 1982), by rafting, human-assisted dispersal or, for land-bridge islands, they could have persisted since the separation (Morrison, 2016). If little is known on ant colonization and community assembly rules on islands (Morrison, 2016; Vepsäläinen & Pisarski, 1982), it seems that ants are nearly always present on islands from the moment it is vegetated (Morrison, 2006). Their ecology and nesting behavior (e.g. in the ground, rock cracks or inside vegetation) allow them to persist on the smallest islands, even with strong natural disturbances, such as inundations or hurricanes (Morrison, 2010a). Studies on ant community structures and dynamics can also benefit from the sessile and long-lived colonies, evidenced by the presence of workers (Lach et al., 2010).

3.2. Ecosystem engineers

In addition to their role of indicator species and the interest they rise in biogeographical studies, ants are also known to significantly and actively affect the ecosystems they live in (De Almeida et al., 2020; Folgarait, 1998). Thus, they are considered as ecosystem engineers for their ability to provide different ecosystem services and to participate in the ecosystem functioning (Del Toro et al., 2012; Folgarait, 1998). Indeed, some species are significant predators (Philpott & Armbrecht, 2006), some participate to seed dispersal and plant reproduction (Lengyel et al., 2010). They also affect the soil structure, as they promote soil aeration during the formation of nest galleries (Frouz & Jilková, 2008), and also influence nutrient cycling (Wagner & Jones, 2006). These ecological functions could as well justify ant monitoring and conservation in itself, omitting their potential role as indicators (Underwood & Fisher, 2006).

Objective of the thesis

The objective of this PhD thesis is to better understand the factors that drive the structure and dynamics of animal communities on small islands. We aim to assess the effects of both space and time, with a particular focus on the effects of habitats, that should be a prevalent factor on small islands (Sfenthourakis & Triantis, 2009; Triantis et al., 2006). Identifying geographical and ecological factors that influence species richness and community dynamics is still among the top-ranked fundamental issue of island ecology and biogeography (Patiño et al., 2017; Santos et al., 2016; Warren et al., 2015). Moreover, discussions about the Small Island Effect (SIE) are still ongoing, and require to better qualify habitat and to assess its influence (Gao & Wang, 2023). These fields can also benefit from conservation and restoration projects on islands to better understand the response to habitat changes (Palmer et al., 2006). For this purpose, we focused on the Mediterranean basin, which, as a biogeographical region, offers relatively homogeneous conditions yet also exhibits significant local diversity (Blondel & Aronson, 1999), especially with its more than 10,000 islands (Médail, 2017). Ants were chosen as biological models, having the advantage of being ubiquitous in insular systems (Morrison, 2006), sometimes being the most abundant organisms, and relatively diversified.

To investigate these questions, this thesis is structured in three chapters. The first chapter aims to explore the ant Species-Area Relationship and the effects of isolation and habitat quantity and diversity on small islands at the scale of the Mediterranean basin. For this chapter, we have compiled ant species richness data of 207 small islands of less than 10km². The second chapter focuses on a subset of small islands around Corsica to study the temporal dynamic of ant communities up to 39 years apart. For 36 small islands, we explored the changes in communities and we tested area, isolation and habitats as predictors of turnover rates. The third chapter focuses on a single small island of the Port-Cros National Park (Var, France) to study ant community dynamics and response to habitat change during a ten-year restoration program including Invasive Alien Species (IAS) eradication, i.e. the iceplant (*Carpobrotus* spp.) and the black rat (*Rattus rattus*).

In the **Chapter 1** we first ask: **What is the best representation for the ant SAR of the small Mediterranean islands?** We expect to find a power model as the best representation of the raw relationship. We hypothesized that while studying the linearized model we should find a positive and significant relationship with a low-slope, in accordance with a previous overview of the ant SAR at the global scale (Ohyama et al., 2021). Within the range of island sizes that we study, we expect to observe a SIE, as there should be a threshold of size below which the species-area relationship is not validated (Lomolino & Weiser, 2001).

In the **Chapter 2** the main question was: **How the ant communities of small Corsican islands have changed in more than 30 years**? According to the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1963, 1967), the species richness should remain stable and the composition of the community should change (turnover). We also hypothesized that certain compositions of ant communities could have higher turnover rates than others.

The **Chapter 1 & 2** allow us to investigate **the predictors of species richness and community dynamics.** The main assumption was that, inversely to species richness, turnover should be negatively correlated to island size, as extinction rates decrease (MacArthur & Wilson, 1963, 1967). As immigration rates should decrease with isolation according to the ETIB, we expect this parameter to be negatively correlated with species richness and turnover. In **Chapter 1,** we also test other isolation calculation than the distance from mainland because it does not necessarily reflect the actual isolation of islands (Itescu et al., 2020). For example, we expect the proportion of landmass around the island to be a better predictor of species richness.

As the SIE suggests that habitat should be more important than area to predict species richness on small islands (Sfenthourakis & Triantis, 2009; Triantis et al., 2006), we also asked: **How habitat diversity influence the species richness and community dynamics?** In **Chapter 1** we hypothesized that habitat diversity and proportion of habitats on islands are positively correlated with species richness. Using plant communities as proxies of habitat diversity in **Chapter 2**, we expect the turnover to be negatively affected with this parameter, as it was found by Goldstein (1975).

The importance of habitats in shaping ant communities was also assessed on a single island in the **Chapter 3**. We asked: **How the eradication of iceplant and black rats affected the community structure and abundance of ants?** We hypothesized that ant species richness and abundance will increase at the four invaded sites after the eradication but remain unchanged at the native vegetation sites, that were not disturbed by IAS removal. However, considering that habitat modification should be a strong driver of ant communities (Andersen, 2019), we expect that the magnitude of change should be higher after the removal of iceplant, that induces modification of plant communities (Buisson et al., 2021), than that of black rats.

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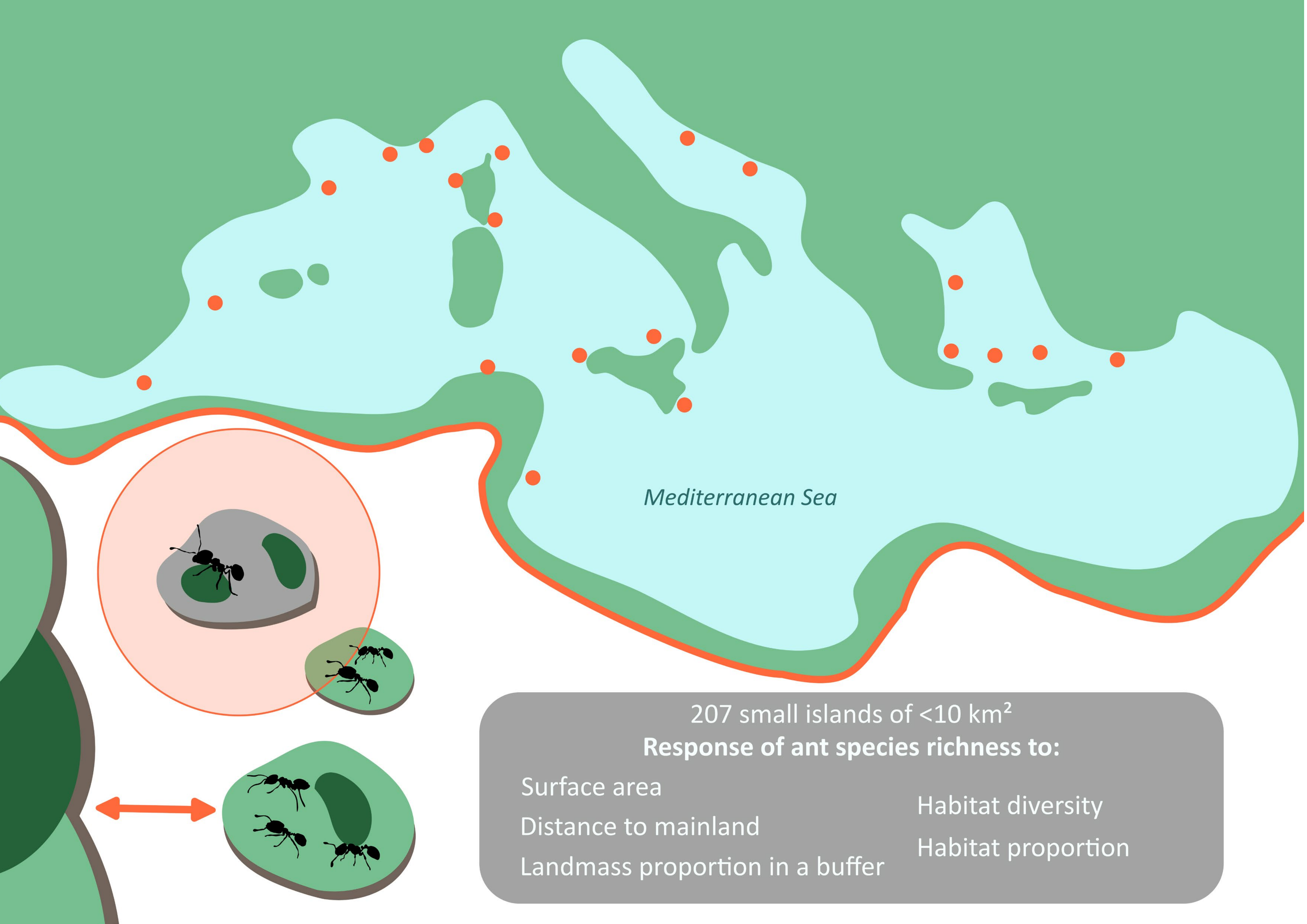
Transition to chapter 1

The objective of this first chapter is to provide an overview of ant community structure on small islands at the Mediterranean basin scale. Ant Species-Area Relationship has already been studied at the world's scale using published data (Ohyama et al., 2021), but here we propose a large dataset mainly including unpublished data, focusing only on small Mediterranean islands. As ants are nearly always present on small islands (Morrison, 2016), sometimes being the most abundant invertebrates, it seems particularly important to understand how they respond to different spatial and ecological factors. This chapter includes the most common spatial factors used as predictors of species richness, as described in the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1963, 1967): surface area and distance to mainland as an estimation of isolation. Its originality lies in the inclusion of less common factors, such as the proportion of landmass within a buffer around the focal islands, which could serve as a good estimator of isolation in contexts such as poorly isolated land-bridge islands. Moreover, we include estimation of habitat proportion and habitat diversity, which may be very important predictors of species richness in the case of small islands.



207 small islands of <10 km²

Response of ant species richness to:

- Surface area
- Distance to mainland
- Landmass proportion in a buffer
- Habitat diversity
- Habitat proportion

Parc National des Calanques © Léo Rocher

CHAPITRE 1

Ant communities on Small Mediterranean Islands: Investigating the Species-Area Relationship, and the role of Habitat Diversity

1. Introduction

Considered as nature's laboratories, islands have fascinated scientists for centuries (Whittaker et al., 2017). They provide an ideal framework to study community ecology and assembly rules (Florencio et al., 2021). MacArthur & Wilson (1963, 1967) used islands and fragmented ecosystems to propose a quantitative method to estimate biodiversity and propose the Theory of Island Biogeography. According to their theory, species richness could be estimated using island size and isolation, considering that bigger islands, that are closer to the continent, are able to host more species than the smaller ones that are more isolated.

The Species-Area Relationship (SAR), i.e. the increase in species number with area, could be one of the rare laws of ecology (Schoener, 1976). It has been the subject of a large number of studies, including those focusing on its statistical modelling (Arrhenius, 1921; Connor & McCoy, 1979; Matthews et al., 2016; Triantis et al., 2003, 2012). The most commonly used model, that has also showed the best representations, is the power model: $S = cA^z$, where S is species richness, A is area, and z and C are parameters depending on the biological model and the context (Triantis et al., 2012). This model is often represented in its linearized form, which imply a logarithmic transformation: $\log S = \log C + z\log A$ (z and C are here parameters respectively corresponding to the slope and intercept) (Matthews, et al., 2019). The parameters of this relationship, i.e. the slope (z-value) and the intercept (c-value) are strongly influenced by the geological history of the islands and the biological group studied (Triantis et al., 2012). The classic SAR model has however been criticized for being too simplistic, scale dependent and for parameters that are difficult to interpret (Lomolino, 2000).

Many authors documented the absence of relationship between island area and species richness when it comes to small islands, calling this phenomenon the Small Island Effect (SIE)

(Lomolino & Weiser, 2001; Triantis et al., 2006). MacArthur & Wilson, (1967) had already suggested that small islands would be more unstable, constituting an anomaly for SAR. Many factors might explain the particularity of the small islands, including the fact that they are more prone to stochastic events and extreme climatic events, such as hurricanes (Lomolino & Weiser, 2001). It was also suggested that habitat distribution on smaller islands is more heterogenous, becoming the main driver of species richness (Sfenthourakis & Triantis, 2009).

Habitat diversity plays an important role in driving species richness (Tews et al., 2004), including on island systems (Hortal et al., 2009). As habitat surface area are classically considered to increase together (MacArthur & Wilson, 1967), and it can be difficult to dissociate their effects (Gentile et al., 2022). This issue has contributed to the debate on how to detect the SIE (Chen et al., 2020; Gentile & Argano, 2005; Lomolino & Weiser, 2001; Triantis et al., 2003, 2006). Nevertheless, while studying the effects of habitat, the difficulty may also lie in defining these habitats, which may vary depending on the taxon studied (Triantis et al., 2003).

On islands, ants are almost always found, their presence has been already documented and studied in many archipelagoes throughout the world for decades, i.e. in the Mediterranean (Baroni-Urbani, 1968, Bernard, 1959), in central and north America (Cole, 1983; Goldstein, 1975; Morrison, 1998), in east Asia (Rizali et al., 2011; Zhao et al., 2020) or in Australia (Woinarski et al., 1998). On islands, ant species richness was often shown to respond to habitat diversity (Torres & Snelling, 1997), vegetation diversity (Morrison, 1998), and cover (Goldstein, 1975) but not isolation (Morrison, 2016; Ohyama et al., 2021). Ohyama et al. (2021), reviewed the SAR of ants for 320 true islands and found a significant relationship but with a relatively low slope (z-value=0.25). In their work, they also showed evidence of a SIE while fitting threshold models, but argued that a lot of predictors should still be assessed, including the study of direct and indirect effects of habitat diversity.

In this study we focus on the ant SAR of Small Mediterranean Islands. We gathered an unprecedented dataset of published and unpublished species lists of islands of less than 10km² (207 islands between 59m² and 10km²). This study is also the opportunity to assess a potential SIE using threshold models. In order to assess the effect of complementary predictors on species richness, we calculated two isolation indices, i.e. the distance to the nearest continent and the proportion of landmass area in a 6-km buffer, and we estimated habitat diversity and quantity on the islands. For the first time, we have used remote sensing data on small islands to estimate the proportion of vegetation cover and the different types of habitats for a large number of entities at once. Since ant are known to respond to habitat complexity (Andersen, 1986; Greenslade & Greenslade, 1977) and openness (Andersen, 2019), we have selected three types of habitats for ants: bare rocks, sparse vegetation and dense vegetation. We expect to find a significant ant SAR, with a low slope, and a SIE within the range of the small island that we studied. We expect that ant species richness will have a stronger positive relationship with habitat diversity and/or quantity. However, we expect that ant species richness will rather be positively explained by the proportion of landmass in a 6-km buffer than negatively by the distance to the nearest continent.

2. Material and Methods

2.1. Island data

Small island typology was chosen upon the definition given by the Small Mediterranean Islands Initiative (PIM Initiative, 2024): islands smaller than 10 km² in size, at least 5 m from the shore, with a permanent water pass and at least one vascular plant. Islands must be located within the Mediterranean basin to be included in the study. For the 207 islands selected, we retrieved geometries from the PIM Initiative private database and the MEDIS public database (Santi et al., 2024), allowing calculation of basic island characteristics such as island surface area and distance to the nearest continent. As suggested by Itescu et al., (2020), we also included the proportion of landmass area in a buffer around a focal island, which can be another good estimate of island isolation. The buffer distance was set at 6 km, as it is the average distance of dispersion of ants sexual individuals around their nests (Helms, 2017). Island surface area, distance to the nearest continent and the proportion of landmass in a 6km buffer were calculated using QGIS 3.22.5 (QGIS Development Team, 2024). Islands were also grouped in 11 geographical clusters: Eastern Spain, Balearic Islands, Southern France, Corsica, Eastern Tunisia, Northern Tunisia, Italy Ligurian, Sicily, Croatia, Greece and Malta.

2.2. Ant data

We gathered ant species lists, and thus species richness of each island matching our criteria, with available data. Published records of ant data were mainly searched on AntCat.org with the key words: “insular”, “islands”, “islets” or “archipelago” in English, French, Spanish, Italian and German. Access to certain documents was facilitated by ant or island specialists (Frédéric Médail, Gregor Bracko and Lech Borowiec). European myrmecologists were contacted for eventual unpublished data (Antonio Alicata, Jelena Bujan, Christos Georgiadis, Dionysos Kryfos, and Enrico Schifani). Personal surveys were conducted on 84 of the 207 small islands of southern France and Corsica, either to collect unprecedented data or to actualize former incomplete surveys. Small islands from southern France were visited either in spring 2021 or spring 2022. Small islands from Corsica were visited in spring 2023. Ants were hand collected with active searches on the islands by flipping rocks, beating vegetation, breaking twigs and looking for foragers on the ground. The time spent prospecting for ants was proportional to the island size and the number of vegetation strata (bare rocks, herbaceous vegetation, shrubs). All collected specimens were identified morphologically, except for those of the genera *Tapinoma* and *Tetramorium*, which were identified genetically. Ant species names were homogenized by actualizing invalid species and groups using AntCat.org catalog.

2.3. Habitat classification

Vegetation on the islands was studied using images from the Sentinel-2 satellite (European Space Agency, ESA). These images are free and available without restriction for Europe. The aim was to differentiate three types of habitats on the islands: rocks, sparse vegetation, and dense vegetation. For this purpose, four channels were selected: Blue, Green, Red and Narrow Infra-Red (NIR), which all have a resolution of 10 meters. We chose to run a pixel-based classification, starting by applying a Principal Component Analysis on the stacked image channels. The K-means algorithm was then used as a non-supervised method for pixel clustering. We used visual comparison with Google Earth Pro (Google Earth Pro, 2024) images and visualization of reflectance curves to determine the cluster identities. These comparisons were also used to perform eventual reclassification of certain clusters by using a mask and reproducing the same workflow on a subset of pixels. The surface of total vegetation (i.e. addition of sparse and dense vegetation clusters) was then calculated, and divided by the cumulated surface of all the clusters, to obtain the proportion of vegetated area of the island. If the method failed to detect any vegetation on one island, we specified a default value of 0.1% of vegetation as we know there is at least one plant present on all small islands included in our study. We also calculated an index of three levels of habitat diversity corresponding of a combination of rocks (or undetectable vegetation due to low image resolution), sparse vegetation and/or dense vegetation.

The concordance of classification was then estimated using high-resolution images from Google Earth Pro. Comparison with these images was performed on 10% the islands of each geographical cluster. We used from 2 to 8 points of verification per class of habitats upon the size of the island.

2.4. Data analysis

2.4.1. Species-Area Relationship (SAR)

The Species-Area Relationship (SAR) was studied using the sars package (Matthews, Triantis, et al., 2019) on raw species richness and area. We first compared the fits of the 20 SAR models available in the package. Performances of the models were compared using the Aikake's Information Criterion (AIC). The linearized power model, with log-transformed variables (logSpeciesRichness~logArea), was then fitted to compare the relationships found in other studies and in particular the one of Ohyama et al., (2021), who synthetizes the SAR of ants at the world's scale from bibliographical data. We used this last model to calculate the slope of the relationship (z-value) and the intercepts (c-value).

2.4.2. Small Island Effect (SIE)

In order to assess a possible breakpoint in the SAR, and indicating a potential Small Island Effect (SIE), we used the available function to fit segmented regression models from the sars package (Matthews, Triantis, et al., 2019). As for the SAR models, we used surface area as the predictor of species richness. The models were fitted while looking for either one or two thresholds. We fitted both continuous and left-horizontal models, in the first case a positive slope is allowed before the breakpoint, while in the second case it is forced to be a null slope. As by default, the thresholds were searched at 0.01km² intervals and only the area was log-transformed, for scale purposes. The threshold models were compared to each other's, and with non-threshold models as well, i.e. the linear and the intercept only model, based on AIC values.

2.4.3. *Predictors of species richness*

Generalized linear mixed models (GLMMs) were fitted using the glmmTMB package (Brooks et al., 2017) in order to assess the potential predictors of species richness. We tested the following predictors: island surface, distance to the nearest continent, proportion of landmass in a 6km buffer around the focal island, proportion of vegetation and diversity of habitats. The geographical cluster was added as a random variable in the models in order to take into account spatial autocorrelation. We controlled the absence of multicollinearity in the models with the package performance (Lüdecke et al., 2024). A selection of models was then performed using the MuMIn package (Bartoń, 2023) to keep only the variables providing the lowest AIC values. We calculated the R^2 between each variable and the species richness by successively removing explanatory variables from the final model.

3. Results

We gathered ant data from 207 islands located between -3,04° and 34,75° longitude and 29,58° and 43,82° latitude (Figure 1.1). Their size range between 58 m² to 10 km², and they are located from few meters to 181 km from the mainland. Ant data originates from published (n = 46) and unpublished records (n = 161). Unpublished data from 77 small islands are shared by European collaborators (Supplementary material S1.1). The remaining unpublished records originate from personal surveys. After species and group name actualization, a total of 195 ants are identified. Habitat clustering had an overall concordance rate of 88.48% with a rate of success of vegetation classification of 91,62% of our control points.

3.1. Species-area relationship

After fitting the 20 SAR models with raw ant species richness and island area, we find that the extended power model (c*A^(z*A^-d)) is the best fit (AIC=1179.42 and R^2=0.21). The shape of the relationship is convex (Figure 1.2). The slope is 0.17 (z-value) and the intercept is 8.04 (c-value). However, the difference of AIC between the extended power model, the Power model and the Power Rosenzweig model is less than 2 points (AIC=1179.68 and 1179.86 and R^2=0.21 and 0.20 respectively). These two last models have convex shapes as well. The linearized form of the power model, with log transformed variables, has a significant adjusted R^2 of 0.13 (Figure 1.3). The log-transformed c-value is 1.83 and z-value is 0.11. However, none of these relationships respected normality and homoscedasticity.

3.1. Small Island Effect

The continuous one threshold model had a lower AIC than the linear model and the one horizontal threshold model (Table 1.1). These two last models had a difference of AIC of less than two points. The model which has the best fit is thus the continuous one threshold model, with an adjusted R^2 of 0.22. This model has a breakpoint at 0.09, which corresponds to the log-transformed area, equivalent to 1.09 km^2 (Figure 1.4). Most of the islands are under the SIE threshold (n=178). The difference of AIC between the continuous one and the continuous two thresholds is less than 2 points. However, the continuous two threshold model is not selected because the number of islands of each segment is unbalanced, with only 4 islands in the middle segment.

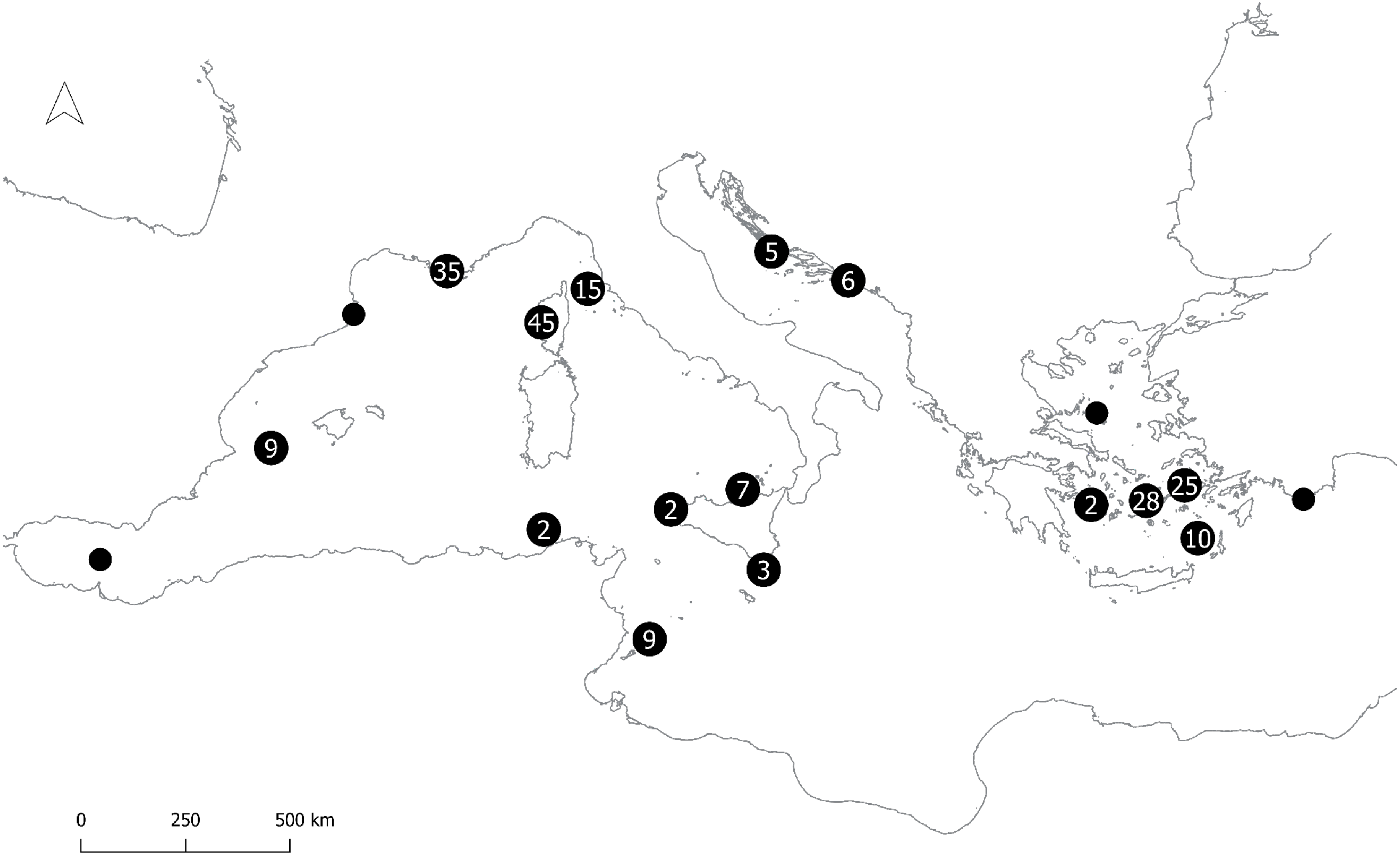


Figure 1.1 : Location of the 207 small islands we studied in the Mediterranean basin. The black dots indicate an island, the larger dots indicate a group of islands, and the number inside the dot indicates the number of islands in the group.

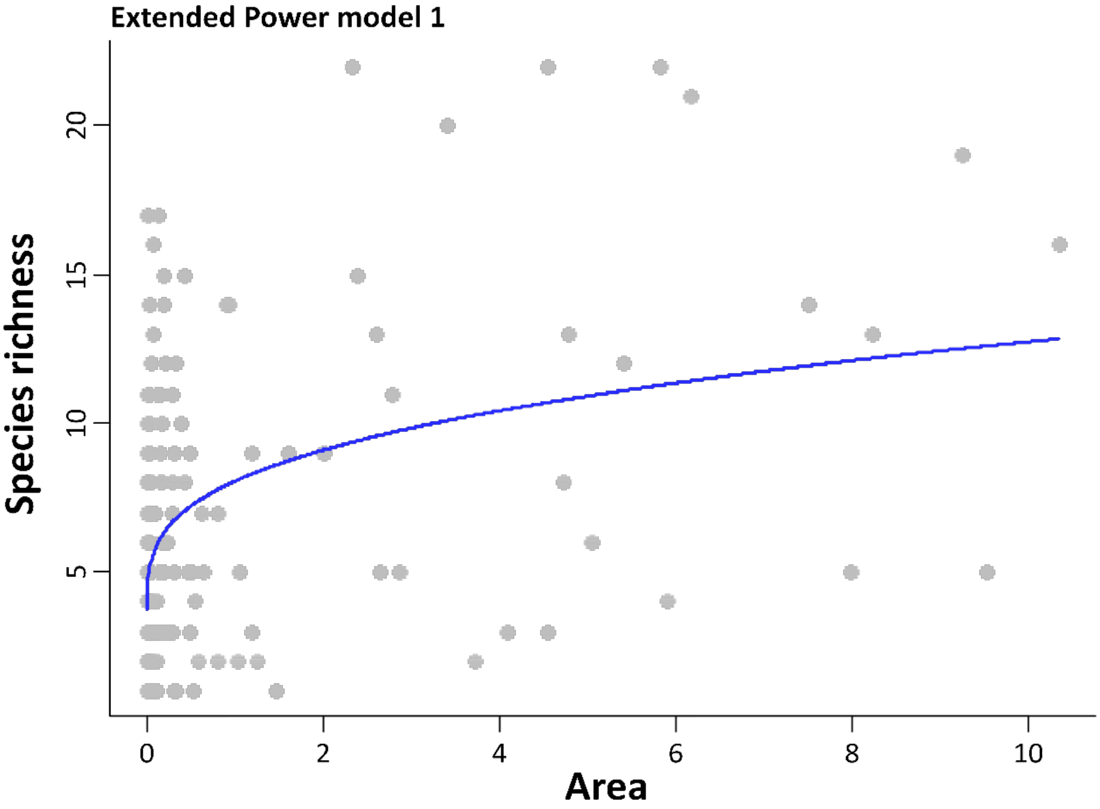


Figure 1.2: Plot of the Extended Power Model with raw ant species richness and area of 207 small Mediterranean islands

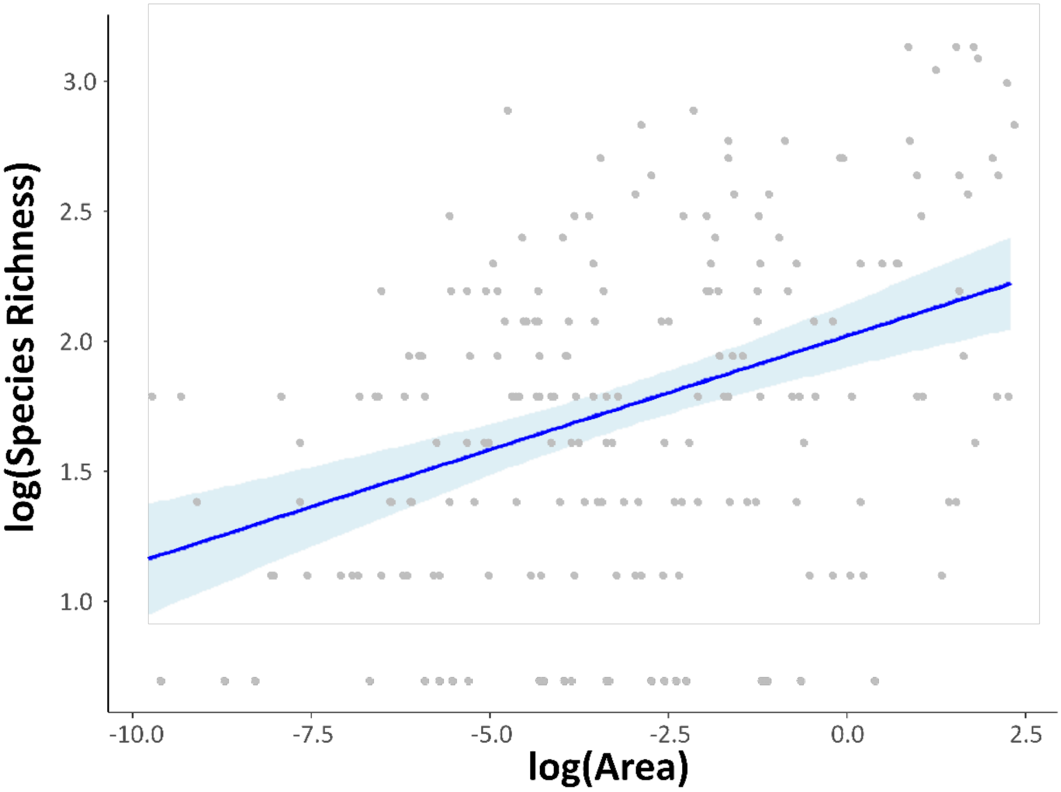


Figure 1.3: Plot of the linear model with both ant species richness and area log-transformed of 207 small Mediterranean islands

Table 1.1: Summary of the comparison between thresholds model and the linear one

Insular: semi-log	**AIC$_c$**	**Adjusted R^2**	**Threshold log(Area)**	**n Islands segment 1**	**n Islands segment 2**	**Slope 1**	**Slope 2**
Continuous one	1177.85	0.22	0.089	178	29	0.08	0.36
Linear	1184.53	0.18				0.13	
Left-horizontal one	1185.4	0.19	-1.121	117	90		0.11

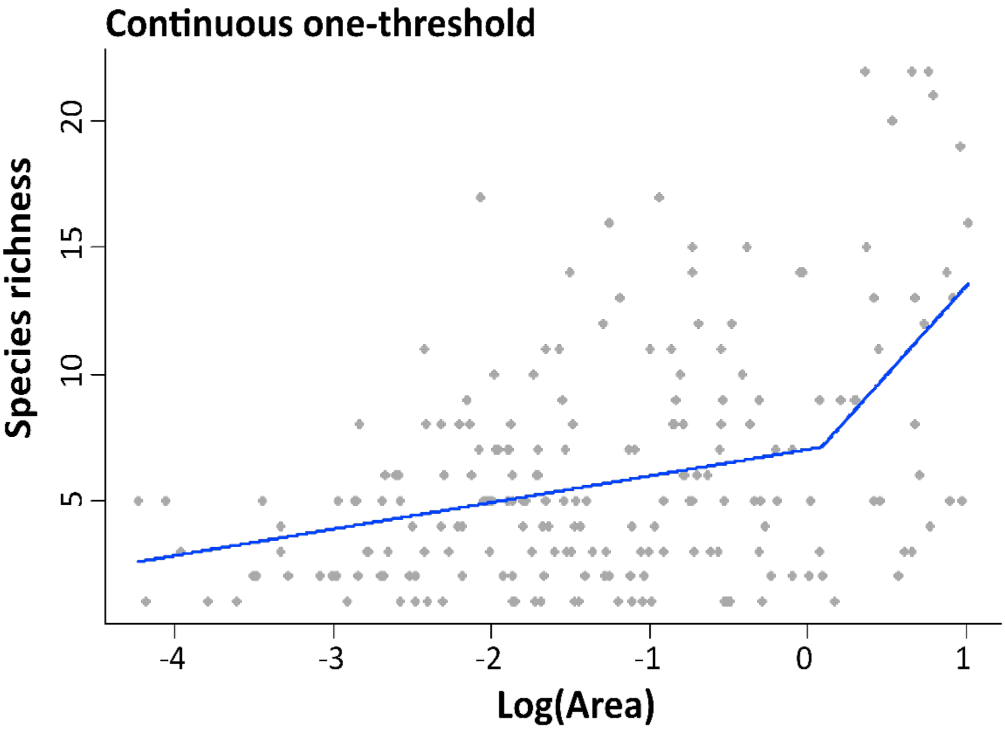


Figure 1.4: Plot of the continuous one-threshold model with both ant species richness and area of 207 small Mediterranean islands. Only the area is log-transformed. The breakpoint is at 0.09

3.1. Predictors of species richness

The mixed model that has the best fit includes three explanatory variables: surface area, proportion of landmass in a 6km buffer and proportion of habitat. Two variables were then excluded from the final model: distance to the nearest continent and habitat diversity. The final model has a R^2 of 0.554. The three selected variables have a significant positive effect on species richness (Table 1.2). Surface area explains the largest percentage of variance of species richness, while the proportion of landmass and the proportion of vegetation have lower R².

Table 1.2: Summary of the results of total ant turnover predictors after a model selection. Results were obtained with a Generalized Mixed Model fitted with negative binomial family.

	Estimate	**SE**	**p-value**	**R²**
log(Surface area)	1.130	0.025	1.25e-07	0.108
Proportion of landmass in a 6km buffer	0.009	0.003	3.19e-04	0.023
Proportion of habitat	0.004	0.002	0.04	0.038

4. Discussion

This study gathers data on ant species richness on 207 small Mediterranean islands, ranging from 58 m² to 10 km². Our personal observations showed that ants were present as long as we found a vascular plant on the island. The presence of ants on small islands of few squared meters was already noticed in former studies (Cole, 1983), from the moment that vegetation was found (Morrison, 2006). It confirms that vegetation is a good indicator for ants to establish on islands. Vegetation may indicate that nesting sites are available, either directly in the vegetation itself (Cole, 1983; Simberloff & Wilson, 1969) or in the soil that made the vegetation able to grow. The vegetation may also provide direct food resources for ants, such as seeds, and indirect resources through associated invertebrates, such as aphids or detritivores.

We found that area is indeed a good predictor of species richness. While fitting the Species-Area Relationship (SAR) models, we find that the best fit was the extended power model with a R² of 0.21, a convex relationship similar to the power model. After linearizing the relationship, we find a lower R^2, of 0.13 and a z-value of 0.11. Previous studies have shown that the SAR is most of the time best represented by the power model (Arrhenius, 1921; Triantis et al., 2012). General reviews about the SAR have also shown that slopes usually range between 0.2 and 0.4 (Connor & McCoy, 1979; Triantis et al., 2012). The slope of our island dataset is lower than what was found for ants on insular systems at the global scale by Ohyama et al., (2021) (0.25 +/- 0.02). Surface area have already been shown to be a weak predictor of ant species richness compared to habitat or vegetation diversity (Morrison, 1998; Torres & Snelling, 1997). As our study focuses on the smallest islands of the Mediterranean basin, the low slope might be attributed to the Small Island Effect (SIE). Small islands could host less species as they are more prone to stochastic events of disturbance, while having smaller populations which are less stable (Lomolino & Weiser, 2001). Moreover, the absence of certain phenomenon on small continental islands, such as speciation, can also explain slower increase in species richness with island area compared to larger islands and oceanic islands that are highly isolated (Triantis et al., 2012).

The threshold models show that there may be a SIE within the range of small islands that we studied. We found a shallow-steep relationship with a breakpoint at 1.09 km^2. Here, even if we failed to get a good fit for the left-horizontal relationship, that could be the classic form of the SIE (Lomolino & Weiser, 2001), we found that under a certain size the increase in species richness is slower. Sizes of the islands that were included in the study are already far below the SIE threshold found by Ohyama et al., (2021), which is around 150km^2. It is however very close from the 1km^2 found by Sfenthourakis & Triantis, (2009) for terrestrial isopods of Aegean islands in Greece, while applying the Lomolino & Weiser, (2001) method, i.e. left-horizontal threshold model. Triantis et al., (2006) suggested that the SIE is a matter of the indirect effects of area through habitat diversity. Island size plays an important role as a predictor of species richness as it often translates the quantity of habitat available (Connor & McCoy, 1979). The surface area is easier to measure than it is to quantify habitats, which are known to be a good predictor of diversity (Tews et al., 2004). However, under the SIE, the distribution of habitats often show more heterogeneity and is not always correlated with area (Triantis et al., 2006).

The proportion of habitats was a significant predictor of species richness, but still weaker than island area. At the contrary, other studies on ants found that habitat and vegetation diversity was a better predictor than island area (Morrison, 1998; Torres & Snelling, 1997). This result still confirm that the effects of surface area and habitat are not necessarily mutually exclusive, but rather complementary (Kallimanis et al., 2008). Here, the weakness of this relationship should be interpreted carefully. In our case, the method we used to determine habitat quantity and diversity can cause some issues. Indeed, the resolution of the image may have been too low in the case of very small islands to detect very sparse vegetation. Even with these issues, we managed to find a positive response of the proportion of habitats on islands, meaning that the link between habitats and ant diversity should be further studied. It is acknowledged that there are still gaps in understanding the effects of habitats on the SAR (Ohyama et al., 2021).

Studies on the SAR agree that more predictors should be added to the models (Chase et al., 2019; Triantis et al., 2003). Here, we showed that the distance to the nearest continent failed to predict ant species richness, similarly to other studies (Torres & Snelling, 1997). Nevertheless, isolation is a central point of the island biogeography theory (MacArthur & Wilson, 1963). Concerning ants and small continental islands, distance to the nearest continent might not be that meaningful considering their dispersal abilities (Morrison, 2016).

Most of the time ants colonize the islands through the mating flights (Vepsäläinen & Pisarski, 1982). The relative proximity of the islands studied with the continent and the almost systematic presence of stepping stones make the colonization even easier. It is then important to adapt the isolation index to the biological group studied (Itescu et al., 2020). It seems straightforward that an increased proportion of landmass in a 6km buffer, the average dispersal distance of ants (Helms, 2017), can promote a diversity of propagules and an increased species richness. Still, in view of the weakness of the relationship observed and the lack of knowledge about ant dispersal abilities, and especially differences among species (Helms, 2017), this index could be further improved.

Many questions remain about ant biogeography and community structures on small Mediterranean islands. The patterns of the SAR and SIE might be different among the geographical clusters, because of the community compositions or the geological history of the areas. At the global scale, Ohyama et al., (2021) showed that slopes of the SARs just like SIE thresholds change among the biogeographical realms. Gentile & Argano, (2005) also showed that the biogeographical complexity of the Mediterranean basin had highly structured the isopod communities on small islands. Along with differences between archipelagoes, it would be important to assess the heterogeneity of small island habitats. The relationship between island area and habitats diversity and quantity should be further studied, as most of the studies on ants and islands have shown how habitats are an important factor to predict the species richness (Goldstein, 1975; Morrison, 2016; Torres & Snelling, 1997). Studies have also shown that the presence of alien species and anthropogenic disturbance are important factors that could impact ant diversity on islands (Rizali et al., 2010, 2011). Our study could then benefit of the addition of more biotic factors, either about habitats, alien species or even bird colonies as they are already known to be in strong interactions with plant dynamics, physical and chemical island characteristics and thus resource availability on islands (Médail, 2017; Polis & Hurd, 1995). Finally, it would be interesting to assess the effects of biotic and geographical factors on not only the species richness but other biodiversity indicator as well, such as phylogenetic diversity and functional diversity, that are worth further studies (Mazel & Thuiller, 2021).

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Supplementary Material

Table S1.1: List of the 207 small Mediterranean islands studied and their location details. The to last columns indicate the source of ant data and either the reference or the name of the persons who shared their data

Name	Geographical Cluster	Latitude	Longitude	Type of source	Source
Ile d Alboran	SOUTH SPAIN	35.93947	-3.03474	Unpublished	Abad, 2006
Meda Gran	EASTERN SPAIN	42.04722	3.22273	Bibliography	Espadaler & Rodà, 1984
S Espardell	BALEARIC ISLANDS	38.79604	1.47688	Bibliography	Espadaler et al., 2013
Es Vedra	BALEARIC ISLANDS	38.86711	1.19738	Bibliography	Espadaler et al. 2013
Es Vedranell	BALEARIC ISLANDS	38.86935	1.21187	Bibliography	Espadaler et al. 2013
S Espartar	BALEARIC ISLANDS	38.95862	1.19509	Bibliography	Espadaler et al. 2013
Escull s Espartar	BALEARIC ISLANDS	38.958643	1.201461	Bibliography	Espadaler et al. 2013
Na Gorra	BALEARIC ISLANDS	38.968205	1.165495	Bibliography	Espadaler et al. 2013
illa des Bosc	BALEARIC ISLANDS	38.9689	1.21708	Bibliography	Espadaler et al. 2013
Na Bosc	BALEARIC ISLANDS	38.972265	1.165755	Bibliography	Espadaler et al. 2013
Sa Conillera	BALEARIC ISLANDS	38.98532	1.20986	Bibliography	Espadaler et al. 2013
Ilot de la gabiniere	SOUTHERN FRANCE	42.98833	6.395287	Unpublished	Personal surveys
Gros Sarranier	SOUTHERN FRANCE	42.99887	6.252806	Unpublished	Personal surveys
Pointe Sainte Anne	SOUTHERN FRANCE	43.00189	6.159811	Unpublished	Personal surveys
Petit Langoustier	SOUTHERN FRANCE	43.00447	6.1614	Unpublished	Personal surveys
Rocher du Rascas	SOUTHERN FRANCE	43.01442	6.389294	Unpublished	Personal surveys
Rocher des Medes sud	SOUTHERN FRANCE	43.02739	6.241893	Unpublished	Personal surveys
Ilot du Cap de Esterel	SOUTHERN FRANCE	43.03273	6.17359	Unpublished	Personal surveys
Les Fourmigues Est	SOUTHERN FRANCE	43.03981	6.069429	Unpublished	Personal surveys
Ile de la Ratonniere	SOUTHERN FRANCE	43.04032	6.087943	Unpublished	Personal surveys
Ile Longue	SOUTHERN FRANCE	43.04115	6.090967	Unpublished	Personal surveys
Ile de la Redonne	SOUTHERN FRANCE	43.04251	6.09804	Unpublished	Personal surveys
Grand Rouveau	SOUTHERN FRANCE	43.080301	5.767611	Unpublished	Personal surveys
Petit Rouveau	SOUTHERN FRANCE	43.084057	5.778444	Unpublished	Personal surveys
Ilot Estagnol sud	SOUTHERN FRANCE	43.10481	6.298982	Unpublished	Personal surveys

Ilot du Jardin	SOUTHERN FRANCE	43.10532	6.304966	Unpublished	Personal surveys
Ilot Estagnol nord	SOUTHERN FRANCE	43.1055	6.299368	Unpublished	Personal surveys
L Estagnolon	SOUTHERN FRANCE	43.10593	6.299689	Unpublished	Personal surveys
Ilot de Leoube	SOUTHERN FRANCE	43.11405	6.282773	Unpublished	Personal surveys
Grand Congloue	SOUTHERN FRANCE	43.17597	5.401273	Unpublished	Personal surveys
Riou	SOUTHERN FRANCE	43.17638	5.385431	Unpublished	Personal surveys
Petit Congloue	SOUTHERN FRANCE	43.17895	5.396069	Unpublished	Personal surveys
Ile Plane	SOUTHERN FRANCE	43.18781	5.385794	Unpublished	Personal surveys
Jarre	SOUTHERN FRANCE	43.19718	5.365064	Unpublished	Personal surveys
Ilot du Planier	SOUTHERN FRANCE	43.1986	5.229774	Unpublished	Personal surveys
Jarron	SOUTHERN FRANCE	43.20035	5.357022	Unpublished	Personal surveys
Le Torpilleur	SOUTHERN FRANCE	43.21044	5.456607	Unpublished	Personal surveys
Maire	SOUTHERN FRANCE	43.21102	5.335404	Unpublished	Personal surveys
Tiboulen de Maire	SOUTHERN FRANCE	43.21407	5.326789	Unpublished	Personal surveys
Ilot de la Crine	SOUTHERN FRANCE	43.267725	5.292645	Unpublished	Personal surveys
Ile d Endoume	SOUTHERN FRANCE	43.27928	5.344662	Unpublished	Personal surveys
Tiboulen de Ratonneau	SOUTHERN FRANCE	43.27943	5.286562	Unpublished	Personal surveys
Caroline	SOUTHERN FRANCE	43.28392	5.321583	Unpublished	Personal surveys
Le Lion de Mer	SOUTHERN FRANCE	43.40694	6.774117	Unpublished	Personal surveys
Ilot pointe Dramont	SOUTHERN FRANCE	43.411545	6.855633	Unpublished	Personal surveys
Ile des Vieilles	SOUTHERN FRANCE	43.42743	6.894163	Unpublished	Personal surveys
Barthelemy	SOUTHERN FRANCE	43.44543	6.908319	Unpublished	Personal surveys
Maubois Sud	SOUTHERN FRANCE	43.45447	6.922958	Unpublished	Personal surveys
Maubois Nord	SOUTHERN FRANCE	43.45515	6.923327	Unpublished	Personal surveys
Ilot C Silene	CORSICA	41.346668	9.255278	MNHN	J. Casevitz-Weurlesse
Isulonu di passu	CORSICA	41.348331	9.25	MNHN	J. Casevitz-Weurlesse
Isolotto Giacinto Paoli	CORSICA	41.348331	9.255	MNHN	J. Casevitz-Weurlesse
Piana	CORSICA	41.550835	9.361389	MNHN	J. Casevitz-Weurlesse
Capense	CORSICA	42.963612	9.341927	MNHN	J. Casevitz-Weurlesse
Sperduto piccolo	CORSICA	41.368889	9.305834	Unpublished	Personal surveys
Sperduto grande	CORSICA	41.369999	9.305	Unpublished	Personal surveys
Porraggia grande	CORSICA	41.391666	9.263056	Unpublished	Personal surveys
Porraggia piccola	CORSICA	41.393055	9.264444	Unpublished	Personal surveys
Ilot du Port	CORSICA	41.473057	9.073889	Unpublished	Personal surveys
Toro piccolo	CORSICA	41.507953	9.380319	Unpublished	Personal surveys
Toro Piccolo 2	CORSICA	41.508386	9.379819	Unpublished	Personal surveys
Toro Piccolo 1	CORSICA	41.508433	9.379242	Unpublished	Personal surveys
Toro Grande	CORSICA	41.509267	9.381597	Unpublished	Personal surveys
Ilot Torello	CORSICA	41.509419	9.383322	Unpublished	Personal surveys
Folaca	CORSICA	41.548527	9.315025	Unpublished	Personal surveys

Rocher Vacca	CORSICA	41.556389	9.387222	Unpublished	Personal surveys
Roscana	CORSICA	41.683334	9.401944	Unpublished	Personal surveys
Ilot de la plage	CORSICA	42.236389	8.5575	Unpublished	Personal surveys
Rocher de Turghiu	CORSICA	42.239057	8.547203	Unpublished	Personal surveys
Sbiro	CORSICA	42.240003	8.547299	Unpublished	Personal surveys
Orto piccolo	CORSICA	42.241847	8.572403	Unpublished	Personal surveys
Orto Grande	CORSICA	42.243628	8.576272	Unpublished	Personal surveys
Guardiola	CORSICA	42.245967	8.586733	Unpublished	Personal surveys
Ilot de Cato Ouest	CORSICA	42.33735	8.569622	Unpublished	Personal surveys
Ilot du chene	CORSICA	42.337939	8.570392	Unpublished	Personal surveys
Cala Maiora	CORSICA	42.345894	8.552131	Unpublished	Personal surveys
Girolata	CORSICA	42.347778	8.609167	Unpublished	Personal surveys
Sud Sulana	CORSICA	42.356945	8.553056	Unpublished	Personal surveys
Purcile Sud	CORSICA	42.3584	8.555644	Unpublished	Personal surveys
Garganello	CORSICA	42.365276	8.539722	Unpublished	Personal surveys
Cala di l Oru 2	CORSICA	42.368991	8.5427	Unpublished	Personal surveys
Gargalo	CORSICA	42.369999	8.539166	Unpublished	Personal surveys
Elbu occidental	CORSICA	42.370342	8.569135	Unpublished	Personal surveys
Elbu Oriental	CORSICA	42.374985	8.573625	Unpublished	Personal surveys
Furmicula	CORSICA	42.375614	8.570494	Unpublished	Personal surveys
Palazzinu	CORSICA	42.379795	8.550322	Unpublished	Personal surveys
Palazzu	CORSICA	42.380385	8.546596	Unpublished	Personal surveys
Porri	CORSICA	42.386112	8.581944	Unpublished	Personal surveys
Elpa Nera 4	CORSICA	42.405591	8.609475	Unpublished	Personal surveys
Elpa Nera 3	CORSICA	42.406132	8.607956	Unpublished	Personal surveys
Rocher Darsana	CORSICA	42.448794	8.667878	Unpublished	Personal surveys
Spano	CORSICA	42.600834	8.799444	Unpublished	Personal surveys
Finocchiarola	CORSICA	42.983612	9.470834	Unpublished	Personal surveys
Mezzana	CORSICA	42.984165	9.468889	Unpublished	Personal surveys
Terra	CORSICA	42.98545	9.466217	Unpublished	Personal surveys
Giraglia	CORSICA	43.025002	9.406667	Unpublished	Personal surveys
Galiton sud ouest	NORTHERN TUNISIA	37.4976	8.87539	Bibliography	Bernard, 1959
La Galite	NORTHERN TUNISIA	37.5258	8.92797	Bibliography	Bernard, 1959
Keblia	EASTERN TUNISIA	34.753077	11.360776	Bibliography	Oueslati et al., 2022
Gremdi	EASTERN TUNISIA	34.75567	11.3204	Bibliography	Oueslati et al. 2020
Jeblia	EASTERN TUNISIA	34.757467	11.362397	Bibliography	Oueslati et al. 2020
Gharsa	EASTERN TUNISIA	34.758264	11.350277	Bibliography	Oueslati et al. 2020
Sefnou	EASTERN TUNISIA	34.79558	11.22512	Bibliography	Oueslati et al. 2020
Roumadia	EASTERN TUNISIA	34.81252	11.31345	Bibliography	Oueslati et al. 2020
Giannutri	ITALY LIGURIAN	42.25117	11.10092	Bibliography	Baroni-Urbani, 1971

Formica G di Gross	ITALY LIGURIAN	42.57679	10.88189	Bibliography	Baroni Urbani 1971
Scola di Pianosa	ITALY LIGURIAN	42.58189	10.08058	Bibliography	Baroni Urbani 1971
Sco Gemini di Fuori	ITALY LIGURIAN	42.71733	10.37284	Bibliography	Baroni Urbani 1971
Sco Gemini di Terra	ITALY LIGURIAN	42.718535	10.374192	Bibliography	Baroni Urbani 1971
Is Di Ortano	ITALY LIGURIAN	42.790185	10.433637	Bibliography	Baroni Urbani 1971
Cerboli	ITALY LIGURIAN	42.85765	10.54695	Bibliography	Baroni Urbani 1971
Palmaiola	ITALY LIGURIAN	42.86569	10.4747	Bibliography	Baroni Urbani 1971
Is Dei Topi	ITALY LIGURIAN	42.87081	10.42343	Bibliography	Baroni Urbani 1971
Gorgona	ITALY LIGURIAN	43.4286	9.8987	Bibliography	Baroni Urbani 1971
Conigli	SICILY	35.510008	12.558497	Bibliography	Bernard, 1959
Lampione	SICILY	35.551788	12.321123	Bibliography	Baroni-Urbani, 1971
Linosa	SICILY	35.866057	12.865989	Unpublished	Enrico Schifani & Antonio Alicata
Isola Capo Passero	SICILY	36.687214	15.149388	Unpublished	Enrico Schifani & Antonio Alicata
Isola di Vendicari	SICILY	36.791973	15.104414	Unpublished	Enrico Schifani & Antonio Alicata
Isola Lachea	SICILY	37.561268	15.166218	Unpublished	Enrico Schifani & Antonio Alicata
Isola Bella	SICILY	37.850191	15.300701	Unpublished	Enrico Schifani & Antonio Alicata
Isola di San Pantaleo	SICILY	37.867549	12.468411	Unpublished	Enrico Schifani & Antonio Alicata
Levanzo	SICILY	37.998827	12.333504	Unpublished	Enrico Schifani & Antonio Alicata
Isola delle Femmine	SICILY	38.210754	13.23536	Unpublished	Enrico Schifani & Antonio Alicata
Alicudi	SICILY	38.544746	14.351929	Unpublished	Enrico Schifani & Antonio Alicata
Filicudi	SICILY	38.572928	14.557823	Unpublished	Enrico Schifani & Antonio Alicata
Panarea	SICILY	38.637218	15.065733	Unpublished	Enrico Schifani & Antonio Alicata
Ustica	SICILY	38.706517	13.176617	Unpublished	Enrico Schifani & Antonio Alicata
SvAndrija	CROATIA	42.646956	17.951184	Unpublished	Jelena Bujan
Lopud	CROATIA	42.694893	17.949709	Unpublished	Jelena Bujan

Ruda	CROATIA	42.710189	17.92931	Unpublished	Jelena Bujan
Misnjak	CROATIA	42.758689	17.831395	Unpublished	Jelena Bujan
Tajan	CROATIA	42.758937	17.797299	Unpublished	Jelena Bujan
Olipa	CROATIA	42.761141	17.779846	Unpublished	Jelena Bujan
Bisevo	CROATIA	42.982685	16.005863	Unpublished	Jelena Bujan
Marinkovac Island	CROATIA	43.15776	16.42008	Unpublished	Gregor Bracko
Piskera Island	CROATIA	43.76763	15.33781	Unpublished	Gregor Bracko
Mana	CROATIA	43.80254	15.268504	Unpublished	Jelena Bujan
Levrnaka	CROATIA	43.823956	15.246711	Unpublished	Jelena Bujan
Armathia	GREECE	35.43758	26.86108	Unpublished	Lech Borowiec
Karofyllas	GREECE	35.45846	26.91152	Unpublished	Lech Borowiec
Anatoliki Divounia	GREECE	35.82563	26.46634	Unpublished	Christos Georgiadis
Chamili	GREECE	35.86317	26.22977	Unpublished	Christos Georgiadis
Astakidopoulo	GREECE	35.87524	26.82382	Unpublished	Christos Georgiadis
Astakida	GREECE	35.88321	26.8224	Unpublished	Christos Georgiadis
Mikro Karavonisi Astypalaia	GREECE	36.000794	26.435248	Unpublished	Christos Georgiadis
Mikros Zaforas Astypalaia	GREECE	36.04727	26.40933	Unpublished	Christos Georgiadis
Mesaios Zaforas Astypalaia	GREECE	36.0573	26.405	Unpublished	Christos Georgiadis
Megalos Zaforas Astypalaia	GREECE	36.0734	26.39961	Unpublished	Christos Georgiadis
Kastellorizo	GREECE	36.14169	29.5808	Unpublished	Lech Borowiec
Christiana	GREECE	36.24917	25.20333	Unpublished	Lech Borowiec
Mikro Fteno Anafi	GREECE	36.311788	25.79539	Unpublished	Christos Georgiadis
Megalo Fteno Anafi	GREECE	36.311896	25.800504	Unpublished	Christos Georgiadis
Kandelioussa	GREECE	36.50235	26.97096	Unpublished	Lech Borowiec
Agia Kyriaki	GREECE	36.54913	26.40366	Unpublished	Lech Borowiec
Pachia Nysirou	GREECE	36.56948	27.07218	Unpublished	Lech Borowiec
Varvaronisi Ios	GREECE	36.648449	25.38687	Unpublished	Christos Georgiadis
Gyali	GREECE	36.66587	27.12173	Unpublished	Lech Borowiec
Agios Efstathios Kimolos	GREECE	36.77476	24.58199	Unpublished	Christos Georgiadis
Kisiri Amorgos	GREECE	36.790593	25.740087	Unpublished	Christos Georgiadis
Gramvousa Amorgos	GREECE	36.80696	25.745396	Unpublished	Christos Georgiadis
Psalida Amorgos	GREECE	36.816173	25.746001	Unpublished	Christos Georgiadis

Petalidi Amorgos	GREECE	36.818987	25.793453	Unpublished	Christos Georgiadis
Mikros Avelas	GREECE	36.827585	25.395364	Unpublished	Christos Georgiadis
Argilos Naxos	GREECE	36.834961	25.525019	Unpublished	Christos Georgiadis
Ofidousa Naxos	GREECE	36.845407	25.520012	Unpublished	Christos Georgiadis
Aspronisi Naxos	GREECE	36.855313	25.546131	Unpublished	Christos Georgiadis
Venetiko Naxos	GREECE	36.855766	25.484871	Unpublished	Christos Georgiadis
Gramvonisi Amorgos	GREECE	36.879117	25.89238	Unpublished	Christos Georgiadis
Nikouria Amorgos	GREECE	36.884893	25.90773	Unpublished	Christos Georgiadis
Kato Koufonisi Naxos	GREECE	36.90961	25.573352	Unpublished	Christos Georgiadis
Nera	GREECE	36.91379	26.93875	Unpublished	Lech Borowiec
Apano Koufonisi Naxou	GREECE	36.941265	25.606553	Unpublished	Christos Georgiadis
Panteronisi Paros	GREECE	36.971393	25.118694	Unpublished	Christos Georgiadis
Despotiko Antiparos	GREECE	36.9724	25.015799	Unpublished	Christos Georgiadis
Tsimintiri Antiparos	GREECE	36.97569	25.018492	Unpublished	Christos Georgiadis
Glaropounta Paros	GREECE	36.979693	25.110802	Unpublished	Christos Georgiadis
Kinaros Leros	GREECE	36.9797	26.2893	Unpublished	Christos Georgiadis
Glaros Leros	GREECE	36.9863	26.3255	Unpublished	Christos Georgiadis
Preza Paros	GREECE	36.9891	25.1012	Unpublished	Christos Georgiadis
Drionisi Paros	GREECE	36.992721	25.240633	Unpublished	Christos Georgiadis
Dytiko Mavri Leros	GREECE	36.99569	26.37313	Unpublished	Christos Georgiadis
Anatoliko Mavri Leros	GREECE	36.9957	26.3818	Unpublished	Christos Georgiadis
Tourlos Paros	GREECE	36.995784	25.09748	Unpublished	Christos Georgiadis
Telendos	GREECE	37.00826	26.9096	Unpublished	Lech Borowiec
Kato Fira Antiparos	GREECE	37.050885	25.087388	Unpublished	Christos Georgiadis

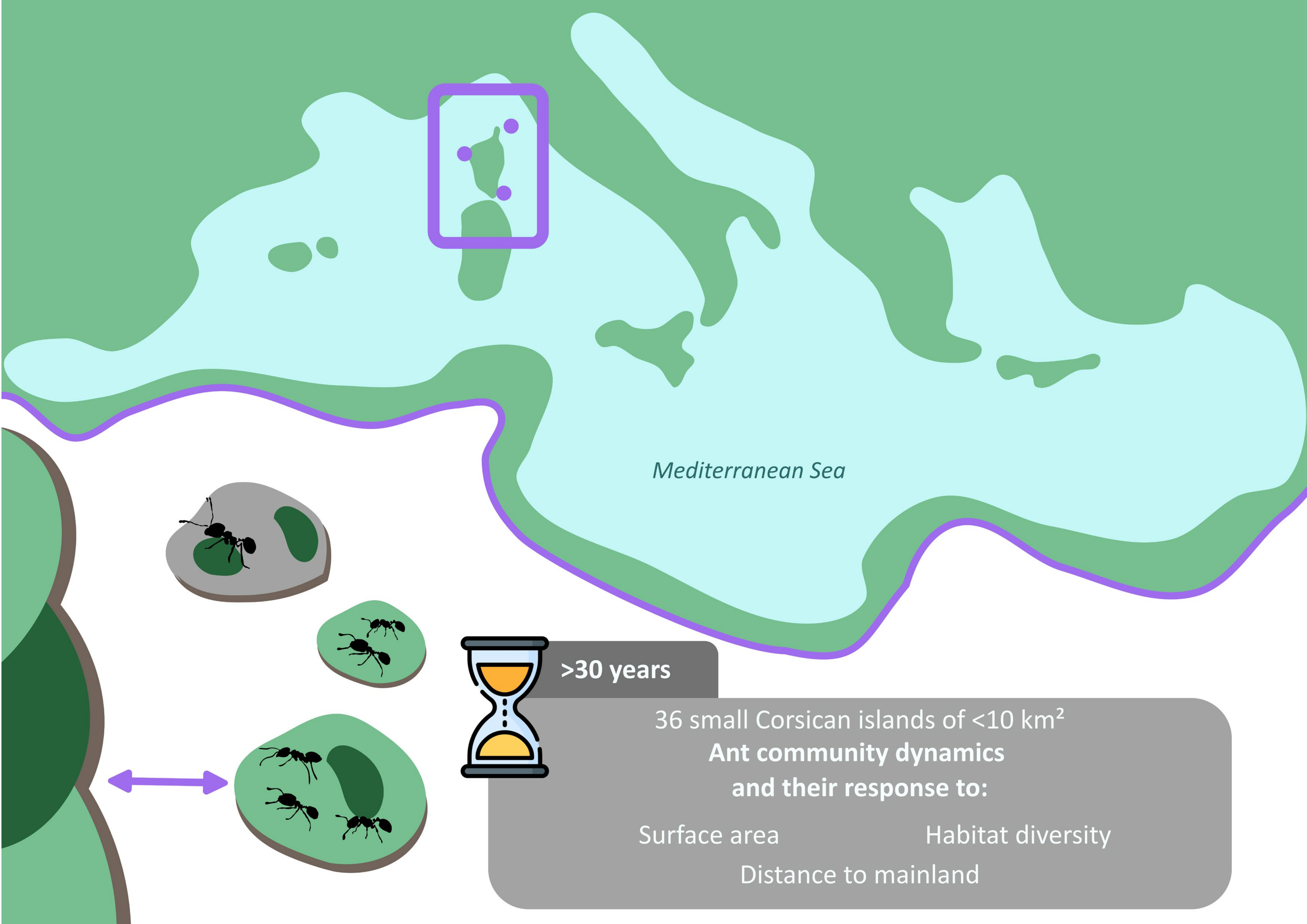
Diplo Paros	GREECE	37.060657	25.085221	Unpublished	Christos Georgiadis
Manto Naxos	GREECE	37.089093	25.361482	Unpublished	Christos Georgiadis
Filidi Paros	GREECE	37.124947	25.289961	Unpublished	Christos Georgiadis
Agia Kali Paros	GREECE	37.130272	25.224506	Unpublished	Christos Georgiadis
Evriokastro Paros	GREECE	37.151744	25.296186	Unpublished	Christos Georgiadis
Gaidouronisi Paros	GREECE	37.157463	25.268183	Unpublished	Christos Georgiadis
Farantonisia Leros	GREECE	37.1928	26.7616	Unpublished	Christos Georgiadis
Saraki Leipsoi	GREECE	37.228	26.7	Unpublished	Christos Georgiadis
Komaros Patmos	GREECE	37.2558	26.7189	Unpublished	Christos Georgiadis
Lira Leipsoi	GREECE	37.2771	26.7705	Unpublished	Christos Georgiadis
Kounoupi	GREECE	37.306422	23.204714	Unpublished	Lech Borowiec
Aspronisia Leipsoi	GREECE	37.3074	26.8031	Unpublished	Christos Georgiadis
Makronisi	GREECE	37.36066	26.75353	Unpublished	Christos Georgiadis
Marathi Patmos	GREECE	37.3682	26.725	Unpublished	Christos Georgiadis
Delos	GREECE	37.39022	25.27084	Unpublished	Lech Borowiec
Fragkos Leipsoi	GREECE	37.4047	26.7244	Unpublished	Christos Georgiadis
Petrokaravo Patmos	GREECE	37.4118	26.4444	Unpublished	Christos Georgiadis
Megalos Anthropofas	GREECE	37.5174	26.5425	Unpublished	Christos Georgiadis
Alatonisi Fournoi	GREECE	37.53193	26.41645	Unpublished	Christos Georgiadis
Vorio Podi Skyros	GREECE	39.018144	24.468043	Unpublished	Christos Georgiadis
Comino	MALTA	36.01163	14.3365	Bibliography	Baroni-Urbani, 1968

Transition to chapter 2

In the first chapter we have shown the importance of island area to predict species richness and to a lesser extent, isolation and habitat proportion on the island. Our data show evidence of a Small Island Effect (SIE), with most islands exhibiting a very slow increase in species richness as area increases. This confirms the complexity of the Island's Species Area Relationship (ISAR) behind its apparent simplicity.

The following chapter is the opportunity to discuss the dynamic vision of the communities proposed in the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1963, 1967). Indeed, stochastic colonization and extinction events do not only affect species richness at a single point in time, as these events are likely to recur, suggesting that species richness remains stable while community composition changes (turnover), with these two processes balancing each other. In order to assess these assumptions, but also the response of turnover to area, isolation and habitat diversity, we used a 36-island subset of the precedent dataset for which we had relatively old records.

Among the small Mediterranean islands that triggered interest, the satellite islands of Corsica have been studied for decades (Paradis et al., 2021), including relatively exhaustive ant sampling on dozens of islands (Casevitz-Weulersse, 2014; Delaugerre, 1986; Delaugerre & Brunstein, 1987; Delaugerre & Guyot, 1995). We took advantage of this data on ants, as well as that on vegetation, to resurvey ant communities and gain a better understanding of how ant communities change over more than 30 years, assessing what are the factors affecting these changes.



>30 years

36 small Corsican islands of <10 km²

Ant community dynamics

and their response to:

Surface area

Habitat diversity

Distance to mainland

Small islands of the Capo Rosso (Corsica) © Romane Blaya

CHAPITRE 2

Towards ant community homogenization: Long-term non-equilibrium on small uninhabited Mediterranean islands

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In prep. for *Ecography*

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6. Université Claude Bernard Lyon 1, LEHNA UMR 5023, CNRS, ENTPE, Lyon, France

Abstract

Studying biodiversity dynamics is a growing challenge in the context of global change. Global changes may cause biodiversity loss, but also an increase of diversity and an homogenization of communities at lower scales. Islands were shown to reach a dynamic equilibrium state characterized by a species richness stability and composition turnover. In order to study community temporal dynamics of ants we focused on 36 well-preserved small islands (<10km²) around Corsica. Ant surveys from the 1980's and 1990's were compared with surveys conducted in 2023 on the same islands. If the regional pool of species remained quite stable, with an increase of one species, island species richness increased. Communities tended to homogenize, with high rates of nestedness and colonization. Meanwhile, very few populations underwent extinctions resulting in low replacement rates. A small pool of species, including *Tetramorium semilaeve*, colonized many islands. Global changes can promote community homogenization as it can provoke an increase in the activity of generalist species leading to a range expansion. Nevertheless, ants underwent low turnover and replacement in accordance with their high longevity and strong resistance to climatic disturbance. Finally, islands with more plant alliances had lower total turnover rates and those that were more isolated had less replacement as well. This result seems to corroborate the Small Island Effect (SIE). According to the SIE habitat diversity and quantity would be prevalent factors on small islands because they are subject to drastic environmental conditions, with more heterogeneity, and inherently less diversified habitats compared to bigger islands. Preserved ecosystems are submitted to the multiple forces of global changes, and small islands show specific dynamics, important to understand the global evolution of communities.

Keywords: temporal dynamics, turnover, nestedness, small islands, ants

1. Introduction

Studying biodiversity dynamics is a growing challenge in the context of global change (Hautier et al., 2015). Our planet is changing rapidly due to a range of threats, including habitat destruction, pollution, biological invasions and climate change. Global changes may cause biodiversity loss, but at local and regional scales it can also lead to an increase in diversity or an homogenization of communities (Chase et al., 2019). This situation is a cause for concern, as changes in the structure of species communities have an impact on the way ecosystems function (Gonzalez et al., 2020). This is particularly true for groups that are involved in many important ecosystem processes, such as ecosystem engineers (Jones et al., 1994).

It is important to understand natural processes of change in communities to implement better conservation policies as we are faced with increasing anthropogenic pressures (Gillespie et al., 2008). Biodiversity conservation is particularly at stake on island that host a disproportionate amount of world's biodiversity and experience higher rates of extinctions (Fernández-Palacios et al., 2021; Russell & Kueffer, 2019). Islands are considered more vulnerable because of their limited sizes, high endemicity, small populations and vacant ecological niches (Fernández-Palacios et al., 2021).

The restricted geographical limits of islands also make them good replicated study systems (Whittaker et al., 2017). In 1961, E.O. Wilson observed ants from Melanasia and described sequential phases of expansion and contraction of species ranges which he called the taxon cycle theory. Community temporal turnover was then a central point of MacArthur & Wilson's theory of island biogeography (1963, 1967). They described that islands experience a dynamic equilibrium through stochastic events of colonization and extinctions resulting in a stable species richness and a composition turnover. Upon their predictions, turnover rates should be inversely proportionate with island area and isolation.

The dynamic equilibrium theory has already been widely studied on fragmented system, applied to various biological groups, showing either cases of equilibrium (Manne et al., 1998; Valente et al., 2017), or ones of non-equilibrium (Lynch & Johnson, 1974; Morrison, 2010a, 2010b; Nuvoloni et al., 2016). The existence of an equilibrium stage on islands can be difficult to observe and its veracity is discussed (Gilbert, 1980). It is often described to be interrupted by non-equilibrium phases (McCollin, 2015; Valente et al., 2015) as climate or dramatic events (e.g. hurricanes) can periodically influence extinction-colonization dynamics (Morrison, 2010b, 2010a; Nuvoloni et al., 2016). Nevertheless, it offers a framework to better understand community dynamics, for which the turnover can be sorted in a continuum between equilibrium and non-equilibrium and high to low bio-dynamism (Whittaker et al., 2023).

More than 50 years after McArthur & Wilson's theory, biodiversity temporal dynamics are still high-ranking priority questions in island biogeography (Patiño et al., 2017).

Due to their wide distribution (Schultheiss et al., 2022) and their diversified ecologies (Andersen, 1997), ants (Hymenoptera: Formicidae) are good biological models to contribute to these questions. Most ants also have great dispersal abilities, they can colonize new habitats several kilometers from their original colony during nuptial flights (Helms, 2017). Their ability to nest in cavities and in soils gives them strong resistance to disturbance (Morrison, 2002). Both Morrison (2010a) and Torres & Snelling (1997) proposed the relative resistance of ants to explain the low temporal turnovers of their communities on islands. Nevertheless, their studies considered relatively short time span, respectively 17 and 18 years, compared to ant record longevity (Hölldobler & Wilson, 1990), and no studies on ant community dynamics were conducted on Mediterranean islands.

The Mediterranean basin is a great candidate for island biogeography studies as it is one of the regions with the largest number of islands, with more than 11,000 islands and islets (Médail, 2017, 2022), and is also recognized as a hotspot of biodiversity (Perret et al., 2023). These islands, and especially the smallest, appear to be highly sensitive to global change (Médail, 2017). If these small Mediterranean islands (<10 km²) are important study systems for conservation, they also represent an ideal framework for equilibrium theory studies, smaller islands close to landmasses being more prone to extinction and colonization events (Whittaker et al., 2023). Luckily many 20th century naturalist surveys are available for these islands, including several small satellite islands of Corsica which have been well studied for different biodiversity groups (Lanza & Poggesi, 1986; Paradis et al., 2021; Thibault et al., 1987) giving opportunities to implement studies of long term biodiversity dynamics.

The objective of our study is to compare ant communities over a relative long-time span, i.e. up to 39 years, in the absence of direct anthropic pressure. Ant community diversity and composition were studied on 36 Corsican satellite islands, which are part of Natural Reserves. Ancient surveys from naturalist reports of the 1980’s and 1990’s were compared with new surveys conducted in 2023. First, we tested the dynamic equilibrium theory, assuming an eventual stability of species richness but a turnover of community composition. In a second phase, we tested which island features could affect temporal turnover, with the following assumptions: (i) turnover should decrease with island size and vegetation diversity, (ii) turnover should decrease with island isolation, and (iii) some ant community composition would be subject to more turnover than others. Even if our study considers a relatively long time-span, we expect turnover to be low in accordance with ant biology and ecology.

2. Materials and methods

2.1. Study sites

Ant communities were surveyed on small satellite islands around Corsica (France). Corsican satellite islands originate from the continental shelf and were separated from mainland Corsica when sea level rose after the last glaciation, around 10,000 years ago (Lambeck et al., 2014). A variety of shapes, altitudes and substrates of 141 islets are described in Paradis et al. (2021). Vegetation has been well studied in the past decades, including recent surveys for most of the small islands studied (Médail et al., 2019; Paradis et al., 2020).

In this study, we focused on 36 small islands where ants had already been surveyed (Casevitz-Weulersse, 2014; Delaugerre & Brunstein, 1987a; Delaugerre & Casevitz-Weurlesse, 1986; Delaugerre & Guyot, 1995b). These small islands are located between 8.36–9.47° longitude and 41.37–42.34° latitude and their sizes range from 0.01 to 21 hectares. None of them are inhabited and most are included in natural reserves: either Bouches de Bonifacio (classified since 1999), Iles du Cap Corse (since 1987), or Scandola (since 1975) with restricted access (Figure 1.1). The closest studied small island is located 5 meters from Corsican main island and the most remote is 7.4 kilometers away. Each studied island had at least one vascular plant.

2.2. Ant data

Species lists of past surveys were gathered from the following publications: Casevitz-Weulersse (2014), Delaugerre & Brunstein (1987b), Delaugerre & Casevitz-Weurlesse, (1986), Delaugerre & Guyot, (1995). First surveys were conducted in 1984 and the last ones in 1995 but most of the islands were surveyed in 1985 (Supplementary material S2.1). Ant communities were resampled in 2023 at similar periods of the year (May and June) and following a similar method. We hand collected ants actively on soil surface, vegetation, underneath rocks and inside rock cracks. Duration of research was proportional to island size. Past surveys sometimes included attractive baits made either of syrup or cat food but many baits were reported unsuccessful because rats knocked them over. Similar baits were put on

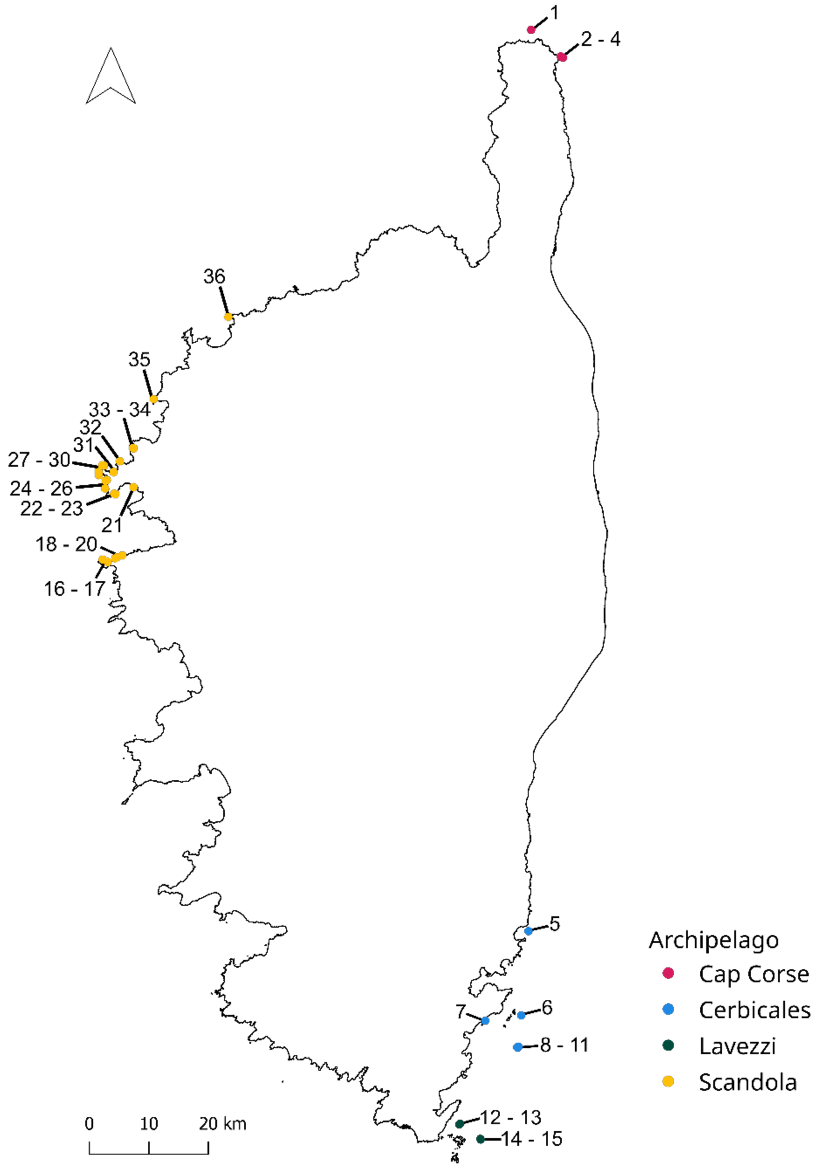

Figure 2.1: Localization of the 36 small islands studied around the main island of Corsica. The islands are grouped by natural reserve/archipelago: Cap Corse in pink, Cerbicales in light blue, Lavezzi in green and Scandola in yellow. Some islands were outside the reserves, like the 5, the 35 or the 36, so they have been grouped with the closest islands.

the biggest surveyed island, Gargalo, but it failed to increase the number of species collected. Due to their limited efficiency on Gargalo and numerous failures in the past this method was not reproduced on other islands. Moreover, hand collecting was already proven to be efficient to estimate species richness (Salata et al., 2020).

Ants collected in 2023 were preserved in 70% alcohol to be identified later on at the laboratory. Ants were identified to species level when possible or species complex, using morphological identification keys (Blatrix et al., 2018; Lebas et al., 2016). *Tetramorium* individuals from 2023 were identified using microsatellite genotyping as in Cordonnier et al., (2019). However, species from *caespitum-impurum* group were kept at the complex level because their status remain ambiguous (Wagner et al., 2017) and we could not use genetics on the specimens from the former surveys. Conserved specimens from the former surveys were morphologically checked at the National Museum of Natural History in Paris to update identifications according to current knowledge on taxonomy of certain genera; i.e. *Lasius* (Blatrix et al., 2020), *Plagiolepis* (Kirschner et al., 2023), *Tapinoma* (Seifert et al., 2017) and the *Tetramorium* species outside the *caespitum-impurum* group (Schlick-Steiner et al., 2006). Species considered cryptic, i.e. which live in the soil matrix and do not forage on the ground, or parasites, were removed from both sampling lists as their detection can be difficult, random and increase pseudo-turnover, i.e. turnover attributed to failed detection during the survey.

2.3. Island characteristics

Island characteristics originated from a database on Corsican small island (Delaugerre et al., In prep). From this database, we used surface area and distance from the Corsican mainland coast. Vegetation and phytosociological data, including two levels of number of plant communities, were extracted from Paradis et al. (2021) or from specific analysis of various publications (Médail, ined). Plant communities from the studied islands were described as greatly stable over decades (Médail et al., 2019), justifying to use community and alliance data even if the absolute number of plant species can change. The plant communities can be proxies of habitat diversity as they represent homogenous assemblages of plant species. Vegetation data we used appreciate these communities at two levels of organization; at a medium scale and a finer scale, i.e. Alliances and Associations as described in (Dengler, 2017). All the island characteristics that were used for the analysis are presented in Supplementary material S2.1.

2.4. Data analysis

2.4.1. Species richness and composition comparison

Difference in species richness between past and present surveys was assessed using the Intraclass Correlation Coefficient (ICC). ICC gives an estimation of the strength of survey resemblance, giving a value between 0 and 1 (Liljequist et al., 2019). The closer the value is to 1, the more similar the two samplings are. To clarify if changes were directed towards a gain or a loss of species, we calculated a standardized effect size by dividing the difference in species richness per the difference in years between the surveys.

Extinction and colonization rates were calculated for each species and each island. (1) The extinction rate per species resulted of the number of islands where the species was only found in the first survey divided by the total number of islands. (2) The colonization rate resulted of the number of islands where the species was only found in the second survey divided by the total number of islands. (3) The extinction rate per island resulted of the number of species found on the island only in the first survey divided by the total number of species found during the study, thus considered the potential colonizing pool. (4) The colonization rate per island resulted of the number of species found on the island only in the second survey divided by the total number of species found during the study.

Changes in community composition were calculated with Jaccard β-diversity index on ant occurrence data. Total turnover was partitioned following Baselga (2010), to distinguish the proportion attributed to replacement, i.e. when species are substituted, from that attributed to nestedness, i.e. a gain or a loss of species with a nested pattern. These three indexes were calculated for each island. A non-parametric test of Wilcoxon was used to compare the proportion of replacement and nestedness in the total turnover. In order to compare our results with those of other studies covering different time periods, we calculated an annual turnover rate by dividing turnover values by the number of years between the two surveys. Annual turnover rates were used for comparison but one has to keep in mind that it underestimates the actual rates, as crypto-turnover can occur between the two dates of surveys.

2.4.2. Predictors of turnover

We studied the response of total turnover, replacement and nestedness to island surface area, distance to mainland Corsica, number of plant alliances and associations with generalized linear mixed models (GLMM) using *glmmTMB* R package (Brooks et al., 2017). Surface area and distance to mainland were log-transformed. To take into account spatial auto-correlation in the data, archipelago ID (i.e. Cap Corse, Scandola, Cerbicale or Lavezzi) was added as a random variable in the models. Models were fitted with binomial distribution and weighted by the total number of species found on each island. Multicollinearity between the explanatory variables was assessed using the R package *performance* (Lüdecke et al., 2024).

After removing variables that contributed to the increase in covariance, we performed a model selection on AIC using the dredge function from the *MuMIn* R package (Bartoń, 2023).

In order to study whether certain composition of species could predict turnover, we started with a clustering on communities of past surveys. Hierarchical clustering analysis (HCA) was performed on a matrix of Jaccard distance with the Ward grouping method. All the islands were included except number 15 (Sperduto piccolo, Bouches de Bonifacio), because it had no ants in 1985 which makes the Jaccard calculation impossible. Then, we studied the differences between compositions of the two sampling dates for each cluster of islands using the non-metric multidimensional scaling (NMDS) of the *vegan* R package (Oksanen et al., 2022) with Jaccard distance. Differences between clusters were assessed using a PERMANOVA test, from the vegan R package, followed by the pairwise adonis test, from the pairwiseAdonis R package, for multicomparison (Martinez Arbizu, 2020). The HCA was also applied on community compositions of the second surveys.

3. Results

Twenty-one ant species were sampled during the two surveys on the 36 studied islands. A total of 17 species were found in the first survey (between 1984 and 1995) and 18 species in the second one (in 2023). Two species were found only in the first surveys: *Plagiolepis delaugerrei*, and *Solenopsis fugax* and three species were only found in 2023: *Cardiocondyla mauritanica*, *Hypoponera eduardi* and *Tetramorium brevicorne* (Supplementary material S2.2). The following analyses were performed on 17 species as three species were removed, *H. eduardi, P. delaugerrei* and *S. fugax*, because we considered they are cryptic and difficult to detect, increasing pseudo-turnover.

3.1. Changes in species richness and community composition

We found a significant ICC of 0.74 (F=6.7, p-value<0.001), which corresponds to a moderate consistency between the two surveys (Koo & Li, 2016). Standardized effect size calculation showed an increase of 0.03 species per year, meaning that the relative stability of species richness is marked by a slow increase through time. This increase is supported by a mean colonization rate per island that exceeds the extinction rate, respectively representing 9.87% and 3.56%. Seven islands had zero colonizations and 17 islands had zero extinctions.

Mean total turnover reached 44.56% and was composed of 11.46% of replacement and 33.10% of nestedness. The percentage of nesteness was significantly higher than the percentage of replacement (V=33.5, p-value<0.001). Mean annual turnover was 1.21% composed of 0.30% of replacement and 0.91% of nestedness.

The species with the highest extinction rate was *Lasius* COR sp1 (23.68% of the islands). *Tetramorium semilaeve* was the species with the highest colonization rate (36.84% of the islands). Half of the 17 species had zero extinctions, and all of them had a positive colonization rate.

3.2. Predictors of turnover

The total turnover was best explained by the number of plant alliances, which is the larger scale of plant communities that we used, indicating a decrease in turnover with an increase in plant communities i.e. habitat diversity (estimate = -0.14, p-value<0.05). Similarly, nestedness was best explained by the number of plant alliances but not significantly (estimate=-0.12, p-value=0.10). Concerning replacement, model selection showed the number of plant alliances and distance to mainland Corsica as the best predictors of replacement. Both variables non significantly affected the replacement.

3.3. Community clustering

Using community data from the first surveys, we found six homogenous clusters of islands (Figure 2.2). While studying cluster typology, we found that islands were quite well mixed, representing wide ranges of sizes, isolation, plant diversity, and archipelagos within each cluster. Cluster 5, which included five islands of Scandola archipelago, was an exception, characterized by smaller islands, located closer to the coast, with very few plant alliances, plant communities and ant species. *Lasius* COR sp1 was found on all of the five islands of cluster five, combined with *Crematogaster scutellaris* on two islands.

Past and recent survey comparison showed that compositions of the clusters remained the same through time, except for the cluster five (Figure 2.3). Most recent surveys on islands composing the cluster five showed that their species composition is now similar to other clusters, i.e. cluster one, three and six. Formerly composed of very poor communities, changes on these islands are driven by an overall increase in species richness and colonizations of *Tetramorium semilaeve*, and *Plagiolepis pygmaea*.

The HCA with data from the second survey showed that island communities are more similar now and can be sorted in only four different groups (Figure 2.4). All types of islands are quite well mixed between clusters, except for the third cluster, which includes only two islands with either one or two ant species.

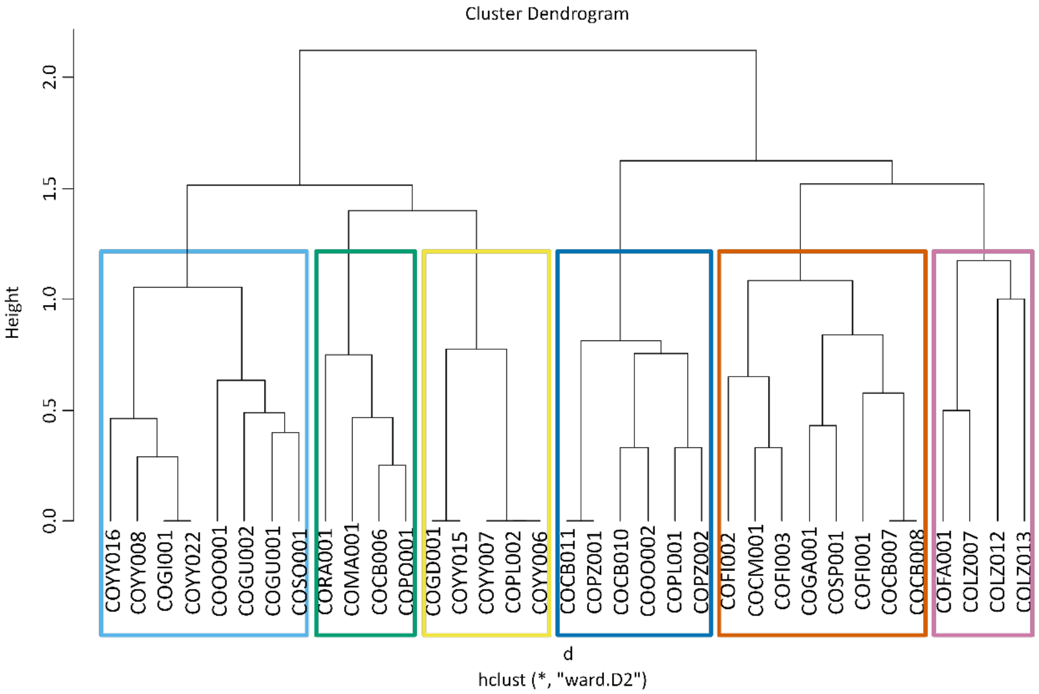

Figure 2.2: Dendrogram representing clusters of the 35 small Corsican islands studied, based on their community dissimilarity, calculated with Jaccard's distance and Presence/Absence of ants on the islands, using only the first surveys. The grouping was performed using Ward’s distance. Six clusters of islands were differentiated, represented by the colored rectangles. Island’s code details are available in Supplementary material S2.1.

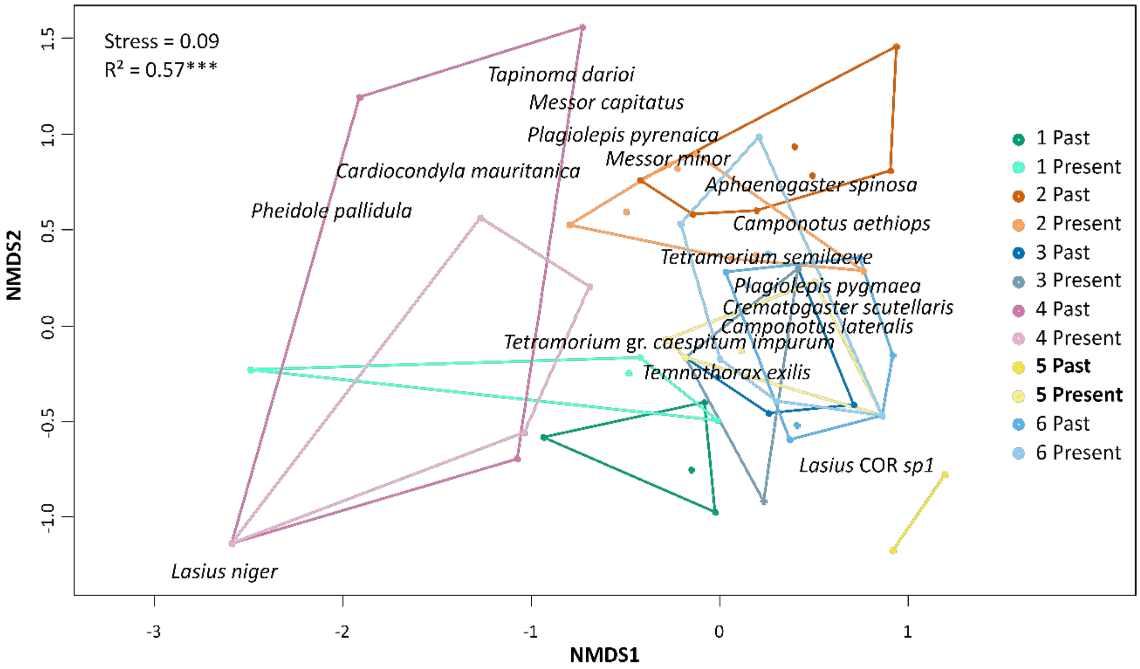

Figure 2.3: Non-metric multi-dimensional scaling (NMDS) ordination of ant communities based on Jaccard’s distance and Presence/Absence of ants on the 35 small Corsican islands studied. Each pair of clusters (Number + community surveyed in the first=past and second=present survey) and their color are referring to the Figure 2.2. Differences inside each pair was assessed using adonis2 (vegan) and a pairwise test, giving the R² and its significance (*P* < 0.05*, *P* < 0.01**, *P* < 0.001***). The cluster 5 is written in bold because it was the only one for which the communities in the first survey significantly differed from those in the second survey.

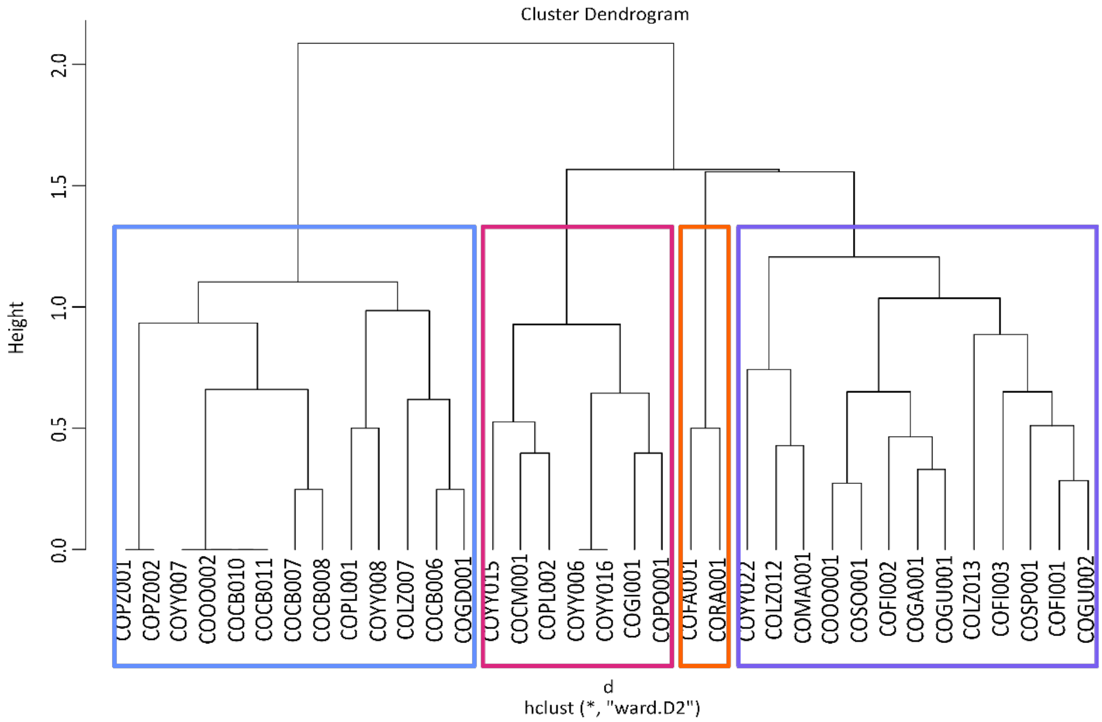

Figure 2.4: Dendrogram representing clusters of the 35 small Corsican islands studied, based on their community dissimilarity, calculated with Jaccard's distance and Presence/Absence of ants on the islands, using only the second surveys. The grouping was performed using Ward’s distance. Four clusters of islands were differentiated, represented by the colored rectangles. Island’s code details are available in Supplementary material S2.1.

4. Discussion

We find no evidence that ant communities of the studied small islands are governed by an equilibrium dynamic. Indeed, we have recorded a significant increase in ant species richness 35 years after the first surveys, that is however associated with a regional homogenization of the communities. An average of around 45% of turnover is observed, with a total turnover negatively correlated with the number of plant alliances.

Our results show that ant species richness increased 35 years after the first survey, although this increase is moderate (0.03 species per year). Various studies on ant community dynamics showed that species richness increased through time, especially in mountainous regions (Munyai & Foord, 2015; Paraskevopoulos et al., 2024), but on islands as well (Torres & Snelling, 1997). Several factors have been proposed to explain this positive dynamic in species richness, such as climate change and temperature increase (Paraskevopoulos et al., 2024) or introduction of alien species (Aulus-Giacosa et al., 2024). The only potential alien present on the islands is *Tetramorium immigrans*, that was identified in the group *caespitum-impurum*, and which is commonly considered invasive in urban areas (Cordonnier et al., 2020). However, it was already present in the first surveys and our results do not indicate any concerning spreading.

If the studied islands are relatively well-preserved from human disturbance (difficult or forbidden access), the Mediterranean islands, including Corsica are known to be particularly susceptible to climate change (Vogiatzakis et al., 2016). Increasing temperatures can alter successions and promote non-equilibrium (Prach & Walker, 2011), notably through the expansion of the distribution range of some species (Paraskevopoulos et al., 2024). In the temperate zones, ants are not expected to suffer from climate change and some species could even benefit from it (Parr & Bishop, 2022). This might be even more pronounced for generalist species, small-sized with large colony sizes, that could benefit from higher temperatures to extend their activity (Parr & Bishop, 2022). This is the case for *Tetramorium semilaeve* which has successfully colonized 14 new islands.

At the opposite, very few ant species went extinct between the two surveys. *Lasius* COR sp1, formerly *Lasius emarginatus* (currently being described by Blatrix et al., 2020), is the species with the highest extinction rate, as it went extinct on 25% of the islands. Species of the *Lasius* genera establish mutualism interactions with aphids in order to exploit honeydew resources (Way, 1963). However, these relationships are complex and versatile as they depend on population dynamics of aphids and host plants, that could both be impacted by climate change (Blanchard et al., 2019). The strategy of relying on honeydew has already been linked to dramatic population fluctuations (Morrison, 2016), and it could have been the case here, as resources and vegetation are already very scarce on the studied islands.

Although island species richness has increased, the regional pool of species was very stable between the two surveys, with only one new species, *Cardiocondyla mauritanica* recorded for the first time in Corsica (Blaya et al., 2024). Therefore, most colonizations involved species already recorded during the first survey. Half of the observed turnover is indeed attributed to nestedness, meaning that a pool of species is becoming increasingly present throughout the islands. This is emphasized by the loss of two community clusters in the second survey. The islands with the lower species richness were those that gained the most species over time, leading to greater resemblance with other clusters. Such trend is not unique and has been previously observed in ant communities (Finderup Nielsen et al., 2019).

As described in MacArthur & Wilson (1963), colonization and extinction dynamics participate in renewing community compositions. Part of this turnover may be attributed to bias in sampling, a phenomenon called pseudoturnover generated by missing species during both surveys (Lynch & Johnson, 1974). To limit this bias, we removed from the analysis the cryptic species that live deeper in the soil and do not forage at the soil surface as they are not easy to find. Moreover, the methods adopted during the second survey were decided in collaboration with the researchers who conducted the first one. Even if the two samplings might have been conducted slightly differently, the relatively high percentage of turnover we recorded here, around 45%, should contain a significant proportion of actual changes in the communities.

This percentage of turnover can also be put in perspective with the long-time span considered, i.e. 37 years. By annualizing the turnover, less than 1.2% per year, we can conclude that rates correspond to a relatively low bio-dynamism according to Whittaker et al., (2023). Annual rates are useful to compare our results to other studies with different time span, but as we only consider two dates in the calculation of the turnover, it can be underestimated (Morrison, 2017). Low rates of turnover are still consistent with previous studies on ant temporal dynamics on islands with time span superior to 15 years (Morrison, 2010a; Torres & Snelling, 1997). The replacement is then accordingly low considering the ecology of ants. Nesting in the soil limits their risk of extinctions while protecting them from climatic perturbations (Morrison, 2010a). Moreover, the remarkable longevity records held by ants (Hölldobler & Wilson, 1990) may allow them a greater persistence. As turnover should decrease with the generation time (Whittaker, 2000), it justifies studying temporal dynamics of ant communities over a relatively long-time span, above the ant generation time.

All components of turnover are negatively influenced by the number of plant alliances, meaning that islands with more plant communities have more stable ant communities. These results are consistent with previous studies on islands concluding that vegetation and habitat diversity may be good predictors of ant species richness (Morrison, 1998; Torres & Snelling, 1997) and turnover (Goldstein, 1975). In accordance with the habitat diversity hypothesis, ant diversity is known to respond well to the structure of the vegetation (Andersen, 2019) that offers a diversity of nesting sites or direct or indirect food resources (Cole, 1983; Simberloff & Wilson, 1969). More specifically, small islands were shown to be exceptions of the island species-area relationship defined by MacArthur & Wilson (1967), due to the Small Island Effect (SIE). As small islands are inherently less complex, habitats diversity and quantity become often better predictors of species richness than area (Matthews et al., 2020; Triantis et al., 2006). Here the response of ant turnover to the number plant alliances, seems to corroborate the SIE: habitats are more important than size for colonization-extinction dynamics.

Ant communities of the small islands of Corsica seem to be at a stage of nonequilibrium with low bio-dynamism (Whittaker, 2000; Whittaker et al., 2023). The relative stability of communities seems consistent with ant ecology, and previous findings (Morrison, 2002). Nonequilibrium was also already observed on ants (Morrison, 2010a; Torres & Snelling, 1997), and it seems that we found a homogenization pattern that coincides with global change trends (Chase et al., 2019). Even when studying small, well-preserved islands without direct anthropogenic disturbance, very low to absent frequentation, the rise in temperature and consequent range expansion of many species may cause regional-scale community homogenization. Studying such relatively preserved ecosystems, is therefore of major importance to better understand the global evolution of communities that under the multiple forces of global change.

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Supplementary Material

Table S2.3 : List of the small islands studied around Corsica, and their spatial and ecological characteristics.

Code	Name	Archipelago	First survey	Latitude	Longitude	Area (m²)	Elevation (m)	Distance to mainland (m)	Plant alliances	Plant communities
COGA001	Giraglia	Cap Corse	1995	43.0250015	9.4066668	76000	65	1600	9	12
COFI003	Terra	Cap Corse	1993	42.9852791	9.4663887	4225	6	195	7	7
COFI002	Mezzana	Cap Corse	1993	42.9841652	9.4688892	4500	12	410	6	6
COFI001	Finocchiarola	Cap Corse	1993	42.9836121	9.4708338	9520	27	570	9	9
CORA001	Roscana	Cerbicales	1986	41.6833344	9.4019442	1690	19	930	1	1
COCB006	Rocher Vacca	Cerbicales	1986	41.5563889	9.3872223	4900	24	3250	2	2
COFA001	La Folaca	Cerbicales	1986	41.5483322	9.3147221	1358	11	275	4	5
COCB007	Toro Grande	Cerbicales	1986	41.5092670	9.3815970	13900	34	7230	3	6
COCB011	Toro Piccolo 2	Cerbicales	1986	41.5083860	9.3798190	980	10	7230	2	2
COCB010	Toro Piccolo 1	Cerbicales	1986	41.5084330	9.3792420	1115	18	7230	2	2
COCB008	Ilot Toro Piccolo	Cerbicales	1986	41.5079530	9.3803190	4900	29	7230	3	5
COLZ013	Porraggia piccola	Lavezzi	1986	41.3930550	9.2644444	2200	6	1800	3	4
COLZ012	Porraggia grande	Lavezzi	1986	41.3916664	9.2630558	8450	19	1750	6	10
COLZ007	Sperduto grande	Lavezzi	1986	41.3699989	9.3050003	5580	12	6220	1	2
COLZ008	Sperduto piccolo	Lavezzi	1986	41.3688889	9.3058338	1210	8	6220	1	1
COSO001	Rocher de Sbiru	Scandola	1984	42.2400030	8.5472990	3360	39	15	3	3
COYY022	Plage	Scandola	1985	42.2363890	8.5575000	365	12	10	1	1
COOO002	Orto piccolo	Scandola	1984	42.2418470	8.5724030	1170	36	250	1	1
COOO001	Orto grande	Scandola	1984	42.2436280	8.5762720	5560	48	4	3	3
COGD001	Guardiola	Scandola	1984	42.2459670	8.5867330	2270	32	185	2	2
COGI001	Girolata	Scandola	1984	42.3477783	8.6091671	1230	11	5	6	7
COYY015	Catò Est	Scandola	1984	42.3379390	8.5703920	520	15	14	4	7
COYY016	Catò Ouest	Scandola	1984	42.3373500	8.5696220	480	15	70	5	5
COCM001	Cala Maiora	Scandola	1984	42.3458940	8.5521310	10700	60	17	11	13
COPL001	Cala di Ponte	Scandola	1984	42.3584000	8.5556440	2050	35	15	4	6
COPL002	Sud di Solana	Scandola	1984	42.3569450	8.5530558	2140	25	30	1	1
COGU002	Garganellu	Scandola	1985	42.3652763	8.5397224	10855	43	255	7	11
COGU001	Gargalu	Scandola	1984	42.3699989	8.5391665	210000	127	0	12	21
COPZ001	Palazzu	Scandola	1984	42.3803850	8.5465960	4700	58	73	4	8
COPZ002	Palazzinu	Scandola	1984	42.3797950	8.5503220	1100	28	40	3	7

COYY008	Rocher occidental Elbu	Scandola	1984	42.3703420	8.5691350	995	15	26	3	3
COPO001	Porri	Scandola	1984	42.3861122	8.5819445	2150	31	170	3	5
COYY007	Rocher Elpa nera 4	Scandola	1985	42.2420120	8.3634080	690	10	2	1	1
COYY006	Rocher Elpa nera 3	Scandola	1985	42.2422160	8.3629100	510	13	30	2	2
COMA001	Capudivella	Scandola	1984	42.4711113	8.6488886	4500	23	0	1	1
COSP001	Spano	Scandola	1985	42.6008339	8.7994442	11400	14	76	3	4

Table S2.4: List of ant species present on each island according to the two samplings. Ø = species found in the two surveys; O = species present only in the second survey; X = species present only in the first survey

	COFI001	COFI002	COFI003	COGA001	COGD001	COGI001	COGU001	COGU002	COMA00	COOO001	COOO002	COPL001	COPL002	COPO001	COPZ001	COPZ002	COSO001	COSP001	COYY006	COYY007	COYY008	COYY015	COYY016	COYY022	COCM001	COCB006	COCB007	COCB008	COCB010	COCB011	COFA001	COLZ007	COLZ008	COLZ012	COLZ013	CORA001
Aphaenogaster spinosa	Ø	Ø	Ø	Ø			Ø	Ø		Ø			O				Ø	Ø							Ø		Ø	Ø								
Camponotus aethiops							Ø	X		O							Ø																			
Camponotus lateralis				O			Ø			X	X						Ø				Ø			O												
Cardiocondyla mauritanica																																			O	
Crematogaster scutellaris				Ø	X		Ø			Ø							O					X														
Hypoponera eduardi																																O				
Hypoponera punctatissima																															O					
Lasius COR sp1					X	Ø	X	X	X	Ø		Ø	Ø	Ø		X	Ø		Ø	X	Ø	Ø	Ø	X	O	X										
Lasius niger																															Ø	Ø				O
Messor capitatus	Ø	O		Ø			O																												Ø	
Messor minor	O	O	O	Ø		O	Ø	O									O	Ø																Ø	O	
Pheidole pallidula																																		O	Ø	O
Plagiolepis delaugerrei				O																																
Plagiolepis pygmaea	Ø	O	Ø	O	O	Ø	Ø	Ø	O	O				O			Ø		O		X	O	Ø	Ø	Ø		O							O		
Plagiolepis taurica	O	O	O	Ø																														O		
Solenopsis fugax		X		X			X																		X										X	
Tapinoma darioi																																		Ø		
Temnothorax exilis			O	Ø	O	X	Ø		O	Ø	Ø	Ø		Ø			Ø	X		O	Ø			X		Ø	O	O	Ø	O		Ø		O		
Tetramorium brevicorne					O				O								O																			
Tetramorium gr. *caespitum-impurum*		O	Ø	O			Ø		X					X				O						O		X						O	O	O		X
Tetramorium semilaeve	Ø	O	O	Ø	O	O	Ø	Ø	O	O	Ø	X	O	Ø	Ø	Ø	O	Ø		O	O	O			O	O	Ø	Ø	Ø	Ø		O			O	

Transition to chapter 3

In the two first chapters we found that area affected ant species richness and ant turnover to a lesser extent. However, the small islands we focus on proved that the relationship between area and species richness is not necessarily linear but rather segmented, suggesting a Small Island Effect (Lomolino & Weiser, 2001). In the case of a SIE, the importance of other factors, such as habitat diversity, is often discussed (Chen et al., 2020; Triantis et al., 2006a). We found that habitat proportion was a predictor of species richness, but it accounted for only a small proportion of its variance. Habitat diversity, define by plant communities, was the main predictor of turnover, promoting more stable communities. Island's species richness increased slightly and island communities tend to homogenize on a regional scale, with less distinct clusters in the second survey. This pattern may corroborate with climate change and the range expansion of certain generalist species (Chase et al., 2019).

The Mediterranean basin could be particularly affected by climate change (Giorgi & Lionello, 2008), as well as by other components, such as Invasive Alien Species (IAS), which often threaten island biodiversity (Traveset et al., 2008, 2009). Considering the vulnerability of islands, and especially of the small ones (Médail, 2017; Whittaker et al., 2017a), many conservation and restoration programs are initiated. Here we take advantage of a 10-year restoration program conducted on a small island of the Port-Cros National Park (Var, France), Bagaud island, to study ant community dynamics after restoration action in response to IAS invasion or in the absence of disturbance. The black rat (*Rattus rattus*) and the iceplant (*Carpobrotus* spp.), two IAS, were eradicated from the island, and 6 years of invertebrate monitoring was conducted in parallel over a 10-year span.

In this third chapter we assess the response of ant communities to eradications, comparing sites that were invaded with ones that were not. Studying the community dynamics over 10 years allows assess the potentially negative effects of IAS, but also the effects of habitat change on ants and community dynamics, even in the absence of any change. Iceplant invasion is known to cause strong changes in habitats because it forms dense monospecific mats (Campoy et al., 2018). It was shown that in contrast, the removal of the IAS plant allowed vegetation diversification (Buisson et al., 2021). This last chapter is then complementary with others, using applied research, with such restoration program and monitoring, to provide important insights of community structure and dynamics to support fundamental questions insights.

10 years

The small island of Bagaud (Port-Cros National Park)

Monitoring ants species richness and abundances

Before-after eradication dynamics

Return of native vegetation after the removal of *Carpobrotus* spp. on Bagaud island © Elise Buisson

CHAPITRE 3

Mixed responses of ant communities to the eradication of black rats and iceplants on a small Mediterranean island

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Abstract

Eradication of invasive alien species (IAS) is often proposed to restore invaded ecosystems, with information on subsequent ecosystem recovery key to conservation policies. Although ants perform major ecological functions in the ecosystem, their response to IAS eradication has received relatively little monitoring. This study investigated ant response to iceplant (*Carpobrotus* spp.) and black rat (*Rattus rattus*) eradications on the small Mediterranean island of Bagaud (Var, France). Ant communities were monitored over a ten-year period, including two years before eradications, at six different sites: two invaded by iceplants, two under high rat pressure, and two native vegetation sites without intervention. We found inter-annual variations in ant communities but no before-after eradication trend at both native vegetation and rat eradication sites. However, there was a clear increase in ant species richness and abundance score after the iceplant eradication. A core of common Mediterranean species, including *Pheidole pallidula*, *Messor bouvieri,* and *Plagiolepis pygmaea*, increased their foraging activity after the removal. As xerophilous and thermophilous species they would benefit from the return of native vegetation with possibly warmer and dryer microclimatic conditions, but also from habitat and resource diversification. The trend was even stronger on the denser and thicker iceplant eradication patch. Our results emphasize the relevance of implementing ant monitoring to evaluate the effectiveness of such restoration and conservation strategies.

Keywords: Formicidae, Restoration, Exotics, Monitoring, Community Recovery

1. Introduction

Islands represent a major challenge for biodiversity conservation, hosting disproportionate levels of biodiversity compared to mainland regions (Fernández-Palacios et al., 2021). Yet much of this biodiversity is threatened by multiple factors, including biological invasions (Russell et al., 2017). Compared to mainland regions, islands suffer from higher invasion rates (Dawson et al., 2017), with invasive alien species (IAS) identified as one of the main causes of species extinctions (Pyšek et al., 2020). Moreover, invasions often cause changes in community structure and modify abiotic characteristics of ecosystems (Pyšek et al., 2012; Strayer et al., 2006). Finally, insular ecosystems are remarkably vulnerable to biological invasions due to their limited size, small populations and vacant niches without competitors or predators (Fernández-Palacios et al., 2021; Russell et al., 2017).

Considered as a hotspot of biodiversity, the numerous islands of the Mediterranean basin (>10,000) are highly threatened by invasions (Hulme et al., 2008; Myers et al., 2000) and could be the ecosystems most impacted by IAS by 2100 (Sala et al., 2000). As they are also hotspots of invasions, many islands are now faced with numerous interacting invasive plants and animals (including seed dispersers), which pose a severe threat to insular biodiversity (Courchamp et al., 2011; Russell & Kaiser-Bunbury, 2019). For example, an invasional meltdown (i.e. the process by which invasive species facilitate each other’s invasion) was described for two invasive taxa, the black rat (*Rattus rattus*) and iceplants (*Carpobrotus* spp., Aizoceae), with rats facilitating seed dispersal and iceplant fruits providing water and energy when resources are scarce (Bourgeois et al., 2005).

The black rat (*Rattus rattus*) is considered as one of the 15 most prevalent IAS on islands (Russell et al., 2017). It has colonized most of the Mediterranean islands over the last 2,000 years (Ruffino et al., 2009), with direct effects on biodiversity through predation. The black rat is widely known to prey on seabird eggs and chicks, and on large-bodied invertebrates, such as beetles, spiders and gastropods (Caut et al., 2009; Nascimento et al., 2019). It also has indirect effects by dispersing invasive plant seeds, including *Carpobrotus* species (Bourgeois et al., 2005; Shiels, 2011).

Also known as iceplants or hottentot figs, *Carpobrotus* species (Aizoceae) were introduced to Europe in the seventeenth century from South Africa, Australia or Chile for ornamental and soil stabilization purposes (Campoy et al., 2018). *Carpobrotus acinaciformis*, *Carpobrotus edulis* and their hybrids (*Carpobrotus* aff. *acinaciformis*) have now colonized a large portion of the western Mediterranean coast (Campoy et al., 2018; Suehs et al., 2004). They establish in a variety of coastal environments, from sandy dunes to rocky cliffs, forming dense monospecific mats with an abundant litter (Campoy et al., 2018). Iceplants are a major threat to native biodiversity in Mediterranean coastal ecosystems (Carboneras et al., 2018; Hulme et al., 2008). They shift soil chemical parameters (Novoa, González, et al., 2013; Vieites-Blanco & González-Prieto, 2018), decrease plant diversity (Badalamenti et al., 2016), and reduce invertebrate abundance and modify community composition (Rodríguez et al., 2020).

In order to mitigate the adverse impacts of IAS on biodiversity, control or eradication operations are implemented, prioritizing the most prevalent IAS, including the black rat and iceplants (Carboneras et al., 2018). In the Mediterranean Basin, controls and eradications have generally led to a positive response in terms of biodiversity (Jones et al., 2016). Iceplant eradications have been shown to positively impact native plants (Buisson et al., 2021; Lazzaro et al., 2020) and spiders and beetles (Braschi, Hélard, et al., 2021; Braschi, Torres, et al., 2021). Black rat eradications have benefited reptiles (Krebs et al., 2015) and breeding bird populations (Bourgeois et al., 2013; Howald et al., 2010). While black rat eradication has also been linked to the recovery of native invertebrates (Ruscoe et al., 2013; St Clair et al., 2011), studies including ants have failed to find any response so far (Sinclair et al., 2005; Vergara et al., 2021).

Ubiquitous and abundant, ants play a key role in ecosystem functioning, in soil structure, as predators, or as promoters of plant dispersal (De Almeida et al., 2020; Del Toro et al., 2012). They respond quickly to environmental change, making them good bioindicators (Andersen et al., 2002; Majer, 1983). Habitat structure, microclimate, resource availability and competitive interactions are indirect factors responsible for ant community modifications (Andersen, 2019). Moreover, the decrease in ant diversity often correlates with habitat simplification and loss of resources such as seeds, pointing to the importance of monitoring ant communities in restoration projects (Underwood & Fisher, 2006). So far, very few studies have focused on ant response to plant or mammal IAS eradication (Lenda et al., 2013; Osunkoya et al., 2011; Parr et al., 2010), even though ant monitoring is a relevant way to assess ecosystem change (Kaspari & Majer, 2000).

The aim of this study was to explore ant responses to iceplant and black rat eradications on the small Mediterranean island of Bagaud (Var, France). Ant communities were compared over a ten-year monitoring period, including two years prior to eradications, at six different sites on the island: two sites invaded by iceplants (ICE), two sites under high black rat pressure (RAT), and two sites with native vegetation (NV), i.e. no iceplants, low rat density and no intervention. We hypothesized that: (i) Ant species richness would increase after the IAS eradication at the four invaded sites and remain stable at the native vegetation sites; (ii) Ant abundance would increase at the eradication sites and remain stable at the native vegetation sites; and (iii) The composition of ant communities would change after the IAS eradication at the four invaded sites and remain stable at the native vegetation sites; (iv) The magnitude of changes in ant communities would be greater after the eradication of iceplants than of black rat, as iceplants impact more ants' habitats.

2. Materials and methods

2.1. Study area

Bagaud island is a small uninhabited Mediterranean island of 58 ha located in the Hyères archipelago (Var, France), which is part of the Port-Cros National Park. It is a strict biological reserve with restricted access since 2007. The continent is 7.5 km away and the main nearest island, Port-Cros, is 1 km away. The archipelago has a Mediterranean climate with annual mean temperatures ranging between 13.5 and 19.5°C and an average 621.5 mm of precipitations per year (1991-2020, Ile du Levant weather station, Infoclimat). Vegetation on Bagaud island is typical of Mediterranean regions, with dominant matorral and halophilous plants on the rocky shores. In addition to its rich native plant communities, two invasive iceplants species, i.e. *Carpobrotus edulis* and *Carpobrotus* aff*. acinaciformis*, were introduced in the nineteenth century by military engineers. Intended to stabilize the soil around the island's forts, these species covered 2-ha of the island at their worst. The only non-flying mammal of the island, the black rat (*R. rattus*), was also introduced, probably during the Roman period (Ruffino et al., 2015). It feeds on *Carpobrotus* spp. fruits as well as potentially on various seeds, beetles, geckos, and seabird eggs and chicks (Ruffino et al., 2015). Eradications of iceplants and black rats were carried out on the island in late 2011 and 2012.

2.2. Study sites

We monitored the temporal dynamics of ant communities via three treatments: (1) iceplants removal (hereafter ICE), (2) black rat removal (hereafter RAT) and (3) native vegetation sites with low black rat density and no intervention (hereafter NV) (Figure 3.1). Limited availability of sites led us to select two sites per treatment only. The two iceplant removal sites were selected for size, being large enough to set up transects of 10 pitfall traps (see section 1.3). The two rat removal sites were selected as having the highest rate of rat captures and being accessible for arthropod sampling.

Iceplants were eradicated from study sites ICE1 and ICE2 between November 2011 and February 2012. Plants were uprooted and left to compost on the site and litter was removed to avoid further dissemination (Chenot et al., 2018). Since then, control operations have been conducted every year since then to prevent the recolonization of the area from the seed bank (Buisson et al., 2021; Ruffino et al., 2015).

Rats were trapped from September 2011 to June 2012 at RAT1 and RAT2 sites. Rat eradication was carried out first via trapping sessions and later supplemented by rodenticide (Ruffino et al., 2015). Twenty permanent bait stations were set up along the coast under biosecurity measures (Ruffino et al., 2015). While traces on baits were spotted in 2015, no rats were caught in 2018; they were however considered as having recolonized the island by 2019, as many traces on baits were observed (Braschi 2021).

Our two native vegetation sites (intervention-free) had the lowest rat densities, i.e. below 37 individuals / hectare (Ruffino et al., 2015), and no iceplants were ever reported. NV1 and NV2 sites represent the island’s two main vegetation types (low and high matorrals). A habitat description for each study site (ICE1 and ICE2, RAT1 and RAT2, NV1 and NV2) is available in Table 3.1.

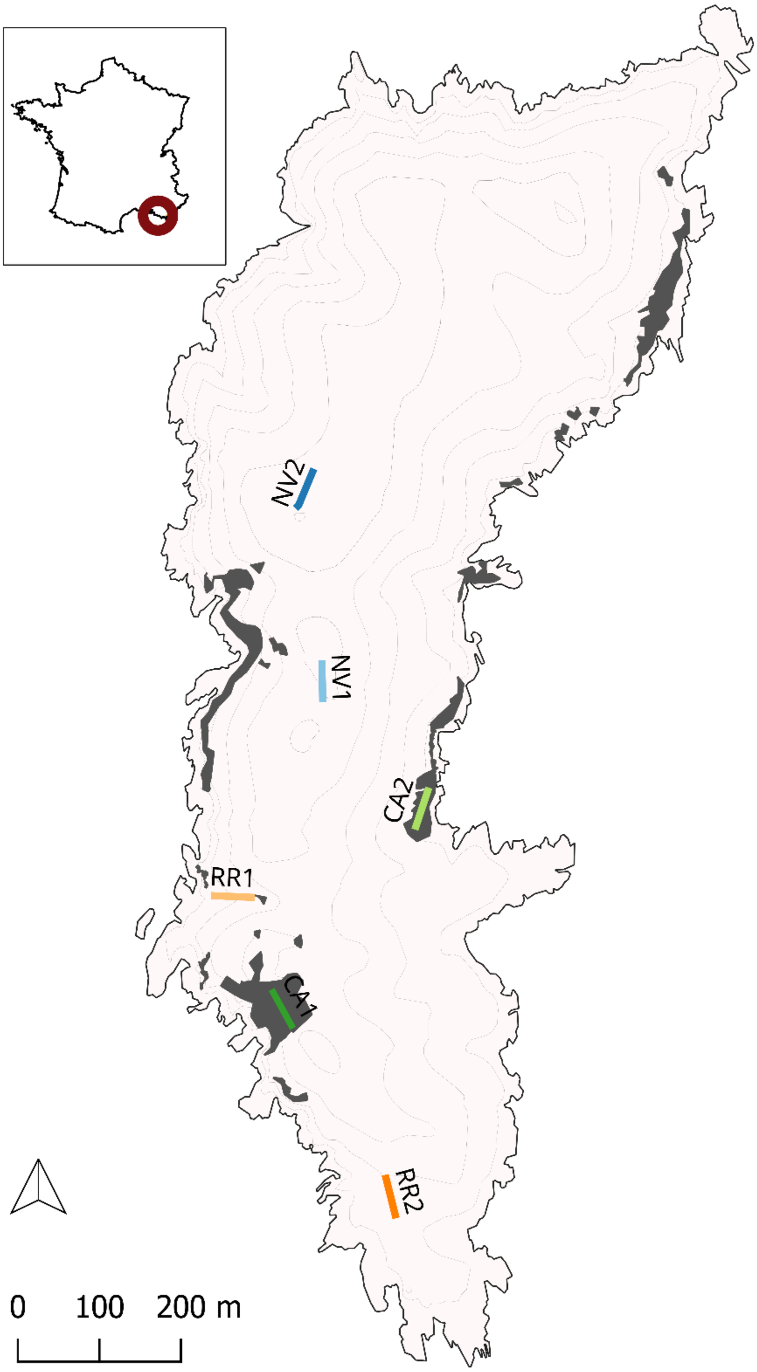

Figure 3.1: Map of Bagaud island, with area invaded by iceplant in dark grey and position of the six monitoring sites. Green lines indicate sites invaded by iceplant (ICE1 and ICE2), orange lines sites with high rat density (RAT1 and RAT2), and blue lines native vegetation sites (NV1 and NV2)

Table 3.5: Site acronym with type and detailed description, main plant species identified by Buisson et al. (2021), and density of black rats (Rattus rattus) recorded by Ruffino et al. (2015)

SITE NAME	TYPE OF SITE	SITE DETAILS	VEGETATION	RAT DENSITY (INDIVIDUALS/HA) (RUFFINO ET AL., 2015)
ICE1	Iceplant eradication	Inland 0.5 ha patch of *Carpobrotus* aff. *acinaciformis* located on top of a 40 m high cliff. Sandy soil.	Low matorral vegetation surrounding the *Carpobrotus* patch. Recolonizing vegetation dominated by *Lotus creticus* subsp. *cytisoides, Sonchus asper* subsp. *glaucescens, Bromus diandrus* subsp. *diandrus*	between 46 and 60
ICE2	Iceplant eradication	Coastal area with *Carpobrotus edulis* intermingled with small halophilous vegetation, sandy soil and rock patches. Altitude 5 m.	Coastal halophilous vegetation and low matorral inland. Main species are *Lotus creticus* subsp. *cytisoides, Sonchus asper* subsp. *glaucescens, Frankenia* sp.	below 37
RAT1	Rat eradication	Nitrophilous grassland highly frequented by seagulls. Sandy soil. Altitude 15 m.	Common species are Hordeum murinum subsp. leporinum, Sonchus asper subsp. glaucescens and Lotus creticus subsp. cytisoides	between 60 and 75
RAT2	Rat eradication	Open low matorral vegetation. Sandy-loam soil. Altitude 25 m.	Small patches of grassland intermingled with shrubs *Lotus creticus* subsp. *cytisoides, Pistacia lentiscus*, and *Frankenia* sp.	between 46 and 60
NV1	Native vegetation	Low matorral vegetation. Sandy-loam soil. Altitude 50 m.	Shrubby vegetation with Pistacia lentiscus, Smilax aspera and Myrtus communis	below 37
NV2	Native vegetation	High matorral vegetation. Sandy-loam soil. Altitude 60 m.	Matorral vegetation with trees such as *Phillyrea* sp., *Pistacia lentiscus* and *Erica arborea*.	below 37

2.3. Sampling design

Ants were collected using pitfall traps, a method commonly used to sample ground-dwelling arthropods and which has proved efficient in assessing ant species richness and spatial patterns (Salata et al., 2020; Steiner et al., 2005). The two first years of sampling, 2010 and 2011, were pre-eradication, while the following four surveys were carried out post-eradication, i.e. in 2013, 2015, 2017, and 2019. Each year, 10 pitfall traps (5 cm diameter and 10 cm depth), half-filled with ethylene-glycol, were installed 5 meters apart on a 45-meter transect on each site. They were collected every three weeks, four times a year. The first three sampling periods were conducted from April to July, and the fourth period started in mid-September. Ants were counted and identified to species level or to species-group level, following Lebas et al. (2016).

2.4. Data analysis

Statistical analyses were performed using R version 4.2.2 (2022-10-31). The temporal dynamics of ant communities was studied for each site independently. Sites were not statistically compared with each other due to the limited number of true site replicates (see section 1.2) (as in Braschi et al. 2021b, a). First, changes in species richness and total abundance of ants over time were assessed. Species richness was calculated for each trap. The total number of ants per trap was not used because these depend on species-specific social behavior (Steiner et al., 2005) and do not reflect the natural unit of ant diversity, the individual nest (Gotelli et al., 2011). Thus, the raw abundance of each species was transformed on a 7-score scale (Hoffmann et al., 2000): 1 = 1 ant; 2 = 2-5 ants; 3 = 6-10 ants; 4 = 11-20 ants; 5 = 21-50 ants; 6 = 51-100; and 7 > 100 ants, and hereafter called abundance score. Total abundance score was obtained by summing the species scores for each trap. Each site was studied independently, using a generalized linear mixed model (GLMM) from the glmmTMB R package (Brooks et al., 2017), with a negative binomial distribution (logit link) with either species richness or total abundance score as response variables. The year was set as a fixed factor and the period of sampling and the trap number were set as random factors. Multiple comparisons between years were performed using post-hoc Tukey tests.

The composition of ant communities was compared over the six years of survey using the non-metric multidimensional scaling (NMDS) approach with the vegan package (Oksanen et al., 2022). For this analysis, abundance scores were averaged over the four sampling periods of each year for each trap. Differences between communities were represented using a Bray-Curtis dissimilarity matrix. Overall significant difference between communities was assessed using PERMANOVA, followed by pairwise adonis tests (Martinez Arbizu, 2020). For each year, the community is represented by ten traps, each having their own species composition. Similarities between traps within a year were visually assessed by estimating the size of the polygons for each year on the NMDS figures. Further individual species abundance score analyses were conducted for the sites showing significant dissimilarity. SIMPER analysis (Clarke, 1993) was used to identify species contributing up to 75% of the community dissimilarity between the pre-eradication grouped years and the post-eradication grouped years. Their individual abundance score response to the year factor was assessed using glmmTMB with the same features as the total abundance score models.

3. Results

A total of 35,414 ants, belonging to 24 species, and 13 genera were identified during the study (Supplementary material S3.1). Most of the individuals belonged to the Myrmicinae family (25,944 individuals), followed by Formicinae (9,491 individuals), and Ponerinae (28 individuals). Site NV2 had the most species, 18, and ICE2 had the least, 11 species. *Pheidole pallidula* was the most abundant and frequently encountered species.

3.1. Species richness and total abundance score

Overall, the pre-eradication years of iceplant removal sites had the lowest species richness of the study (Figure 3.2). The two iceplant removal sites showed significant increase in species richness after the eradication (Figure 3.2). At ICE1, species richness was significantly higher than both pre-eradication years, 2010 and 2011, starting in 2015. It reached its highest in 2019 with an average of 5 species per trap. At ICE2, species richness after 2015 was only significantly higher than in 2010 (not 2011). At RAT1 species richness changed slightly over time, with significantly higher values in 2019 than in 2013 and 2017 (Figure 3.2). The other sites did not show any significant differences between years (Supplementary material S3.2).

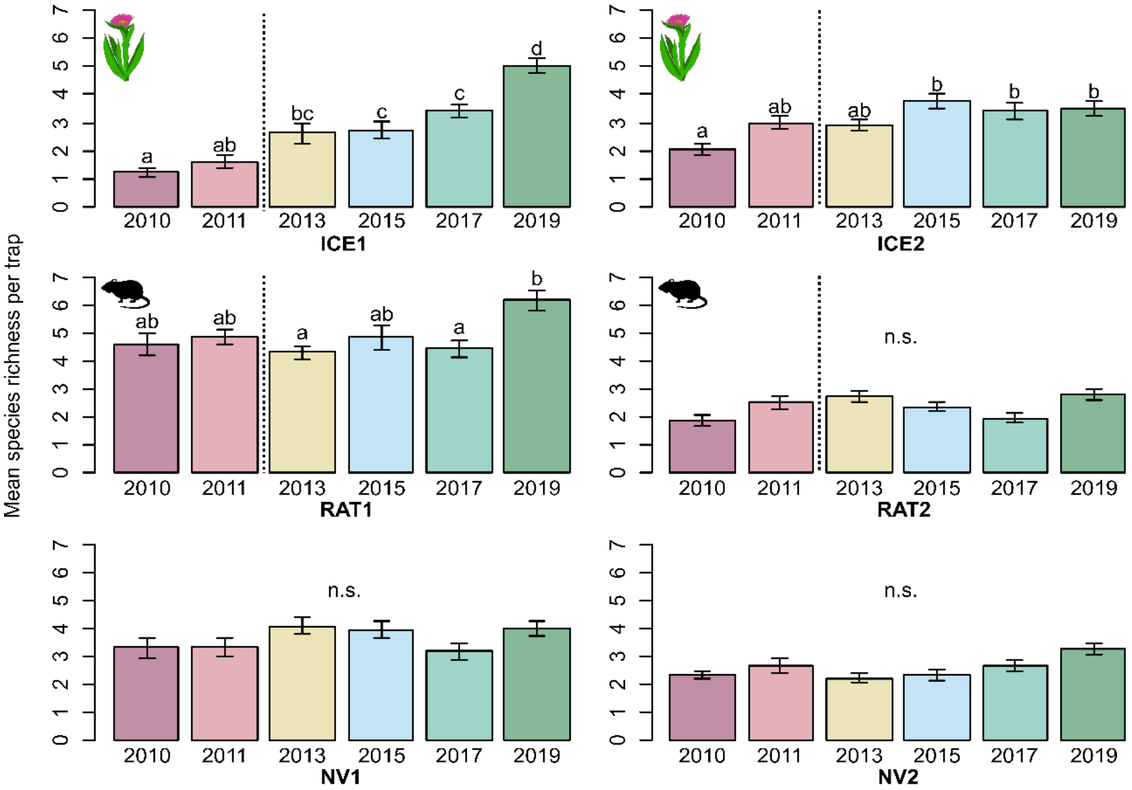

Figure 3.2: Mean ant species richness per trap over the six-year sampling at the six different sites (mean value ± standard error). The black dotted line indicates period of eradication (between late 2011 and mid-2012), of black rats at RAT1 and RAT2 and of iceplant at ICE1 and ICE2. Tests were performed using generalized linear mixed model and a negative binomial distribution. Letters above the bars indicate significant differences between years ($p < 0.05$). If no significant difference was found we added "n.s." above the graph.

Ant abundance score increased significantly and gradually after the eradication at ICE1 (Figure 3.3). Ant abundance score in 2019 was up to 5 times higher than pre-eradication years. At ICE2, the total abundance score increased slightly over the years. Pre-eradication years had significantly lower values than 2015 and 2019. At RAT1, RAT2 and NV1, abundance scores fluctuated, with no particular trend (Figure 3.3), although they were significantly higher in 2019 compared to 2010 at both RAT1 and RAT2. Ant abundance scores did not change over the years at NV2 (Supplementary material S3.2).

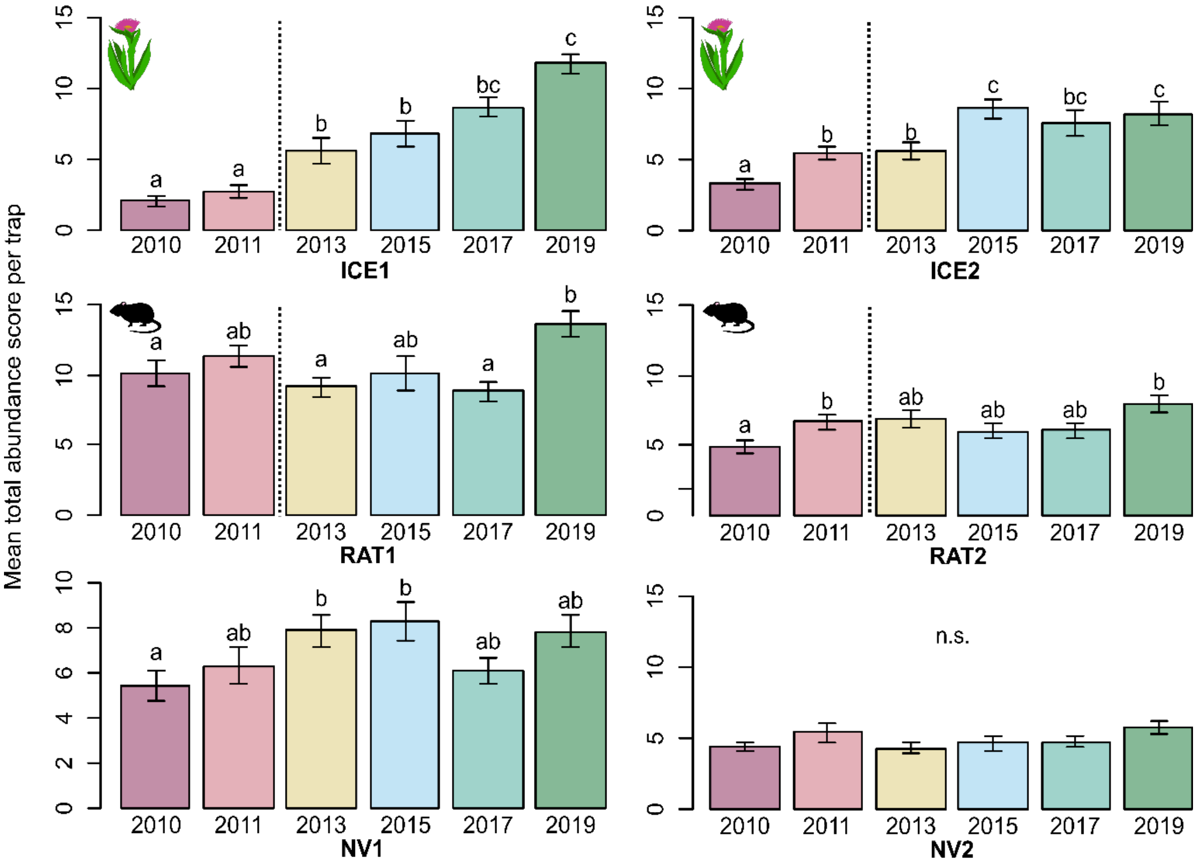

Figure 3.3: Mean ant total abundance score per trap over the six-year sampling at the six different sites (mean value ± standard error). The black dotted line indicates period of eradication (between late 2011 and mid-2012), of black rats at RAT1 and RAT2 and of iceplant at ICE1 and ICE2. Tests were performed using generalized linear mixed model and a negative binomial distribution. Letters above the bars indicate significant differences between years ($p < 0.05$). If no significant difference was found we added “n.s.” above the graph

3.2. Community composition

The communities of ICE1, ICE2, RAT1 and NV2 varied significantly among years. With an R^2 of 32%, ICE1 communities differed the most across years, followed by ICE2 with 19% and RAT2 and NV2 with respectively 14% and 15%. At ICE1, ant communities significantly changed after eradication. Communities shifted over the years, from communities driven by *Hypoponera eduardi* to communities with a strong species core composed of *Pheidole pallidula, Plagiolepis pygmaea, Crematogaster scutellaris,* and *Crematogaster sordidula* (Figure 3.4). This trend was weaker at ICE2, where polygons overlapped much more (Figure 3.4). In 2010, community composition differed from all the subsequent years and, composition of 2011 was only significantly different from 2019. At both iceplant eradication sites, trap compositions within a year were more dissimilar before eradication than after (Figure 3.4). At RAT1, only the year 2010 was significantly different from post-eradication communities. Species compositions of 2019 traps were once again more similar than previous years (Figure 3.4). At NV2, the communities of 2010 and 2011 were significantly different from those of 2017 and 2019. At RAT1 and NV2, polygons overlapped much more than at the iceplant eradication sites.

3.3. Individual species abundance score

At the ICE1 site, three species contributed to 75% of the pre-/post-eradication community dissimilarity: *P. pallidula, Messor bouvieri,* and *P. pygmaea*. For these three species, individual mean abundance score increased after eradication (Figure 3.5). This trend was stronger for *P. pallidula* and *P. pygmaea,* as their abundance scores values were nearly zero before iceplant eradication and, increased significantly and steadily in the following years. At ICE2, the same three species contributed to most of the dissimilarity between pre- and post-eradication years. While *P. pygmaea* abundance score did not change over the years, *P. pallidula* began

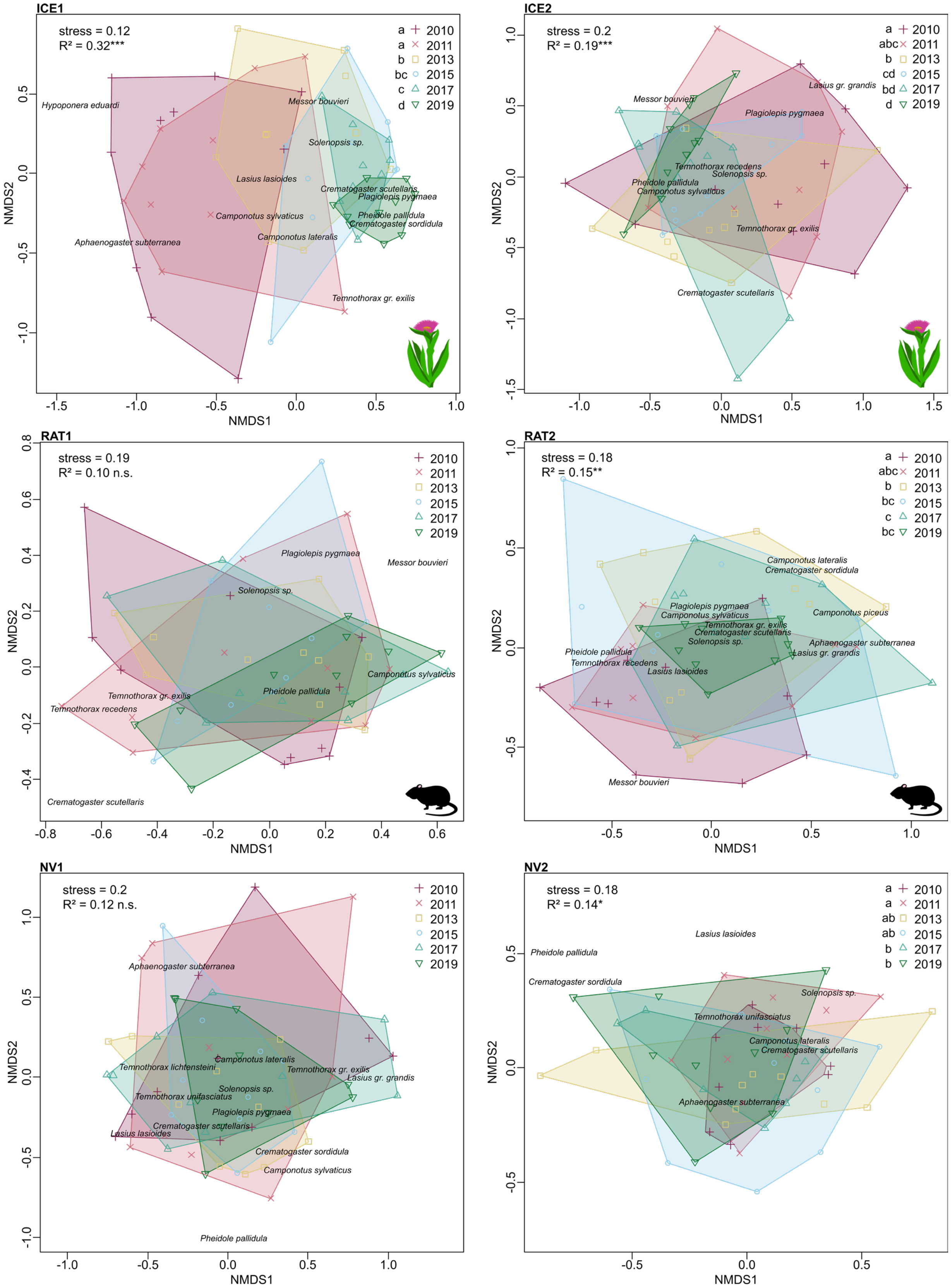

Figure 3.4: Non-metric multi-dimensional scaling (NMDS) ordination of ant communities based on Bray–Curtis dissimilarities with pitfall trap abundance scores. Differences between the years' communities were assessed via the adonis2 (vegan) package, giving the R2 and its significance ($P < 0.05$*, $P < 0.01$**, $P < 0.001$***). Communities differed significantly according to year at the two iceplant eradication sites (ICE1 and ICE2), at one of the black rat eradication sites (RAT2 but not RAT1), and at one of the native vegetation sites (NV2 but not NV1). Letters next to the year entries indicate significant differences between years found with pairwise comparisons. If no significant difference was found we added "n.s."

to be significantly more abundant from 2015 on and *M. bouvieri* from 2017 on (Figure 3.5). At RAT2, 75% of the pre-/post-eradication dissimilarity was attributed to six species: *P. pallidula*, *Lasius* gr. *grandis*, *M. bouvieri*, *C. scutellaris*, *P. pygmaea,* and *Camponotus sylvaticus*. In contrast to the iceplant eradication sites, no before-after trend was observed for the rat eradication sites. (Figure 3.5). Concerning NV2, among the three main species contributing to pre-/post-eradication community dissimilarity, only *C. sordidula* abundance score was

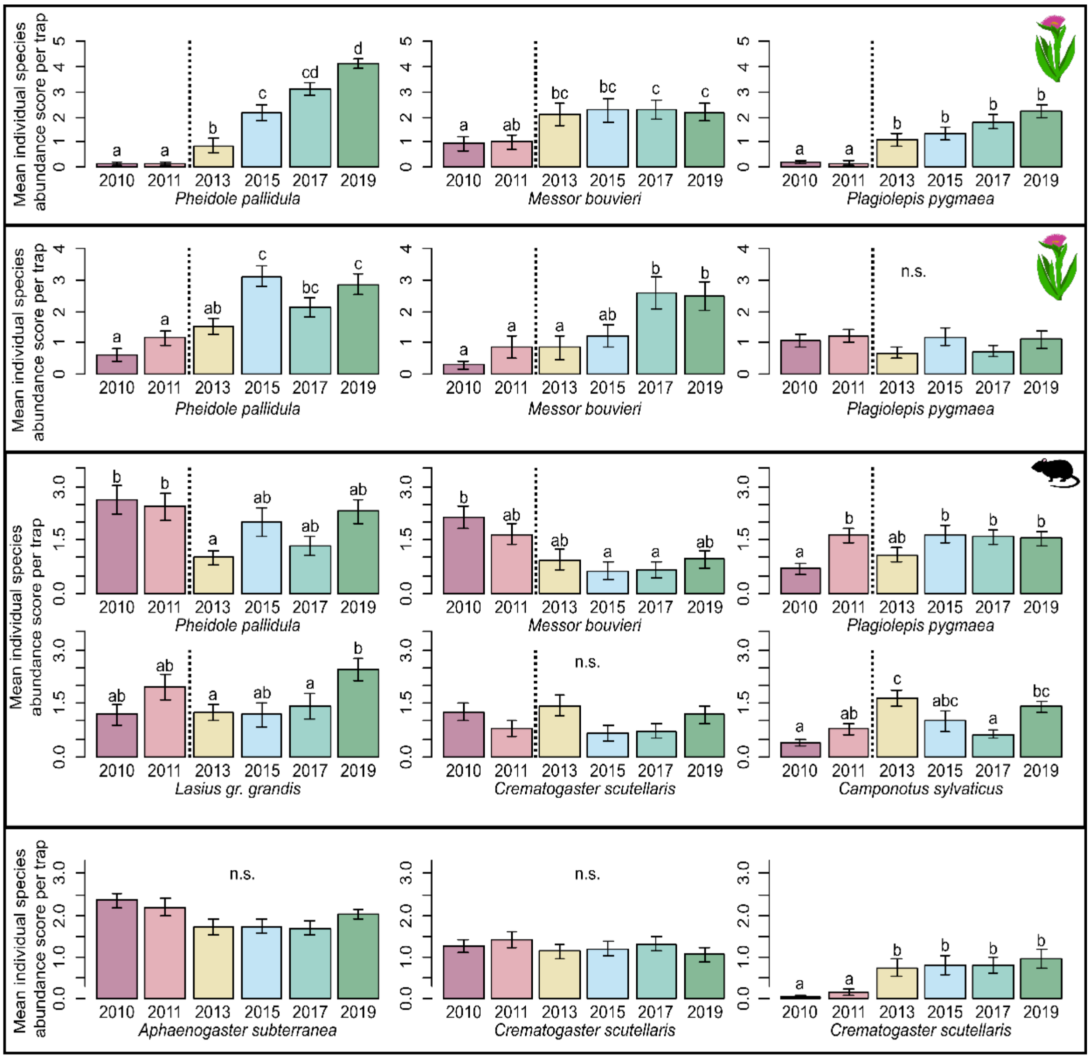

Figure 3.5: Mean abundance scores of individual species per trap over the six-year sampling (mean value ± standard error) at the two iceplant eradication sites (ICE1 and ICE2), at the second black rat eradication site (RAT2) and at the second native vegetation site (NV2). Only sites that presented significant community dissimilarities were considered. Selected species were those contributing up to 75% to before-after eradication dissimilarity, according to SIMPER analysis. The black dotted line indicates the eradication period (between late 2011 and mid-2012). Letters above the bars indicate significant differences between years ($p < 0.05$) assessed with a generalized linear mixed model and a negative binomial distribution. If no significant difference was found we added “n.s.” above the graph

significantly influenced by years (Supplementary material S3.3). It was significantly less abundant in 2010 and 2011 compared to the subsequent years (Figure 3.5).

4. Discussion

We show that, in line with expectations, ant communities changed significantly after the eradication of iceplants. However, such a trend was not observed at the native vegetation sites. Indeed, while the global pool of species found at the iceplant sites did not change after eradication, we observed an increase in the abundance score and number of species caught in the traps. The eradication promoted common Mediterranean ants, including *Pheidole pallidula, Messor bouvieri* and *Plagiolepis pygmaea* giving them opportunities to increase site spatial occupation and exploration with a higher foraging activity. This trend was stronger at the iceplant eradication site located on the cliff top and surrounded by low matorral (ICE1), where we observed an overall steady increase in ant abundance scores.

These changes in the ant communities can be attributed to ecosystem modifications following eradication efforts. As a succulent and with its ability to create dense litter and mats, iceplant induces changes at the soil surface: it reduces evapotranspiration, incident solar radiation, and thus temperature at a small scale (Molinari et al., 2007; Novoa, Rodríguez, et al., 2013). Conversely, we assume that the eradication led to an increase in temperature and a decrease in moisture at the soil surface, as observed by Novoa et al. (2013b) when comparing invaded and non-invaded sites. Native vegetation quickly recovered after eradication, with native Mediterranean species including *Lotus creticus*, *Sonchus asper subsp. glaucescens*, and *Bromus diandrus*, inducing changes in habitats, from poor and homogeneous dense mats of iceplant to higher plant species richness (Buisson et al., 2021). This vegetation diversification is combined with a decrease in litter cover, and fluctuation of bare ground cover with seasons and years (Buisson et al., 2021). At a small scale, the return of native vegetation added habitat structure (Buisson et al., 2021). Moreover, vegetation diversification may have increased the temporal spread of certain food resources, such as nectar or seeds, contrasting with the few weeks of iceplant flowering during spring (Campoy et al., 2018).

Positive impacts of iceplant eradication have already been observed on other invertebrates (Braschi, Hélard, et al., 2021; Braschi, Torres, et al., 2021) but were never assessed on ants. Nevertheless, ants are known to be sensitive to habitat disturbance through the indirect effects of change in habitat structure, microclimate, resource availability, and competitive interactions (Andersen, 2019). Ant species richness and abundance are closely correlated to vegetation variables, such as vegetation cover and strata (Lassau & Hochuli, 2004; Retana & Cerdá, 2000). Ants may have been promoted by an increase in microhabitats diversity (Hill et al., 2008; Martello et al., 2018; Vasconcelos et al., 2008). The increase in resource diversity and availability may have also benefited ants with a specialize diet (Hahn & Maschwitz, 1985; Sundström, 1993), such as *Plagiolepis pygmaea* that feed on liquid food and *Messor bouvieri* that feed on seeds (Arnan et al., 2014). Moreover, the dynamics of the resource use of many ant species is also strongly influenced by microclimatic conditions (Cerdá et al., 1998), in particular by fine-scale temperature changes (Stuble et al., 2013). In our case, most of the trapped species being xerophilous and thermophilous, they may have benefited from a return to warmer and dryer conditions at the soil surface to build their nest and/or to expand their foraging range. Nevertheless, the removal of the abundant litter produced by iceplants and/or the soil disturbance it caused might have been detrimental to other specialized species, such as the hypogaeic species *Hypoponera eduardi*, which was characteristic of the pre-eradication communities of the ICE1 site.

While our results clearly showed the benefits of iceplant eradication on ant spatial occupancy at ICE1, located on the cliff top and surrounded by low matorral, there was less evidence of benefits at ICE2. At ICE1, iceplant was denser and thicker, thus eradication led to drastic changes in the ecosystem, which could explain a higher success in the restoration. The coastal site (ICE2) had patchy vegetation with some native species before eradication and higher rock cover, which remained at the same level throughout the study (Buisson et al., 2021). The eradication of iceplant probably did not trigger enough changes to the ecosystem to induce strong modifications in ant presence over the site.

In contrast to the impact of iceplant eradication, rat eradication had no discernible effect on ant communities. Likewise, we did not observe any distinct pattern at the native vegetation sites. The composition of each site's community remained relatively stable over the years, and we did observe fluctuations in abundance scores, with an overall peak occurring in 2019. Ant species richness and abundance score at rat eradication sites were already at similar or higher levels than those of the native vegetation sites. Individual responses were mixed, depending on species identity and sites. *Crematogaster sordidula* abundance score was an exception, increasing slightly for unknown reasons after 2011 at NV2.

Although eradications initially decreased rat densities on Bagaud island, the population density rose again in 2015 and 2017. Still, the lack of response from ants to rat eradication in the first years is consistent with previous findings that ants are not commonly a prey of black rats (Courchamp et al., 2011; Riofrío-Lazo & Páez-Rosas, 2015). Other studies showed that ant abundance remained similar with or without rats (Sinclair et al., 2005; Vergara et al., 2021).

The absence of habitat modification, and relative stability of plant communities outside iceplant removal sites (Buisson et al., 2021), is consistent with relative stability of ants at rat and native vegetation sites. Small changes could be explained by climate variations (Pelini et al., 2014; Resasco et al., 2014) and/or by demographically volatile species (Samways, 1990), as some species with a highly flexible behavior show changes in their nest distributions from year to year (Gordon, 1991). The Mediterranean climate is known for the strong inter-annual variability of temperatures and precipitations (Deitch et al., 2017), and these parameters can strongly influence ant foraging activity (Lasmar et al., 2021; Levings, 1983; Whitford & Ettershank, 1975).

In Mediterranean open vegetation, temperature is the main driver of changes in ground ant communities (Cerdá et al., 1998; Retana & Cerdá, 2000). Most of the time foraging activity increase with temperatures, but responses can vary according to the thermal tolerance of the species (Cerdá et al., 2013; Stuble et al., 2013). According to Porquerolles weather station which is the closest island where climatic conditions were recorded, 2019 was one of the warmest and dryest year of our sampling (Appendix D). These conditions could have promoted an increased in the activity of common Mediterranean heat-tolerant species (Cros et al., 2016), which represent most sampled species in our study. Apart from climatic variability, resource availability can also be a strong driver of demographic changes and foraging behavior in ants (Bernstein, 1979; Davidson et al., 1985; Traniello, 1989).

Our data come from eradications carried out on a single small Mediterranean island, and this study should therefore be replicated on other islands to confirm the generality our results. The harmful effects of iceplants are leading to an increasing number of eradication campaigns, particularly in the Mediterranean area. In addition to the findings mentioned, it is worth noting that ants are very rarely included in restoration monitoring surveys, yet they play a crucial role in ecosystem functioning (De Almeida et al., 2024) and can provide valuable insights into the effectiveness of restoration and conservation strategies. While they may not be the ideal taxon for evaluating the benefits of rat eradication, their quick response to ice plant eradication highlights their potential as indicators of restoration success.

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Supplementary Material

Tableau S3.5: List of ant species and their individual counts by site. All species are Formicidae identified from the pitfall traps of the 6-year arthropod sampling included in the monitoring of the restoration program of Bagaud island.

Species	**ICE1**	**ICE2**	**RAT1**	**RAT2**	**NV1**	**NV2**
Aphaenogaster dulciniae (Emery, 1924)			1			
Aphaenogaster subterranea (Latreille, 1798)	24		11		233	982
Camponotus lateralis (Olivier, 1792)	17	2	58	1	177	151
Camponotus piceus (Leach, 1825)	3		144	1		
Camponotus sylvaticus (Olivier, 1792)	86	109	499	6	80	6
Colobopsis truncata (Spinola, 1808)						1
Crematogaster auberti (Emery, 1869)					1	11
Crematogaster scutellaris (Olivier, 1792)	35	123	634	119	709	495
Crematogaster sordidula (Nylander, 1849)	31		209	1	69	385
Hypoponera eduardi (Forel, 1894)	22					
Lasius gr. *grandis*	1	150	1713		1122	42
Lasius lasioides (Emery, 1869)	20	1	20	1	2816	57
Messor barbarus (Linnaeus, 1767)			7			
Messor bouvieri (Bondroit, 1918)	4488	2311	968	1694	4	2
Pheidole pallidula (Nylander, 1849)	1516	1327	2359	5503	120	41
Plagiolepis pygmaea (Latreille, 1798)	548	333	542	102	648	15
Ponera testacea (Emery, 1895)						3
Solenopsis sp. (Mayr, 1851)	55	89	169	135	169	11
Temnothorax aveli (Bondroit, 1918)					2	
Temnothorax gr. *exilis*	74	25	115	152	17	1
Temnothorax lichtensteini (Bondroit, 1918)	2				33	
Temnothorax recedens (Nylander, 1856)	3	57	81	214		
Temnothorax unifasciatus (Latreille, 1798)	3				42	53
Tetramorium gr. *caespitum*						1

Tableau S3.6: Statistical results of the year effect on mean species richness per trap, mean abundance level per trap and assemblage composition (Bray-Curtis dissimilarity). Results were extracted from the generalized linear mixed models for the species richness and abundance, giving the Chisq statistic. Results from PERMANOVA tests were used for the assemblage composition, giving the F statistic. Bold numbers show the significant responses to the year factor and stars indicate significance levels (p<0.05=*; p<0.01=**; p<0.001=***). Results are given per site.

	Species Richness	Abundance	Assemblage Composition
	Chisq	Chisq	F
ICE1	**107.75*** **	**158.65*** **	**5.10*** **
ICE2	**16.25** **	**57.01*** **	**2.50*** **
RAT1	**16.43** **	**22.97*** **	**1.95** **
RAT2	10.81	**20.59*** **	1.20
NV1	8.98	**20.11** **	1.40
NV2	9.77	8.94	**1.79* **

Tableau S3.7: Statistical results of individual species abundance responses to the year per site. Results were extracted from the generalized linear mixed models. Given numbers are the Chisq parameter of the models. Bold numbers show the significant responses to the year factor and stars indicate significance levels (p<0.05=*; p<0.01=**; p<0.001=***). For each site, species considered where these contributing up to 75% of the dissimilarity between pre and post eradication assemblages.

	ICE1	ICE2	RAT1	NV2
Pheidole pallidula	**128.34*** **	**61.23*** **	**15.74** **	
Messor bouvieri	**22.11*** **	**29.99*** **	**16.81** **	
Plagiolepis pygmaea	**60.96*** **	3.96	**19.16** **	
Crematogaster scutellaris		**20.41** **	8.03	2.41
Lasius gr. grandis			**11.10* **	
Camponotus sylvaticus			**35.23*** **	
Aphaenogaster subterranea				7.75
Crematogaster sordidula				**30.28*** **

Tableau S3.8: Summary of the main weather data from the Porquerolles weather station (located 9 kilometers from Bagaud island) during the four sampling periods (April to July and September to October)

	2010	**2011**	**2013**	**2015**	**2017**	**2019**	**Mean over the six years**
Mean maximum temperature (°C)	22.65	25.52	22.60	24.70	23.70	25.22	24.07
Mean minimum temperature (°C)	13.64	14.31	13.94	14.61	14.16	14.7	14.23
Annual cumulated precipitation (mm)	298.4	34.5	165.2	180.7	65.7	104.3	141.5

Summary of the results

Chapter 1

A total of 195 species were found on the 207 small Mediterranean islands studied. The species-area relationship is convex, close to the shape of the power model. The linearized SAR (log-log transformation) had a significant R^2 of 0.13. However, the continuous one threshold model provides a best fit than the linear model. We find that 86% of the islands are below the breakpoint which is 1.09 km^2. In studying predictors of species richness, the best-fitting model includes surface area, the proportion of landmass in a 6km buffer and the proportion of habitat on islands as explanatory variables. Species richness increases with all of the selected predictors. Surface area is the variable with the strongest influence on species richness.

Chapter 2

Twenty-one ant species were found on the 36 small Corsican islands, two species were found only in the first surveys (between 1984 and 1995) and three species only in the second survey (2023). Species richness has increased between the two surveys, but at a very low rate, i.e. 0.03 species per year. Mean colonization rate exceeds mean extinction rate. This results in a turnover predominantly composed of nestedness, with nestedness accounting for 33.10 of the total 44.56% turnover. Moreover, all species have at least colonized one new islands and half of the species have become extinct on at least one island.

The total turnover is negatively affected by the number of plant alliances. Community clustering on the first surveys show that islands can be sorted in 6 clusters in which islands are not grouped by archipelago, size or isolation. Only one cluster is composed of five islands that shared more similar characteristics, and this is also the only cluster for which the composition changed between the surveys. This cluster was composed of very small islands, close from the coast with very few plants and low ant diversity. Their species richness has increased in the second survey. Using data from the second survey for clustering shows that only four groups of communities can be differentiated.

Chapter 3

The 10-year restoration program of the small island of Bagaud allows to list 24 ant species. Species richness and abundance increased after the eradication at the two iceplant removal sites. At the rat eradication sites and the native vegetation sites, species richness and abundance either fluctuated without trends or did not show any significant differences through time. The two iceplant eradication sites also had shifts in the community composition after eradication, a trend that was not observed at the others sites. These trends were stronger at the site that had the larger and more homogeneous patch of iceplant, and thus that had the strongest habitat change. Some species responded more to the iceplant eradication than others, including the most abundant and common: *Pheidole pallidula*, *Messor bouvieri*, and *Plagiolepis pygmaea*.

General Discussion

The main objective of this thesis was to better understand the structure and dynamics of ant communities on small islands. While studying ant response to spatial and ecological characteristics of small islands, we also focus on the effects of habitat diversity and quantity, particularly in a context of global change. Given the particular conservation challenges that islands face due to their vulnerability, we also discuss how our results can contribute to this field and how fundamental questions can benefit from conservation/restoration programs.

1. Effects of island spatial characteristics on ant community structure and temporal dynamic

Area is shown to be the strongest driver of ant species richness, but not of ant temporal turnover on small Mediterranean islands. Conversely, the effect of isolation on species richness and turnover is weakly supported by our results, particularly when using the distance to mainland. Turnover rates are not influenced by this parameter and ant species richness respond positively but weakly to the proportion of landmass in a 6-km buffer around the island.

While choosing the isolation parameter it is important to consider the particular context of the islands, and if mainland is an important pool of species for islands, it was shown to weakly predict species richness for continental islands (Weigelt & Kreft, 2013). Here, most of the studied islands are continental (or land-bridge) islands, poorly isolated, often included in chain of numerous islands. Adjacent islands may represent important alternative sources compared to mainland, playing an important role in colonization dynamics. Low isolation is correlated with low spatial beta-diversity (Zhao et al., 2021). The similarity of communities, due to proximity, can also explain that turnover is not affected by isolation, as colonization and extinction dynamics could maintain a same small species pool. Nevertheless, in most cases isolation remains a weaker predictor even of island's species richness compared to area, as concluded by other studies (Itescu et al., 2020; Matthews et al., 2019; Zhao et al., 2020), and particularly for ants that have high dispersal abilities (Helms, 2017; Morrison, 2016).

Since the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1963, 1967), the Island's Species-Area Relationship (ISAR) has been extensively studied and validated, sometimes elevating this relationship to the rank of law in ecology (Schoener, 1976).

According to the ETIB, colonization and extinction rate are indeed influenced by island area, affecting in turn the turnover. It follows the assumption that small islands are more prone to stochastic events, hosting smaller and so less stable populations, without evolutionary mechanisms, such as speciation (Lomolino & Weiser, 2001; Triantis et al., 2012), which may justify the slower increase in species richness with area, and eventually a higher turnover. If our data supports this positive relationship between ant species richness and area, area weakly affect the turnover of ant communities. Other studies on ants, showed that area is not always the best predictor of species richness (Morrison, 1998; Torres & Snelling, 1997) or even of turnover (Goldstein, 1975). Ant ISAR synthesis at the global scale describe the relationship with a low slope (Ohyama et al., 2021), but in our case we find an even lower slope. A reason to this particularly slow increase may be supported by the fact that the range of island sizes that we included in this study, i.e. 58m^2 to 10km^2, is already way below the Small Island Effect (SIE) threshold they found in their synthesis, i.e. 150km^2. Finding a SIE is indeed dependent on the method used (Sfenthourakis & Triantis, 2009), but also the island context (Lomolino & Weiser, 2001). The particular context of poorly isolated very small islands can result in lower thresholds (Schrader et al., 2020). Discussions about the SIE often focus on the importance of other factors than area on species richness, mainly through indirect effects, as it may be the case for habitat diversity (Chen et al., 2020; Sfenthourakis & Triantis, 2009; Triantis et al., 2006).

2. The importance of habitat diversity and quantity in shaping ant communities

Species richness and turnover of ants on small Mediterranean islands respond significantly to habitats. In the case of species richness, at the scale of the Mediterranean basin, we find a positive relationship with the quantity of habitats, defined in our study by vegetation cover. Vegetation can benefit ants both directly and indirectly by changing abiotic and biotic conditions. Vegetation modifies soil availability, to establish their nest (Goldstein, 1975), and also affects humidity and temperature by creating shaded areas. Vegetation also provides direct food resources, with seeds and extrafloral nectars for example, but also indirectly by affecting the availability of preys, such as detritivores or aphids. Islands with higher proportions of vegetation could then promote greater colonization possibilities. This result corroborates with the habitat heterogeneity hypothesis (Tews et al., 2004). However, there would be an island size threshold above which habitats increase significantly with size. As small islands often present a more heterogenous availability of habitats (Sfenthourakis & Triantis, 2009), it seems appropriate that it contributes significantly to predict species richness in addition to area on smallest islands.

As the community becomes richer thanks to habitat diversity, it seems that it also becomes more stable. Indeed, habitats also negatively affect turnover, through the number of plant alliances. Plant diversity may be used as a habitat proxy (Dennis et al., 2003), as it represents a diversity of resources. Turnover rates may decrease due to lower extinction probabilities, as enhanced protection reduces the impacts of stochastic and extreme climatic events. This corroborates with the SIE and highlights the importance of vegetation, compared to area, in buffering disturbances and maintaining communities.

The rapid response of ant communities to habitat changes, i.e. iceplant (*Carpobrotus* spp.) removal, further highlights the importance of habitat diversity for ant spatial occupancy and species richness. On a single island and at a site scale, ants quickly recolonized and increased their spatial occupancy of the area after the return of native vegetation, a few years after the removal. Iceplant is known to cause habitat simplification by forming dense monospecific mats (Campoy et al., 2018), in contrast to the diverse plant communities that return after its removal (Buisson et al., 2021). As abundance increases, it is generally admitted that extinction rates decrease, because bigger populations are more stable (Frankham et al., 2002). If no new species colonizes the area, ant communities may benefit once again from habitat diversity to increase their stability. Monitoring other sites of Bagaud island have also showed that without habitat change, ant communities have low to zero temporal turnover over a 10-year time span.

3. Insights into the effects of global change on ant communities and small island conservation

At a larger scale, the dynamics of ant communities of 36 small Corsican islands have shown a relatively high percentage of turnover, a little less than 50%, through more than 30 years. However, communities have changed slowly compared to the relatively long-time span, with a nested pattern. Many islands have gained species that were almost exclusively already present in the regional pool, except *Cardiocondyla mauritanica*, which is a recent finding for Corsica (Blaya et al., 2024). This result, of a slight increase in the mean number of species per island, may reflect a non-equilibrium pattern. We also found that fewer clusters of islands with similar communities could be distinguished in the second survey compared to the first one. These patterns corroborate with homogenization of communities, which is often attributed to global change or the spread of Invasive Alien Species (IAS) (Chase et al., 2019).

The structure of ant communities can be contrasted between islands presenting anthropogenic disturbance and the most preserved ones (Rizali et al., 2011). Nevertheless, although most of the studied islands are relatively well-preserved, either because they are very difficult to access or because public access is prohibited, indirect human disturbance may still affect them. Such trends of homogenization in relatively undisturbed ecosystems have already been observed, as thermally generalist species expand their range (Paraskevopoulos et al., 2024) Climate change and the resulting increase temperatures, could indeed benefit some generalist species to increase their activity (Parr & Bishop, 2022). As ants increase their activity they may also improve their resource exploitation, which could affect their investment in reproductive ants (Morales & Heithaus, 1998), resulting in higher colonization probabilities. However, putting in perspective the turnover with the time-span, it seems that changes in the communities operated at low rates, similarly to what was found in previous studies (Morrison, 2010; Torres & Snelling, 1997). Low or zero turnover was also observed at the site scale on a single island over 10-year monitoring, which supports that the absence of direct disturbance promotes stability in community composition at the regional scale as well, even if we lacked data between the 30+ years separating the surveys of small Corsican islands.

Slow changes in ant communities are sometimes justified by their ecology, as they are able to bury their nests, offering protection against disturbance (Morrison, 2010), and biology because of the remarkable longevity of colonies (Hölldobler & Wilson, 1990). Nevertheless, we also showed that communities can respond very fast to habitat change. The ability of ants to respond clearly to environmental changes highlights their importance as indicator species (Andersen et al., 2002; Tiede et al., 2017). In this context of global change, including IAS spread, they may be appropriate biological models to monitor to understand the effects of invasions on communities or to evaluate the efficiency of conservation/restoration projects. Ants can provide good insights of insular community dynamics as they strongly, and most of the time positively, affect their environment. However, among ant species, a small number is spreading from their native range and have detrimental impacts on their environment (Wong et al., 2023). This is the case of the notorious *Solenopsis invicta* in Sicily (Menchetti et al., 2023) which disperses through nuptial flight and therefore is able to colonize islands. These spreads also justify monitoring ant communities, especially on islands that are often more vulnerable than adjacent mainland (Whittaker et al., 2017). In the case of the biotic resistance hypothesis, where diverse communities should be more resistant to invasion than less diverse ones, disturbance of habitats may promote alien ant arrival, thus, preserving and eventually restoring island habitats becomes even more important (Morrison, 2016). This is especially relevant given that we show that ant communities are more diverse and stable in islands with greater habitat variety and quantity.

Perspectives

4. The response of other diversity indices to spatial and ecological characteristics and time

The data gathered for this PhD thesis project offer many opportunities of research questions. Among the fundamental research questions at stake in island ecology and biogeography, there is a recent strong interest for studying the response of diversity indices, other than taxonomic, such as functional or phylogenetic diversity (Patiño et al., 2017; Whittaker et al., 2014). Studying the functional space of ant communities could help to avoid excessive taxonomic disparities between communities, particularly on the scale of the Mediterranean basin. As predictors of functional diversity may not be the same as species richness ones (Santos et al., 2016), this would contribute to understand community assembly and ecosystem processes (Mason & de Bello, 2013) at a larger scale.

Benefiting from previous studies on ant functional traits (Arnan et al., 2010, 2014; De Almeida et al., 2024), the idea would be to study which traits are filtered according to the island spatial and ecological characteristics (surface, habitat, isolation...), along with the effect of these factors on the global functional space. The restoration program of Bagaud island would also be an opportunity to understand how ant traits respond to habitat change. The selection of traits should focus on those relative to dispersal, such as ability to do mating flights, wing size or queen size, or even size of the colony that could influence the ability of propagules to colonize islands. Traits relative to establishment success and competitivity, such as the size of workers, polymorphism, polygyny, polydomy and foraging strategy are also important to include.

Using other diversity indices, it would be interesting to assess how they fluctuate through time. It was shown that ETIB can be extended to functional diversity, notably for plants (Schrader et al., 2023). They found, for example, that extinct species are compensated by others with similar traits, which results in a stability of functional diversity. Moreover, it would also provide an opportunity to identify traits that contribute to higher turnover. In our case, as we observed an increase in species richness with a nested pattern, it would be interesting to assess how the functional space is affected by these changes. Notably, the issue would be to understand if the species that are causing homogenization of the taxonomic composition at the regional scale (archipelagos) also participate in functional space homogenization.

5. Comparative study of the SAR and the SIE among archipelagos

Ohyama et al. (2021) suggested that ant SAR may be variable among different biogeographical realms, with a high variability for the Palearctic. In turn, it was shown that the breakpoint of the SIE could be influenced by scale, including size and isolation of islands that compose the studied archipelagos (Schrader et al., 2020). Thus, it would be interesting to further study this variation inside the Mediterranean basin, related to the spatial turnover of the communities. For example, while studying isopods of Mediterranean islands, Gentile & Argano (2005) have shown distinct communities between the eastern and western part of the basin, affecting the shape of the SAR and the SIE. Our study could then benefit from community clustering to better understand how beta diversity of ant communities affects the SAR and SIE trends we found at the scale of the Mediterranean basin. The Mediterranean Sea is divided in nine seas or basins related to tectonic plate dynamics leading to the formation of the area during Oligocene and Miocene (Blondel et al., 2010). The complex biogeographical history of the area has been shown to strongly influence plant diversity (Médail, 2022), and could in turn influence ant community composition and species richness. Our study would then benefit to take into account the geological history of the archipelagos, to better understand how it participated in ant community shaping.

6. Estimation of habitat quantity and diversity, and their effects

The term habitat in itself is controversial (Fattorini et al., 2015). It is often used to translate environmental heterogeneity, as we did, and it can be particularly difficult to estimate upon the biological model. For ants, we chose to use vegetation parameters, and more specifically cover, density or diversity, as these have been shown to contribute to ant diversity and turnover (Greenslade & Greenslade, 1977; Pacheco & Vasconcelos, 2012; Torres & Snelling, 1997). Acquiring homogeneous vegetation data on a large scale therefore presents a considerable challenge, that remote sensing can help to resolve by making it possible to process a large quantity of images remotely (Hsu et al., 2008; Lazuardi et al., 2021). Nevertheless, the remote sensing data used to process vegetation cover and density showed some limitations. The efficiency of the method upon the size of the island could influence the relationship between habitat diversity and proportion with ant species richness. We suggest that the effects of island size on habitat classification, and the parameters derived from it, should be further explored, as this method offers interesting data acquisition possibilities over a large number of entities in a limited time. As we increase reliability of this estimation, it would be interesting to assess the proportions of direct and indirect effects of habitat on species richness and eventually turnover using structural equation models (Matthews et al., 2019).

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