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Soil unsealing in Mediterranean schoolyards: what factors drive ant communities?

Louise Eydoux[1], Pierre Jay Robert[1], Bernard Kaufmann[2], Mickael Hedde[3], Alan Vergnes[1]

1. CEFE, Univ Paul-Valéry Montpellier 3, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
2. Université Claude Bernard Lyon 1, LEHNA UMR 5023, CNRS, ENTPE, F-69622, Villeurbanne, France
3. Eco&Sols, Univ Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France

Corresponding author: louise.eydoux@univ-montp3.fr – UPVM3, Route de Mende 34199 Montpellier Cedex 5

Abstract

Soil unsealing, the process of removing the impermeable top layer of soil, is increasingly advocated by urban planning policies. The role of unsealed areas in biodiversity conservation, particularly soil biodiversity, remains strongly understudied and especially in understanding the recolonization dynamics of soil biodiversity in these new habitats. Besides, the various types of soil cover resulting from soil unsealing could potentially influence the recolonization kinetics.

This study focused on 79 unsealed plots located in 14 schoolyards along the French Mediterranean coast, investigating ant communities through the placement of 485 baits on unsealed plots. Two variables were considered: the duration since soil unsealing (1 or 2 years) and the type of soil cover (wood chips, plantations mulched with wood chips or lawns).

Remarkably, these unsealed areas act as habitats for ants from their very first years of creation: a rich number of ant species (21 species; a fifth of the regional pool and 10% of the metropolitan French species) has been observed. Additionally, notable changes in ant communities were evident within a single year: plots unsealed for 2 years exhibited significantly higher indices of ant abundance and species richness compared to those unsealed for 1 year. However, the construction of these spaces influences the present communities, with wood chip-covered areas significantly less rich and abundant in ants compared to other ground cover types.

These findings represent a promising starting point and offer insights into the potential of such projects for soil biodiversity conservation.

Keywords: *Formicidae, soil biodiversity conservation, urban ecology, urban soils*

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1. Introduction

Urban areas are expanding at an unprecedented rate, with projections indicating that they will cover more than 7% of the world's land surface by 2050 (UNFPA 2011). This change in land use has led to an increase in soil sealing, i.e. the elimination of biophysical exchanges between subterranean and superficial soil layers through the addition of impermeable materials such as concrete or asphalt (Bardgett 2016). The proportion of sealed surface varies across cities, but it frequently reaches more than 50% (Fuller and Gaston 2009; Prokop, Jobstmann and Schönbauer 2011). The detrimental effects of this process on ecosystem functioning include disruptions in the water cycle, degradation, fragmentation and pollution of habitats for the living organisms (Scalenghe and Marsan 2009; Haase 2009). Soil sealing is indeed considered one of the greatest threats to soil functioning (EC 2012; Tobias et al. 2018). These alterations subsequently have both an impact on human populations by affecting health and agriculture, but also on biodiversity (Béchet et al. 2017; Braaker et al. 2014; Concepción et al. 2016; Pickens et al. 2017; Vergnes et al. 2017).

In this context, soil unsealing, which entails the replacement of impermeable surfaces with permeable alternatives such as draining synthetic materials or open ground, appears as a necessity. This approach is encouraged by the US Environmental Protection Agency (US EPA 2014) or the EU soil monitoring law proposal (European Commission 2023), illustrating the growing support for restoring soil functionality. Notably, many European cities (Barcelona, Brussels, Paris, Rotterdam, …) have launched projects targeting school grounds (Baró et al. 2022). Indeed, predominantly asphalted school ground represents substantial surfaces which can potentially be unsealed and are pivotal in environmental education issues (OASIS Schoolyards 2023). The focus on soil unsealing is primarily driven by anthropocentric concerns, such as the mitigation of flooding (Gomez-Baggethun et al. 2013; Haase et al. 2014; Kareiva et al. 2007; Morel et al. 2015). In addition, soil unsealing provides a unique opportunity to study primary succession, the establishment of new ecosystems on barren substrates such as volcanic islands or mining sites (Odum 1969).

Urban landscapes have long been perceived as an unfavorable environment for biodiversity (Aronson et al. 2016) despite the presence of vegetated habitats, often referred as green spaces. This type of habitats is characterized by its heterogeneity resulting from various historical and present human activities (O'Riordan 2022; Vergnes et al. 2017) affecting all compartments of ecosystems and especially soils (Pickett et al. 2011; Pouyat et al. 2010). While relics of pseudo-natural or agricultural soils are present in cities, a large proportion of unsealed urban soils are constructed soils, also known as technosols, and are therefore potential novel habitats for a large number of organisms (Aronson et al. 2016; Dijon et al. 2023; Morel et al. 2015). However, this diversity of greenspaces fosters highly variable levels of species diversity and abundance, influenced by both local (soil properties) and landscape factors (configuration and spatial composition) (Guilland et al. 2020). Despite the increased understanding of urban soil biodiversity, studies specifically examining soil ecology remain limited (Guilland et al. 2020). A dearth of scientific knowledge persists regarding colonization, community trajectories over time, and biodiversity maintenance in urban soils (Hedde et al. 2018; Pruvost et al. 2020).

Ants (Hymenoptera Formicidae), as ubiquitous, diverse, and particularly connected to terrestrial ecosystems' properties, are ideal models to address these research gaps (Alonso and Agosti 2000; Andersen 2021). As Andersen (2021) points out, the close interrelation of ants with their ecosystems makes them effective bioindicator species. Known as ecosystem engineers, i.e. capable of modifying the availability of resources to other species, by causing physical state changes of their own biotope (Jones et al. 1994), ants significantly impact their biotic and abiotic environment through bioturbation and their role as predators or recyclers of organic matter (Folgarait 1998; Kaufmann 2019; Schultheiss et al. 2022). They are also directly involved in the water cycle through tunneling activities (galleries and nests), which allow water to infiltrate the soil (Bardgett et al. 2001). Ants predominantly colonize an area by foundation after nuptial flight, or by budding, particularly for invasive ones (King & Tschinkel 2016). Some species, driven by foraging needs, can traverse fairly long distances, contributing to the ecosystem even before establishing in the novel habitat (Blatrix et al. 2013). They may also show strong evidence of habitat selection. For example, King and Tschinkel (2016) demonstrates that exotic species select disturbed patches more often than native species.

Past studies on ants and urban soils have primarily focused on urban green spaces like parks, private gardens, or cemeteries (Clarke et al. 2008; Pacheco and Vasconcelos 2007; Trigos-Peral et al.

2020; Yamaguchi 2004). However, to the best of our knowledge, there is a lack of data on soil biodiversity in unsealed areas, particularly in unsealed schoolyards. Consequently, there is a pressing need to enhance our scientific understanding of the initial stages of colonization in order to gain deeper insights into these novel environments. This knowledge is essential for informing public policy decisions in addressing the critical challenges associated with the unsealing of urban spaces.

This study aims to elucidate factors driving ant communities in recently unsealed soils within schoolyards located in the European Mediterranean biogeographical region (Roekaerts 2002), which is a hotspot for insects and particularly for ants (Blatrix et al. 2013). Two variables are considered in this study: (i) the duration since soil unsealing categorized into two modalities: very early (1 year) or early (2 years) pioneering stage of colonization and (ii) the type of ground cover implemented post-unsealing including lawns, wood chips or plantations mulched with wood chips.

First, we assume that 2 years unsealing foster more diverse and abundant ant populations due to increased colonization and establishment opportunities. Prior studies have revealed that soil biodiversity and especially ants, increases over time in urban sites (Hedde et al. 2018; Majer et al. 1984; Vergnes et al. 2017). Ant communities exhibit ecological successions, showcasing gradual changes linked to variations in vegetation and environmental modifications caused by the ants themselves (Dauber and Wolters 2004). This includes the existence of pioneer species alongside equilibrium species, a phenomenon not extensively documented, particularly in the Mediterranean region.

Secondly, the initial conditions of the constructed area influence the recolonization kinetics (Vergnes et al. 2017). Consequently, we anticipate fluctuations in ant abundance and species richness based on distinct ground cover types. We also expect more homogenous areas with a single component stratum (wood chips) to exhibit lower species richness and abundance compared to heterogeneous areas (plantations mulched with wood chips and lawns).

2. Materials and Methods

2.1 - Study sites

Fourteen schools located along the French Mediterranean coast near Montpellier (Figure 1a-1b; covering a region approximately 60 km by 20 km inland) were selected as sampling sites. The region is characterized by dry summers and mild, wet winters, with sudden and intense rainfall episodes frequently leading to flooding events. Over the past 60 years, rapid demographic growth has led to a threefold increase in the urbanized area along the entire coastline (DREAL Occitanie 2015).

Types of unsealed areas

Each school, influenced by its city affiliation, unique history and location, boasts various layouts for its unsealed spaces. Despite their spatial heterogeneity, all these schools share a common objective: to provide recreation areas for children. Soil cover diversity of unsealed spaces is therefore relatively limited.

A comprehensive typology of unsealed areas within each schoolyard led to the identification of three primary types of soil cover:

- *Wood chips (25 plots):* These areas feature of a layer (approx. 30 cm) of wood chips (Softwoods between 6 and 30mm, complies with the standard NF EN1177), primarily designed for recreational uses, and thus usually centrally located where children spend considerable leisure time. Some may incorporate scattered plantations or pre-existing trees. The thick layer of wood chips absorbs heat and exhibits low humidity levels, with temperatures similar to those of lawns (averaging 19° C).
- *Plantations with wood chips (40 plots):* They are surfaced with wood chips (approx. 10cm) serving as mulch for plantations, comprising two main strata: perennial shrubs and trees. These spaces require regular maintenance, such as drip irrigation resulting in higher soil humidity and cooler soil temperature (averaging 18° C) compared to other habitats. Because of the plantations, these spaces are generally less accessible to children and therefore have less compacted soils.
- *Lawns (14 plots):* These areas are mainly planted with grass, with a scattered density of other plantings (perennials, shrubs or trees) without mulching. They maintain higher soil temperature than areas with wood chips (averaging 20°C) but retain a significant level of soil moisture.

These three types were unevenly represented in the various schoolyards and, within each, scattered across several plots of different sizes and shapes.

Year of the soil unsealing operation

All the schoolyards were unsealed during July and August, the summer holidays, to ensure the absence of children during these operations. Schools included in this study were divided into two groups based on the year of concrete removal operations: summer 2021 or summer 2022. Consequently, 4 schools have been sampled during their first year after unsealing, and 10 during their second year.

2.2 - Ant sampling and identification

Sampling was conducted using an attractive bait method. Ant baiting is a common method for exploring ground-foraging ant communities (Wong and Guénard 2017). It was chosen over alternatives such as pitfall trapping (Bestelmeyer et al. 2000) or direct detection of nests (Seifert 2017) because we worked in schoolyards, where indiscriminate destruction of biodiversity by trapping or digging soil in newly planted greenspaces would not have been accepted by school authorities. To attract a wide spectrum of ant species, baits comprised a protein source (a pellet of tuna rillettes) and a sweet source (a drop of honey), placed on a microscope slide (Figure 1d) (Kaufmann et al. 2014). The objective of bait placement was to measure the spatial and numeric presence of ground-foraging ant species. Ant baiting was therefore carried out on all unsealed plots in all schoolyards of the study (Figure 1c). Baits were placed 3 meters apart, covering the entire plot area. This distance was chosen so that most ground-foraging ant colonies would be able to reach at least one bait. This also means that some large colonies could be attracted to more than one bait, which allowed us to evaluate the spatial dominance of each detected ant species. This spatial dominance is determined by nest densities, number of workers per nest and behavioral patterns of competition (Gotelli 1996; Seifert 2017). Additionally, a 1.5-meter distance from plot borders was maintained to prevent overlap with neighboring plots.

A plot is delimited by changes in soil cover, such as a lawn area surrounded by concrete or adjacent to areas with wood chips. Plot area is the size of the plot expressed in square meters, and varies from 9 to 270 m^2. Specifically, we selected all plots that were part of the soil unsealing operations in schoolyards, characterized by one of three types of ground cover (wood chips, wood chips with plantations, or lawns), and of sufficient size to place a bait at the center of a 3-meter diameter buffer zone to maintain a minimum distance from surrounding plots. Given the diverse spatial layout of each school and the proportional allocation of baits based on plot area, the study generated varying numbers of baits and plots across different types of unsealed areas and years of soil unsealing. Table 1 provides a summary of the plots and bait numbers categorized by area types and the year of soil unsealing. A more detailed summary of each school characteristics is available in Supplementary Material 1. A total of 485 baits were placed flat on the surface, ensuring accessibility even for the smallest ant species.

After one hour, to limit the impact of the study on these recent ecosystems, only a limited number of ants gathered on the microscope slide, along with those within a 20 cm radius, were collected using a mouth aspirator and transferred into 96% ethanol. Concurrently, the number of ants present on each bait was estimated.

Table 1: *Number of plots and baits per types and year of unsealed areas*

Types of soil cover on unsealed areas		Year of unsealing	Number of plots	Number of baits
	Wood chips	2021	10	106
		2022	15	127
	Plantations with wood chips (perennial shrubs and trees)	2021	10	56
		2022	30	106
	Lawns areas	2021	3	20
		2022	11	70

Observations occurred during the Easter holidays (from 24th to 27th April) in 2023 to ensure optimal temperatures for ant activity and avoid interference from children. The observations spanned four days, from 9 am to 5 pm, to ensure relatively consistent temperatures between 17 °C and 22 °C. These temperature ranges align with ideal conditions for ant species found in France (Kaufmann et al. 2014), coinciding with their most active period between April and July.

The identification of ants was conducted at species level using a stereomicroscope and the taxonomic keys of Seifert (1996), Blatrix et al. (2013) and Seifert (2018). Ants of the genus *Tapinoma* which encompasses species challenging to differentiate solely based on morphological characteristics (Seifert 2017) were identified using microsatellite markers following Centanni et al. (2022), as were ants of the genus *Tetramorium* (Cordonnier et al. 2019;). *Lasius cinereus* and *Lasius grandis* are similarly complicated to identify, even using DNA sequences (as in Talavera et al. 2013: mtDNA sequences of the two species were near identical), and were therefore grouped under *Lasius grandis cinereus.*

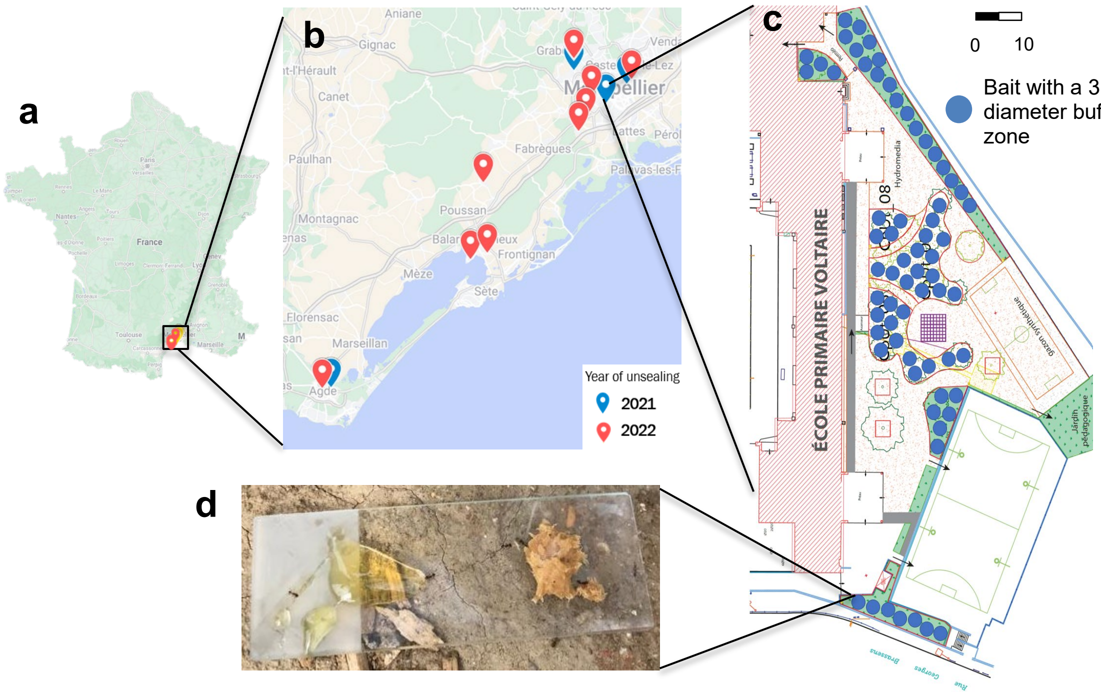

Fig. 1: *Location of the study area in France and of the 14 schools (a and b; Google satellite basemap) according to their year of unsealing. Plan of Voltaire school (c), with the distribution of baits (at the center of 3 m in diameter blue circles) in the different plots (each plot corresponds to one type of soil cover). Photo of a bait (d) with a protein source (tuna rillette, right) and a sugar source (honey, left).*

2.3 - Data analyses

All analyses were conducted with R software (version 3.1.0; R Development Core Team 2014) and R Studio (RStudio Team 2020).

Response of species richness and abundance classes

Generalized Linear Mixed Models (GLMMs) were employed to evaluate the differences in species richness and abundance of ants across various types of unsealed areas and time since unsealing.

These models accounted for the double nested structure of the data, considering baits placed within plots, which in turn were situated within schools (Bolker et al. 2008; Zuur et al. 2009).

Because baits provided a snapshot of ground-foraging ants in a specific area at a given moment, two indices were employed as response variable to characterize the observed ant communities: species richness, defined in the study context as the number of ground-foraging ant species attracted to the bait, and ant abundance as the number of ants counted. As counts made in the field cannot be accurate, to limit this bias, we have divided ant abundances in 6 classes adapted from Andersen (1997) and structured to ensure a balanced distribution across classes: 0 = 0 ants; 1 = 1 ant; 2 = 2-5 ants; 3 = 6-10 ants; 4 = 11-20 ants; 5 = 21-50 ants.

In GLMMs models, *School* and *Plot* variables to which the baits belonged were counted as random effect. Initially, a first model (Model 1) was constructed with fixed effects including the *Soil Cover* variable, corresponding to the type of unsealed area, and the *Year of unsealing* variable, indicating the time since unsealing, and computed separately for species richness and abundance as response variables.

Model 1: ~ Year of unsealing + Soil Cover + (1/School/Plot)

Subsequently, a second model (Model 2) was developed, adding the *Plot Area* variable (the size of the plot expressed in square meters) as a fixed effect to the existing variables.

Model 2: ~ Year of unsealing + Soil Cover + Plot Area + (1/School/Plot)

The "glmer" function from the 'lme4' package is utilized for model generation, while "relevel" is employed to conduct pairwise tests on the effects of the variable's modalities.

Autocorrelation between baits within plots was tested using Moran’s I test ("Moran.I" function from 'ape' package) and was found to be non-significant for both response variables.

Response of Communities – Multivariate analyses

To gain a comprehensive understanding of how these variables influenced the ant communities within schools, a partial Canonical Correspondence Analysis (CCA) was conducted (Cushman & McGarigal 2002; Schweiger et al. 2005) with the 'cca' function from the 'vegan' package (Oksanen et al. 2019). CCA is well-suited for analyzing contingency tables containing numerous null occurrences (Legendre and Gallagher 2001). The variation partitioning technique was utilized to explain the total variation in community composition based on environmental variables (Legendre 2008). This approach involved testing "marginal effects" that describe the global variation explained by a set of variables, and "pure effects" indicating variation explained after removing the confounding effect of other variables (Schweiger et al. 2005). The significance of effects was tested using a pseudo-ANOVA with a Monte Carlo permutation test (1000 permutations). The analyses were performed on occurrence data at the plot scale by adding up the occurrences found for each bait (Gotelli et al. 2011), and using as explanatory variable the type of soil cover of the unsealed area (Soil Cover), the year of the unsealing operations (Year of unsealing), the size of the plot (Plot area) and the school in which the baits were placed (School).

3. Results

3.1 – Description of ant communities

A total of 21 species corresponding to 12 genera were recorded. Species richness per bait exhibited a range between 0 and 3.

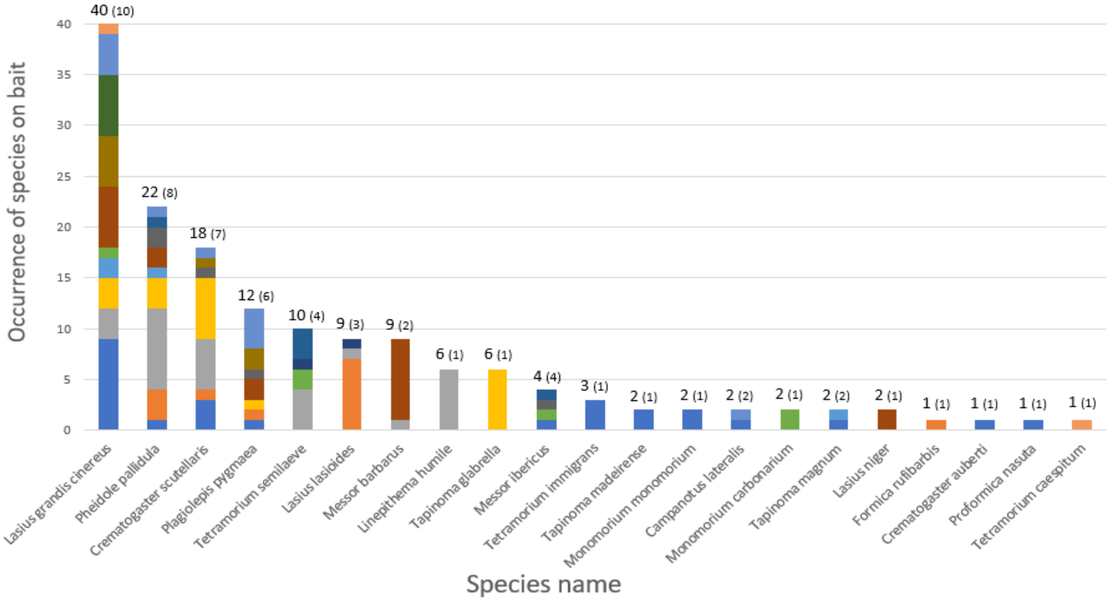

Fig. 2*: Total occurrences of ant species on bait and in brackets the number of schoolyards in which they were observed, also represented by the different colors on the bars.*

The three species most commonly found through the different schoolyards are *Lasius grandis cinereus* (25.9% occurrence rate; i.e., the number of times this species was observed out of the total number of times species were observed on all the baits) present in 10 sites, *Pheidole pallidula* (14.3%) in 8 sites, and *Crematogaster scutellaris* (11.7%) in 7 sites (Figure 2). An example of the distribution of observed ant species using baits placed in a schoolyard is given in Supplementary Material 2.

3.2 – Effects of soil cover and unsealing time

Response of species richness

Model 1, testing as fixed effects the soil cover type and the duration since unsealing, showed significant effects for both (respectively $p < 0.01$ and $p < 0.05$). Regarding the soil cover type, significantly lower species richness was observed in wood chip areas (mean = 0.193) compared to the other two types of soil cover. Conversely, plantations with wood chips (mean = 0.407) and lawns (mean = 0.364) exhibited similar levels of species richness (Figure 3a). For the duration since unsealing, areas unsealed one year prior (in 2022) displayed significantly lower species richness (mean = 0.248) than those unsealed two years prior, in 2021 (mean = 0.379) (Figure 3b). Richness means were calculated as the mean number of species observed at each bait of a plot. Baits that failed to attract ants were counted as having 0 species.

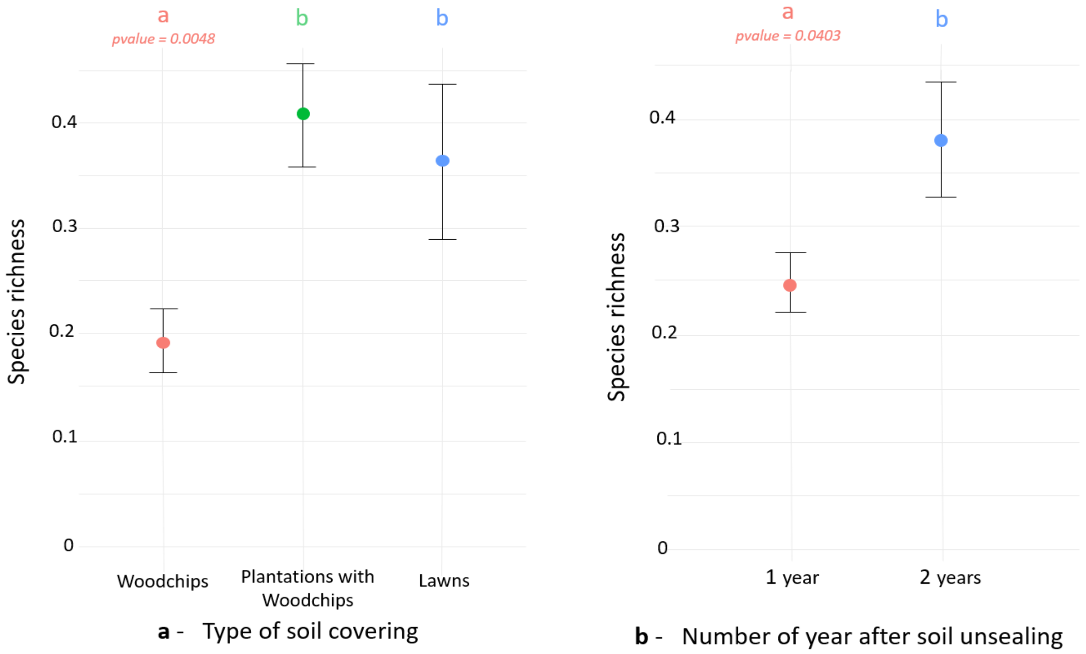

Fig. 3: *Ant species richness observed on baits depending on the type of soil cover (a) and the time of soil unsealing (b). The color dot represents the average of observations with the corresponding error bar. Letters represent any significant differences between modalities of the variables with the associated p-value, highlighted by the GLMM.*

Model 2, incorporating *Plot Area* as an additional fixed effect did not enhance the model's fit compared to the initial model. Following the principle of parsimony, the first model was chosen. Comprehensive outputs of both models are accessible in the Supplementary Material 3.

Response of abundances classes

To evaluate abundance classes, Model 1 employed a quasi-Poisson transformation to address overdispersion (Bolker et al. 2008). Both soil cover type and duration since unsealing showed significant effects (respectively $p < 0.05$ and $p < 0.001$). Areas featuring wood chips exhibited significantly lower ant abundance level (mean = 0.373) compared to those under plantations with wood chips (mean = 0.957) and lawns (mean = 0.870) (Figure 4a). Areas unsealed one year prior showed significantly lower ant abundance (mean = 0.508) in comparison to those unsealed two years earlier (mean = 0.917) (Figure 4b). Subsequent inclusion of *Plot Area* did not enhance the model's explanatory capacity (Supplementary Material 3).

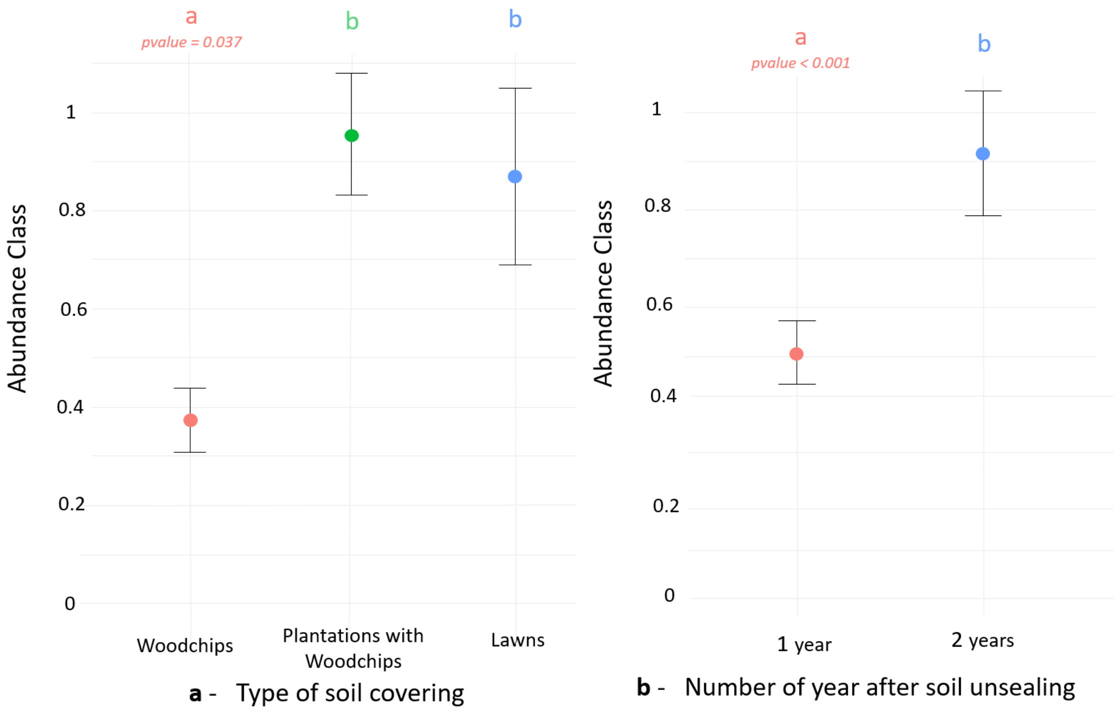

Fig. 4: *Abundance classes of ants observed on baits depending on the type of soil cover (a) and the time of soil unsealing (b) using Generalized linear mixed models (GLMM). The color dot represents the average of observations with the corresponding error bar. Letters represent any significant differences between modalities of the variables with the associated p-value.*

3.3 – Response of ant communities

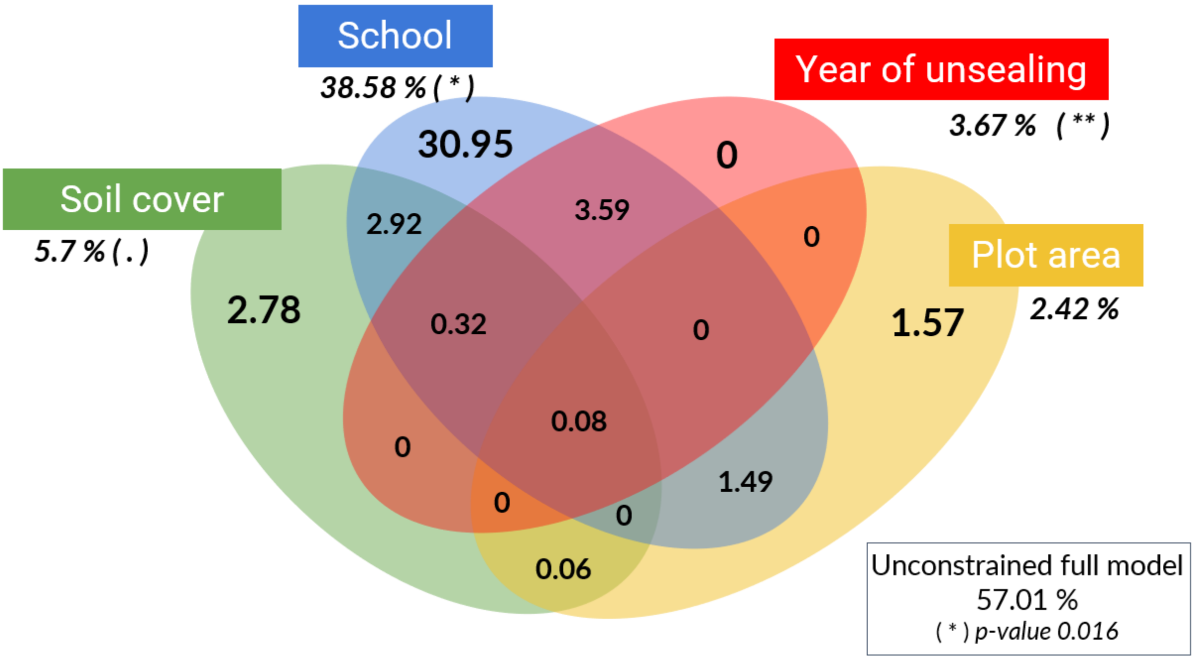

Fig. 5: *Venn diagrams representing the hierarchical variance partitioning (%) of the influence of soil cover, year of unsealing, plot area, and school on ant community composition. Values outside the ellipses represent marginal effects, while values inside the ellipses represent pure effects. The level of significance is indicated in parentheses as follows: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

The full model (Figure 5) integrating soil cover, school, year of unsealing, plot area elucidated 42.99% of the total variance and significantly explained ant community composition (p-value = 0.016). The effects of the different variables taken separately were also significant, except for the variable "plot area". Its marginal effect accounted for only 2.42% of variance, while for "year of unsealing" it constituted 3.67%, for "soil cover" 5.7% and "school" 38.58% of the total variability. Regarding pure effects (without interactions with other variables), plot area explained 1.57% of the variance, soil cover 2.78% and school 30.95%. The pure effect of the year of unsealing was null, but there was a strong interaction with the school subset (3.74%).

Most other interactions showed relatively weaker impacts, emphasizing the relative independence of each variable.

Canonical correspondence analysis of ant communities

The ordination diagrams gave insight into the variables' effects on communities through pCCA visualization (Figure 6). Concerning soil cover type, the first and second axes (3.92% and 1.78 % of the model variance, respectively) segregated the variable into three distinct parts, distributing species according to soil cover types. Some species appeared associated with specific covers, such as *Formica rufibarbis*, *Crematogaster auberti* or *Tapinoma magnum* with wood chip areas, or *Lasius niger* and *Monomorium carbonarium* with lawns. Conversely, species like *Tetramorium semilaeve* or *Pheidole pallidula* appeared in multiple environments.

Regarding the variable *duration since unsealing*, the CCA1 axis separated species according to the two duration modalities. Species proximal to the '1-year' modality seemed specific to newly unsealed schools, while those nearer to the '2-years' modality, like *Linepithema humile* and *Tapinoma glabrella* were exclusive to schools unsealed over a year ago. Species positioned at the axis center, such as *Plagiolepis pygmaea* or *Tetramorium semilaeve*, were not distinctive in relation to this variable.

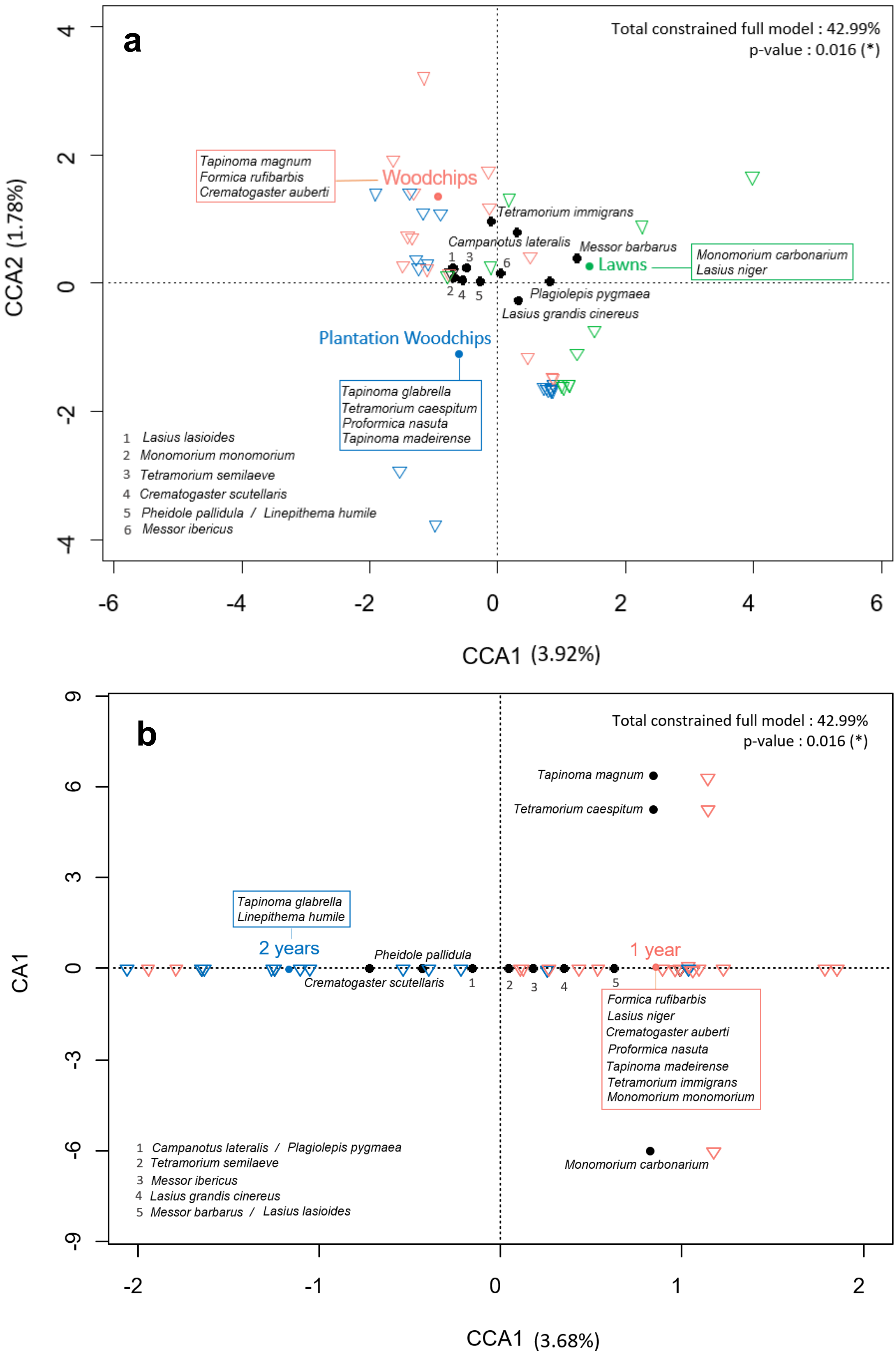

Fig. 6: *Triplots of (a) the marginal effects of the variable Soil cover and (b) Year of unsealing from an analysis of canonical correspondences on the occurrences of species observed on baits. Triangles represent study sites, with different colors according to the variable to which they belong.*

4. Discussion

4.1 - A surprisingly high activity for recently unsealed schoolyards

Given the scarcity of scientific studies on macrofauna colonization in newly unsealed spaces (Hedde et al. 2018; Pruvost et al. 2020; Tobias et al. 2018), it was challenging to anticipate the activity of ground-foraging ants these areas might shelter. Unsealed spaces are often promoted as a chance for pioneer ecosystems to foster (US EPA 2014). Ants are also known for the high dispersal capabilities of most species: actively through independent nest foundations following nuptial flights, or passively by budding, where a queen establishes a new colony from the existing one, as it is the case in urban environments by being transported with topsoil and plantations of ornamental plants or by simply walking from an existing greenspace (Helms 2018). The urban environment, with multigenerational movements hindered by the lack of habitat for queens to colonize, coupled with the specific characteristics of school environments—restricted spaces intensively used by children—may have implied limited ant colonization (Sanford et al. 2008; Yamaguchi 2004). However, a total of 21 ant species were discovered across all school sites, representing more than 10 % of the metropolitan French species and a fifth of the Montpellier district species pool (Hérault; Blatrix et al. 2013).

The three most dominant species (*Lasius grandis cinereus; Pheidole pallidula; Crematogaster scutellaris*) present in 13 of the 14 schoolyards in the study, come as no surprise — the first two are ubiquitous, generalist species thriving in anthropized environments, particularly in southern France and *Crematogaster scutellaris* is an arboreal specialist ant that nest in wood (Blatrix et al. 2013). These species are characterized by populous colonies (several thousand workers) and an omnivorous diet, adapting to varied environments (Carpintero et al. 2003). Furthermore, they are known for undertaking extensive nuptial flights, making them relatively unaffected by fragmentation (Blatrix et al. 2013). Materials commonly found in urban settings such as rubble, bits of asphalt or wood possess the ideal conditions for the development of their brood: retaining moisture and absorbing heat, an environment especially favourable for potential invasive species (Blatrix et al. 2013; Dijon et al. 2023; Yamaguchi 2004). However, in our case, we could have expected to observe more: only three species considered invasive (*Linepithema humile, Monomorium carbonarium,* and *Tapinoma magnum*) were detected at respectively one and two sites.

The presence of *Tetramorium caespitum* is surprising as it has been shown that this species is absent from Mediterranean urban areas (Cordonnier et al. 2019). As for *Tapinoma glabrella*, recently described by Seifert et al. (submitted), it is a new species for France that closely resembles *Tapinoma erraticum,* and whose known distribution spans from Italy to Kyrgizstan. Species identity was confirmed by Seifert as well as by molecular methods (microsatellite markers as in Centanni et al. 2022). *Tapinoma glabrella* could be native of France and still undetected, but the closest known site in Italy is less than 650 km away. Alternatively, it may have been imported from Italy or the Balkans with ornamental plantations (Seifert et al. submitted).

4.2 - A rapid colonization in the early stages

Even in the early stages of newly unsealed soil habitats, the GLMM analysis reveals a significant positive correlation between the duration since unsealing and both the number of ground-foraging ant species attracted to the bait, and their abundance. This finding aligns with our expectations: with longer periods post-unsealing, populations had more time to colonize and establish within these new environments, as observed in constructed soils (Hedde et al. 2018; Vergnes et al. 2017) in urban context or in restored quarries (Majer et al. 1984). As suggested by concepts such as the Island Biogeography Theory (MacArthur and Wilson 1963), this progressive enrichment of plots (considered as continental islands amidst a matrix of impermeable soil) may exhibit a linear trend initially. Eventually, biodiversity would reach an equilibrium—linked to its maximum capacity positively tied to the relative size of the plot, and consequently its available food resources and potential habitats (Gibb and Hochuli 2002). Depending on the species, ant colonies can take several years before being deemed mature i.e., capable of producing reproductive. Workers have lifespans of a few months to 2 years while queens can live between 5 and 30 years (Blatrix et al. 2013). Thus, observed ants might originate from relatively young nests. The equilibrium point usually takes a long time to reach, with urban environments introducing heterogeneity due to various pressures: ant population can sometimes take more than 20 years to establish, particularly in disturbed areas (Kaufmann 2019; Majer et al. 1984; Pacheco and Vasconcelos 2007). Unsealed environments are likely to progressively increase in biodiversity and abundance non-linearly, impacted by school-related human activities (children's activities on the plot, land management, etc.), with a possible succession from pioneer species to more dominant species (Dauber and Wolters 2004; Hedde et al. 2018; Kaufmann 2019). Long-term studies would track this trajectory and comprehend these distinctive assembling communities in these recently altered environments.

Using Canonical Correspondence Analysis (CCA), a closer look at the composition of communities reveals that some species were found exclusively in plots unsealed for 1 year (e.g. *Crematogaster auberti, Lasius niger, Formica rufibarbis, Tapinoma immigrans*), while others are observed more in plots unsealed for 2 years (*Linepithema humile, Tapinoma glabrella, Crematogaster scutellaris*). Certainly, the latter species are sensitive to the habitat's developmental stage. For instance, *Crematogaster scutellaris* shows a preference for habitats with mature tree cover rather than newly planted areas, such as those found in schoolyards unsealed just a year ago, in 2022. The longer the habitat has been established, the more opportunity vegetation has had to mature, grow, and generate organic matter (Majer et al. 1984). The species distribution across the plots likely involves not just the duration of unsealing (1 or 2 years) but also the school's geographic situation and potential colonization opportunities nearby (Dauber and Wolters 2004). The Venn diagram (Figure 5) emphasizes both the significant impact of unsealing duration on ant community distribution and the relative importance of school’s characteristics, particularly their geographic uniqueness within the urban landscape. A forthcoming study on landscape ecology, considering existing ant communities in established plots that could serve as colonization reservoirs for newly unsealed plots, is planned to integrate this dynamic.

4.3 - Significant impact of ground cover on ant communities

As depicted by the variation partitioning, the type of ground cover, classified into three modalities (woodchips, plantations with woodchips, and lawns), has a slightly significant effect on the distribution of ant communities, albeit significantly smaller (5.7%) than the effect of schools themselves (38.58%).

GLMM analysis reveals that woodchip cover harbors significantly lower indices of ground-foraging ants compared to the other two types of ground cover. This aligns with our initial hypothesis and the literature: Uno et al. (2010) highlights significant differences in ant communities according to the urban habitat type, varying in ground cover factors (number and size of trees, leaf litter, amount of concrete and buildings). It is known that temperature and humidity are key factors for the presence of ants (Kaufmann 2019; Seifert 2017). These parameters are directly linked to the type of soil cover. In habitats with a litter layer, colonies take advantage of moisture retained under wood chips and warmth absorbed by this mulch (Majer et al. 1984; Seifert 2017), as it is probably the case in our study for the category of habitat “Plantations with woodchips”. But in the case of a thick layer, here for the habitat with 30 cm of woodchips, Seifert et al. (2017) highlights a significant decline in ant communities due to a strong decrease of soil temperature as the sun radiation is unable to heat up the soil under the chips. Additionally, it is acknowledged that ant community structure varies depending on available food resources, themselves directly linked to temperature and humidity parameters (Arnan et al. 2007; Feldhaar 2014). Thus, our results can be explained by the trophic relationships ants have with plants (e.g. aphid honeydew and plant nectar consumption, granivory, predation on phytophagous insects), which are absent in this habitat (Blatrix et al. 2013; Cerda et al. 2013; Uno et al. 2010).

The three most prevalent species of woodchips cover (*Crematogaster auberti, Formica rufibarbis, Tapinoma magnum)* exhibit particular diets (especially *T. magnum*, which relies on aphids, and *F. rufibarbis* on preys), yet they demonstrate extensive foraging abilities. Their presence is also characteristic of open environments with nests directly in the soil or beneath stones (Blatrix et al. 2013). Conversely, the other two habitats do not seem to significantly affect the species richness and abundance of species.

4.4 - A suitable method despite its biases

Bait trapping is well-adapted for our study sites: it is non-destructive, minimally impacting these young ant communities. As mentioned in Materials and Method, alternative methods could not be justified in a schoolyard environment. The dual food bait offering—tuna (protein source) and honey (sweet source)—diversifies ant attraction based on their preferences (Andersen and Brault 2010; Wong and Guénard 2017): for instance, *Plagiolepis pygmaea* and certain *Lasius* are known for their preference for sugar. This trapping method primarily attracts species that swiftly detect food sources (*Lasius*, *Tapinoma*), potentially excluding other species, resulting in underestimated species richness (Bestelmeyer et al. 2000; Gotelli et al. 2011). Other species may not be sampled by baits, such as exclusively hunting species (genera *Ponera* and *Hypoponera*), or strictly underground species (e.g. *Lasius myops, Solenopsis sp.*). This bias is acknowledged and does not detract from the study, as the objective was to observe the spatial and numerical presence of ground-foraging ant species in relation to the type of ground cover and the year of unsealing.

Kaufmann et al. (2014) recommend a minimum of 70 baits for robust information. Yet, their study was conducted in expansive semi-natural settings, unlike our study with restricted spaces. In the case of unsealed schools, the areas that could be sampled were already completely covered, so it would not have been possible to add baits. Ant baiting was indeed carried out on all unsealed plots in all schoolyards. To comprehensively assess ant communities across unsealed plots, baits were placed every 3 meters to cover the maximum area, ensuring that most ground-foraging ant colonies could reach at least one bait. While this distance suits smaller species (*Tetramorium, Plagiolepis*, etc.), larger species like *Camponotus* or species that form supercolonies as is the case with *Tapinoma*, may be overrepresented (Gotelli et al. 2011; Wong and Guénard 2017). Nevertheless, it is not a concern as it allowed us to evaluate the spatial presence of each detected ant species. By sampling in this manner, the study does not aim to provide a complete inventory of all species present in the unsealed areas of schoolyards. Instead, it provides a new insight into the activity of ground-foraging ant communities and how certain factors impact them.

5. Conclusion

It is promising to note that these unsealed areas can, in just two years, host rich ant communities. While the importation of topsoil and plants, as inoculum, likely plays a fundamental role in these communities, future studies integrating the landscape dimension will provide further insights into colonization dynamics. Long-term observations across various taxa will facilitate a comprehensive understanding of these environments, all of which are planned for future research. These initial findings mark a significant step towards unravelling the previously unexplored ecosystems of unsealed schoolyards environments.

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Statements and Declarations

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Competing Interests

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

Author Contributions

All authors, Pierre Jay Robert, Bernard Kaufmann, Mickael Hedde, Alan Vergnes and Louise Eydoux, contributed to the study conception and design. Material preparation, data collection and formal analysis were performed by Louise Eydoux. The first draft of the manuscript was written by Louise Eydoux and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The authors declare that the data supporting the findings of this study are available within the paper and its Supplementary Materials. Should any raw data files be needed in another format they are available from the corresponding author upon reasonable request