Short communication

Relative efficiency of pitfall vs. bait trapping for capturing taxonomic and functional diversities of ant assemblages in temperate heathlands

Axel Hacala[1,2,*], Clément Gouraud[1], Wouter Dekoninck[3] & Julien Pétillon[1]

[1] UMR CNRS 6553 Ecobio, Université de Rennes, 263 Avenue du Gal Leclerc, CS 74205, 35042 Rennes cedex, France

[2] EA Géoarchitecture: Territoires, Urbanisation, Biodiversité, Environnement, Université de Bretagne Occidentale, CS 93837, 29238 Brest cedex 3, France

[3] Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussels, Belgium

[*]: Corresponding author; Tel: +336 16 50 76 52, Email: axel.hacala@gmail.com

Simple Summary: Ant's community, due to their ecological diversity, are a challenge to properly sample. This issue was tackled by many authors through multiplying sampling techniques. Depending on the habitats sampled, the effectiveness and complementarity of the sampling techniques may vary. Here, in open temperate habitats, the assessment of sampling methods complementarity hadn't be done yet. This study aimed at assessing the effectiveness of the association of two common traps, pitfall traps and bait trap. The comparison was done through species count but also with a functional approach (i.e. acknowledging for ecological characteristics of species to describe an assemblage of species). Pitfall traps assessed more species and a wider set of functional traits than bait traps, every species caught with baits were also caught with pitfall traps. It therefor appear that in our context of open temperate habitats, bait traps are ill advice to use with pitfall traps for it will add costs to the study without information gain and that pitfall should be favored in that context.

Abstract: Whereas bait and pitfall trappings are two of the most commonly used techniques for sampling ant assemblages, they have not been properly compared in temperate open habitats. In this study, taking advantage of a large-scale project of heathland restoration (3 sites along the French Atlantic Coast forming a north-south gradient), we evaluated the relative efficiency of these two methods for assessing both taxonomic and functional diversities of ants while accounting for a north south diversity gradient. Ants were collected and identified to species level, and 6 traits related to morphology, behavior (including diet, dispersal and maximum foraging distance) and social life (colony size and dominance type) were attributed to all 23 species. Both observed and estimated species were significantly higher in pitfalls compared to spatially pair-matched bait traps. Functional diversity followed the same pattern, with consistent results for both community weighted mean (CWM) and Rao's quadratic entropy. Taxonomic and functional diversities from pitfall assemblages increased from North to South locations, following a frequently reported pattern at larger spatial scales. Bait traps can hardly be considered a complementary method to pitfall traps for sampling ants in open temperate habitats, as it appears basically redundant with pitfall traps at least on maritime cliff-tops of the East-Atlantic coast.

Key-words: sampling method, estimated richness, functional diversity, maritime cliffs, Western France.

1. Introduction

Because of their high abundance and diversity except in Polar Regions, ants play a key-role in ecosystem functioning in many terrestrial habitats, from open ecosystems like deserts to forests, and from the floor to the canopy (Lach *et al.*, 2010). Ants are known to be good bioindicators (Ellison, 2012) with a high ecological importance (Lach *et al.*, 2010). As many other groups, ants are globally more diverse in the tropics than in temperate areas (Higgins & Lindgren, 2012), and the level of knowledge in sampling methods overall follows this pattern (Romero & Jaffe, 2014). Pitfall trapping is expansively used and recognized as a good way to sample epigaeic arthropods (Ward *et al.*, 2001), including ants (Lopes *et al.*, 2008). It is also criticized not being an exhaustive technique (Lang, 2000), and suffering from several biases like microhabitat complexity or trap diameter reported for decades (e.g. Luff, 1975; Adis, 1979). The limits of pitfall trapping are particularly obvious for ants due to their heterogeneous use of space (Romero & Jaffe, 2014) and pheromone distress signals that can induce artificially high abundance in single traps (Steiner *et al.*, 2005). On the other hand, bait trapping is recognized as the most common method for sampling ants (Agosti *et al.*, 2000), and sometimes compared to pitfall trapping but mostly in tropical habitats (Underwood & Fisher, 2006). Few examples can be found for temperate areas, but they are restricted to forest habitats (Wang *et al.*, 2001; Ellison *et al.*, 2007; Lessard *et al.*, 2009; Véle *et al.*, 2009). In this study, we compared the efficiency of pitfall vs. bait trapping for assessing the taxonomic and functional diversities of ant assemblages in temperate open habitats (maritime heathlands). We used the sampling design provided by a large-scale project where heathland restoration is evaluated. Arthropods were sampled in 3 heathlands along the French Atlantic Coast covering a gradient of restoration time that we did not test here because of its small spatial scale. We especially tested the hypothesis that, in an open habitat, pitfall trapping performs well (see e.g. Privet *et al.*, 2020) and is consequently expected to capture ant diversities in similar proportions than bait trapping. Conversely, we expect functional diversity to be inferior with bait trapping as only some species are targeted by baits (Ellison *et al.*, 2007). Lastly, we expect taxonomic, but not functional, diversities to differ among sites, with species richness increasing from North to South (Kaspari *et al.*, 2004) as, even if the gradient is geographically short, our southern location are known to have a warmer microclimate (Bioret *et al.*, 1988).

2. Material and methods

2.1. Study sites

Fieldwork was done in three coastal sites of Brittany, Western France. Sites were coded according to the north-south gradient they form. La Pointe de Pen-Hir (S1), located on the mainland (48° 15′ 03″ N, 4° 37′ 25″ W), was degraded by human trampling which was reduced. La Pointe de l'Enfer (S2) (47°37'18.3"N 3°27'46.9"W) was degraded by frequent vehicle access and human trampling. L'Apothicairerie (S3) (47°21'44.0" N, 3°15'34.9" W) was heavily degraded by infrastructures (car park and hotel) that were removed in 2012 (see Hacala *et al.*, 2020 for a full description, and pictures, of the sampling sites).

2.2. Sampling design

Two 400 m² plots of homogeneous vegetation were designed for each degradation state, and four pitfall traps (80mm in diameters and 100mm deep) were set at each plot. Traps were half-filled of salted solution (250 g.L^{-1}) with a drop of odorless soap and settled 10 meters apart in order to avoid interference and local pseudoreplication (Topping & Sunderland, 1992). This resulted in 71 traps (fig. 1) (in one station, the sampling area was too restricted to set 4 traps spaced of 10m apart, so 1 was removed) active between mid-March to mid-June 2017, and emptied every two weeks. One bait trap was associated to every pitfall trap. The sampling device (fig. 2) consisted in a cardboard square (4cm x 4cm) on which approximately 1cm^3 of tuna rillettes and few drops of honey were deposited. A wooden stick was drove through the cardboard which anchor it to the ground to ease both sampling and detection in the field. Bait traps were set 5 times, two weeks apart between March and June. The traps were set for 2 hours in the middle of the day and by sunny weather only.

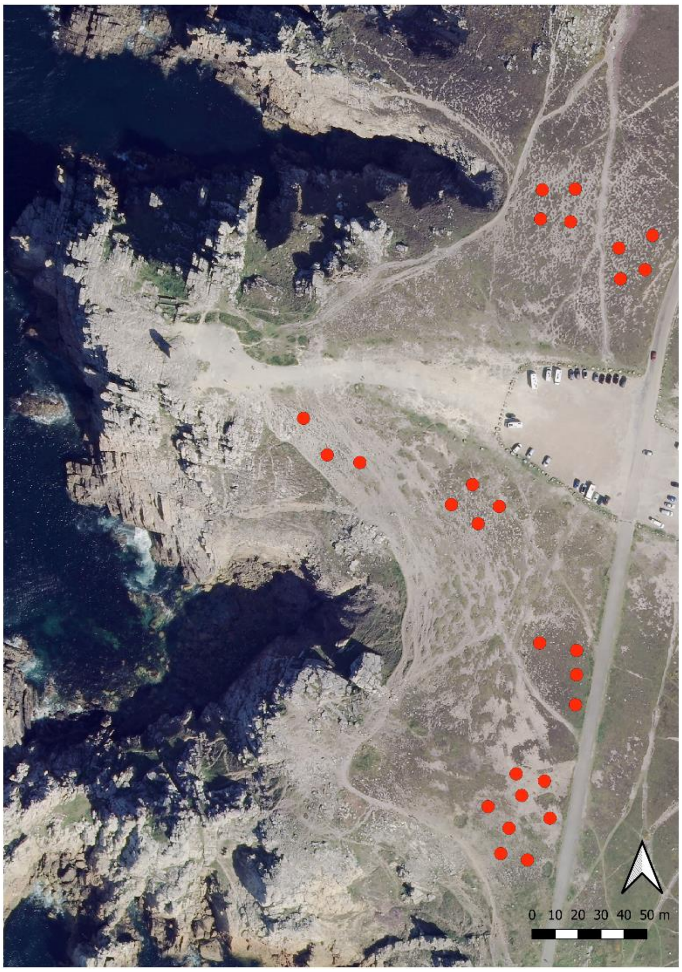

Figure 1. Example of trap placement in space with the map of one of our sites

Figure 2. bait trap

Samples of pitfall and bait traps were sorted, transferred to ethanol 70°, and stored at the University of Rennes 1. Ants were identified to species level using keys of Seifer & Schultz. (2009), Blatrix *et al.* (2013), Seifert (2018, 2020). Data were pooled together by state of degradation and by site.

2.3. Functional traits

Several traits related to morphology, behavior (including diet and dispersal) and social life (colony size and dominance type) were attributed to all the 23 species (Appendix A), using different bibliographic traits (Appendix B).

2.4. Statistical analysis

Data were transformed to presence/absence data to avoid abundance bias from difference in species activity rate and/or in sensitivity to environment structures (Menke & Vachter, 2018). Species richness was calculated with the vegan package (Oksanen *et al.*, 2007) while functional diversity as well as Rao's quadratic entropy and the CWM (community-level weighted means) where calculated with the FD package (Laliberté *et al.*, 2015). Alpha-diversity (species richness) was also compared between methods using estimated richness based on the methods developed by Chao (1984, 1987) through the "iNEXT" function from iNEXT package (Chaos *et al.*, 2014). This method was selected to account for possible influence of sampling coverage. The test was ran with 40 knots and 200 bootstrap replication. Significant differences were assessed through the absence of overlapping confidence intervals on iNEXT curves (Chao *et al.*, 2014).

The influence of the methods on species Richness, functional diversity and Rao's quadratic entropy were tested through a Poisson GLMM with sites as a fixed factor as ant's diversity is known to increase toward warmer climates (Majer & Beeston, 1996). The type of error (Poisson vs quasi-Poisson) was assessed following O'Hara & Kotze (2010). Functional patterns were compared between the methods with CWM and Rao's quadratic entropy to respectively asses shift in main trait value and trait divergences (Ricotta & Moretti, 2011). Being numerical, the CWM colony size score and the Foraging distance were tested with Wilcoxon test.

In order to asses sites effect and include them as a fixed factor of our model, their effect were tested on taxonomic richness and functional metrics through Kruskal tests with Wilcoxon post hoc tests.

All analyses were carried out using R software (version 3.6.1 2019-07-05).

3. Results

Pitfall trapping and bait trapping resulted in the collection of 4976 individuals and 4419 individuals respectively (Appendix A), altogether representing 23 species, all collected by pitfall traps and 10 by bait traps (Table 1). Yet *Formica pratensis* was sampled by bait traps only in S1 and S2, it was sampled with both method in S3. Overdispersion was detected in the richness data and was corrected by using a quasi-GLM model Observed. Species richness was significantly higher in pitfalls traps ($\chi^2 = 0.74$; $p < 0.0001$) (Fig. 3a).

Tableau 1. Occurrence of ant's species in the three sites (S15; S11; S5) for both bait traps and pitfall traps

species	**S1**		**S2**		**S3**		**All Sites**	
	Bait	Pitfall	Bait	Pitfall	Bait	Pitfall	Bait	pitfall
Aphaenogaster gibbosa (Latreille, 1798)	0	0	0	1	0	0	0	1
Aphaenogaster subterranea (Latreille, 1798)	0	0	0	0	0	1	0	1
Formica cunicularia (Latreille, 1798)	1	1	1	1	1	1	1	1
Formica pratensis (Retzius, 1783)	1	0	1	0	1	1	1	1
Hypoponera eduardi (Forel, 1894)	0	0	0	1	0	1	0	1
Lasius alienus (Foerster, 1850)	1	1	0	1	0	1	1	1
Lasius emarginatus (Olivier, 1792)	0	0	0	1	0	0	0	1
Lasius flavus (Fabricius, 1782)	0	0	0	0	0	1	0	1
Lasius niger (Linnaeus, 1758)	1	1	0	0	1	1	1	1
Lasius platythorax (Seifert, 1991)	0	0	1	1	0	0	1	1
Lasius psammophilus (Seifert, 1991)	1	1	0	0	0	0	1	1
Messor capitatus (Latreille, 1798)	0	0	0	1	0	0	0	1
Myrmecina graminicola (Latreille, 1802)	0	1	0	1	0	1	0	1
Myrmica ruginodis (Nylander, 1846)	0	0	0	0	0	1	0	1
Myrmica sabuleti (Meinert, 1861)	0	1	1	1	1	1	1	1
Myrmica scabrinodis (Nylander, 1846)	0	0	0	1	1	1	1	1
Plagiolepis pallescens (Forel, 1894	0	1	0	0	0	0	0	1
Ponera coarctata (Latreille, 1802)	0	1	0	0	0	0	0	1
Solenopsis fugax (Latreille, 1798)	0	1	0	1	0	1	0	1
Tapinoma erraticum (Latreille, 1798)	1	1	1	1	1	1	1	1
Temnothorax unifasciatus (Latreille, 1798)	0	0	0	0	0	1	0	1
Tetramorium atratulum (Schenck, 1852)	0	0	0	0	0	1	0	1
Tetramorium gr. caespitum- impurum	1	1	1	1	1	1	1	1
Only bait/ shared / only pitfall	1/6/5		1/5/8		0/7/9		0/10/13	

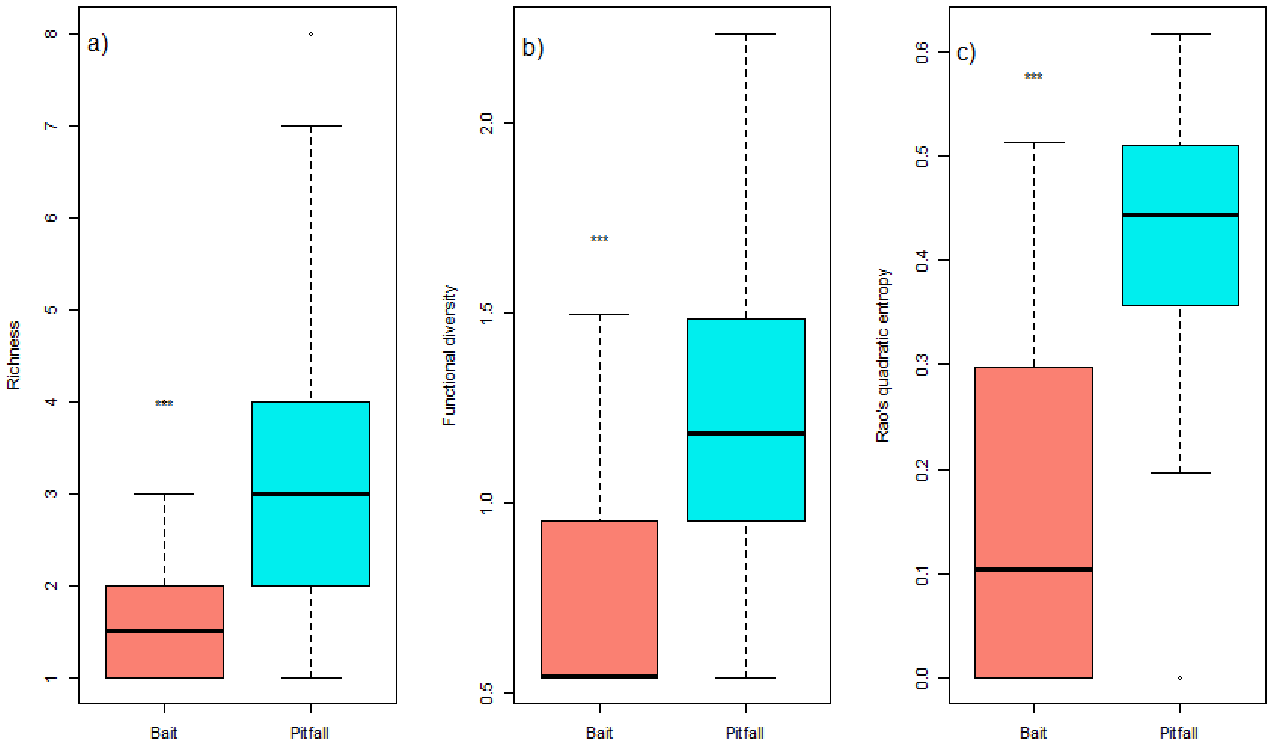

Figure 3. Comparison between bait traps and pitfall traps of a) Species richness; b) Functional diversity and c) Rao's quadratic entropy. Significant differences are indicated *** for p-values < 0.0001

Sampling coverage for both sampling methods reached asymptotes (Fig. 4), and were above 90% coverage, indicating a very good sampling intensity. Estimated species richness was significantly higher in pitfall traps than in bait traps, whether plotted against the number of samples or vs the sampling coverage (Figs 3b and 3c, respectively).

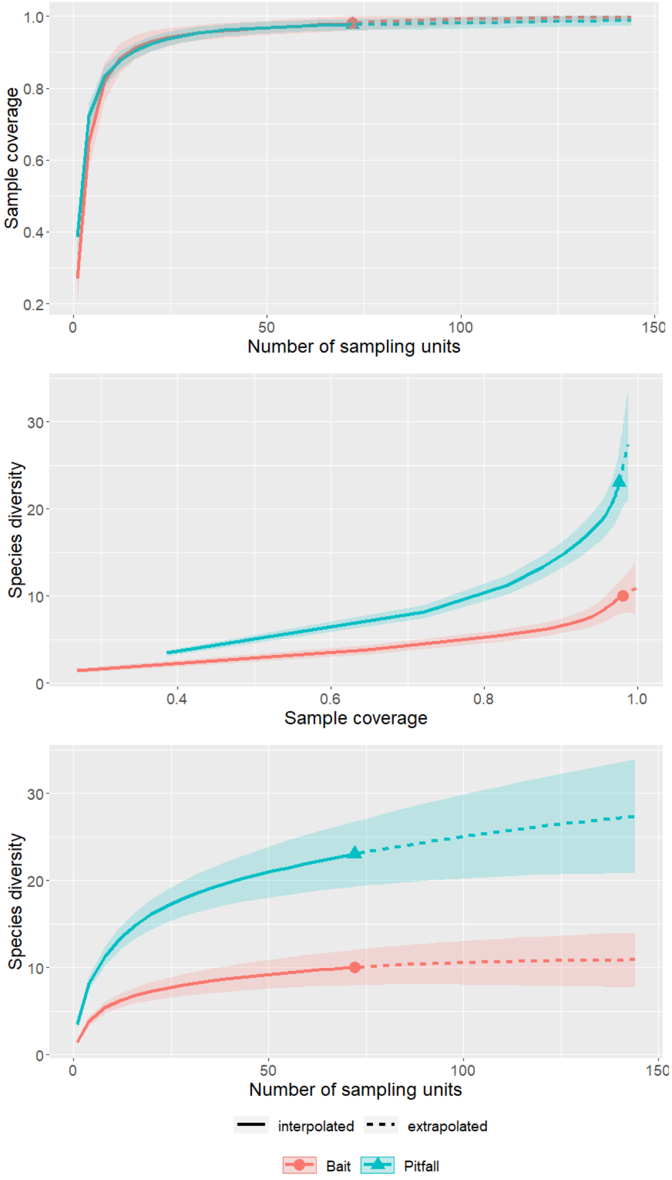

Figure 4. Estimated richness of ant's assemblages between bait traps (pink) and pitfall traps (blue) for each sites and all sites combine. a) Coverage vs number of sampling units; b) Species diversity vs sampling coverage; c) species diversity vs number of sampling units.

The same pattern was observed for functional diversity with higher FD in pitfall traps compared to bait traps ($\chi^2 = 0.49$; $p < 0.0001$) (Fig. 3b). The CWM displayed the same main trait value with same categorical variable (e.g. large dominant omnivorous epigaeic ants with independent colony formation), while no significant differences were observed in colony size score (W = 207, p-value = 0.546). The foraging distance was significantly greater in pitfall traps than in bait traps (W = 2880.5, p-value = 0.002). Rao's quadratic entropy was significantly higher in pitfall ($\chi^2 = 0.89$; $p < 0.0001$) compared to bait traps (Fig. 3c).

Both methods confounded, significant differences following the north-south gradient were observed in both taxonomic and functional metrics (Fig. 5) with higher richness in the south ($\chi^2 = 6.20$; p= 0.045), lesser functional diversity in the north ($\chi^2 = 8.21$; p= 0.01) and higher Rao's quadratic entropy in the south ($\chi^2 = 11.12$; p= 0.004).

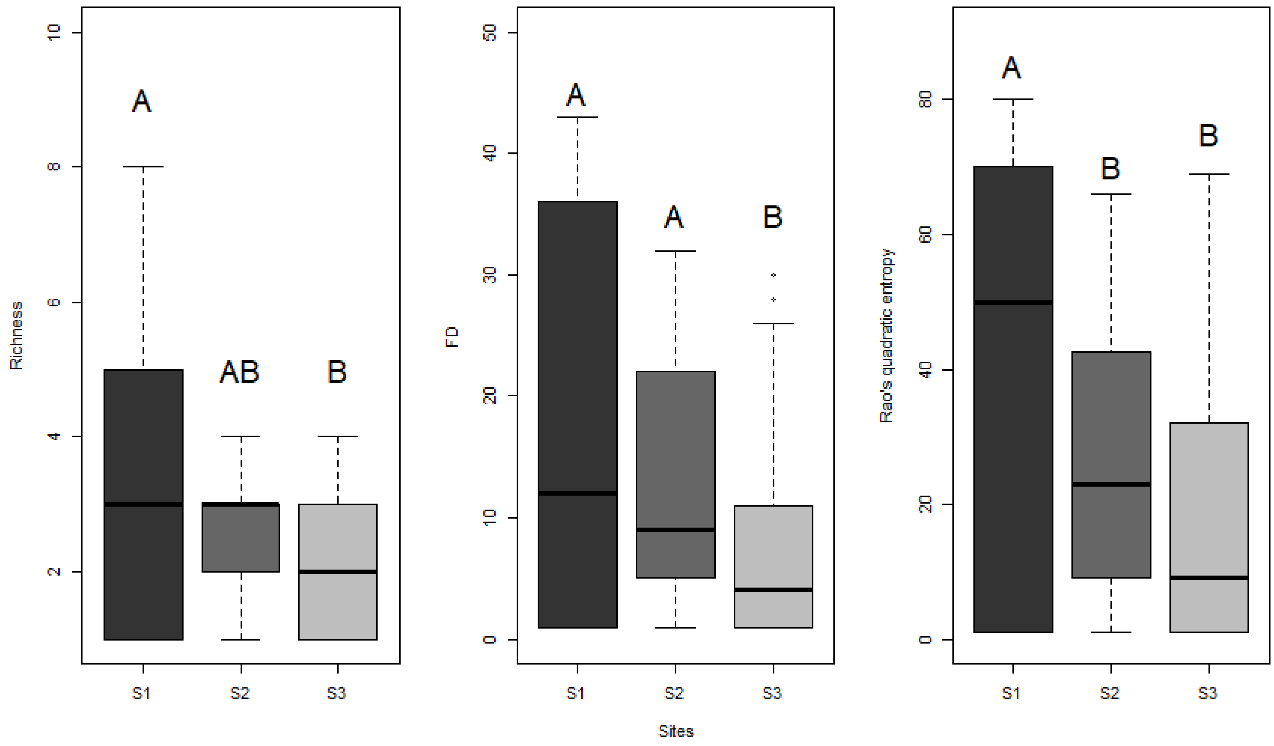

Figure 5. boxplot displaying diversity metrics (Taxonomic richness, functional diversity (FD) and Rao's quadratic entropy) compared between the three sites that form a north-south gradient with S1 at the south and S3 in the north. Significant differences ($p < 0.05$) are represented with groups of letters (*e.g.* A & B).

4. Discussion

Contrary to our first assumption, the observed and estimated species richness was higher in pitfall traps than in bait traps, with bait traps capturing only a fraction of what the pitfall traps do. This differs from what we expected, yet this redundancy of bait traps is concurring with results from other habitats (Lessard *et al.*, 2009; Véle *et al.*, 2009). Several hypotheses can be formulated to explain such a result. One could argue that the sampling effort greatly differed between the two methods, with pitfall traps being active for two months in a row (pitfall) and bait traps for a total of ten hours covering 5 event of sampling with a 2h span (bait). Although the sampling time (2h) of the bait traps could be a reason for the lesser effectiveness of the baits, the sampling coverage of the two methods was high for both methods and previous study with higher sampling effort with baiting showed similar trends (Wang *et al.*, 2001). The sampling time might still had an effect since ants are known to have a high interspecific variability of circadian activity (Tavares *et al.*, 2008). Therefore species being actives at night, early day or late afternoon could have been missed from the bait traps with the protocol used here. Another bias known to the bait traps is exclusive competition (Gotelli, 2010). Some competitive ants could have indeed monopolized the baits and limited the access to competitive ants only, which would explain a high coverage with at the same time missing species from the local pool. The functional analysis showed that the two methods caught mainly dominant ants, and that ant assemblages from bait traps did not expand away from the mean trait. This problem could have been avoided by longer bait trap sessions since less competitive species tend to be active during colder times of the day to avoid inter-specific competition (Agosti *et al.*, 2000). Multiplying the number of observation during the two hour span the trap was active could have lessen the impact of potential exclusion phenomenon (Agosti *et al.*, 2000). Another phenomenon can also help explain this result, i.e. the redundancy of the two methods, species captured by bait traps being considered populous and active (Ellison *et al.*, 2007). These characteristics are factors known to increase the probability of capturing ants in pitfall traps (Agosti *et al.*, 2000), concurring together with the CWM results to the high similarity between the two sampling methods. On the other hand, several species missed by bait traps have traits that could explain their absence. Slow-moving species (i.e. *Aphaenogaster subterranea*, *Myrmecina graminicola*, *Solenopsis fugax*) could have a lower probability to contact the baits as suggested by the shorter foraging distance observed in ant sampled by baits. Some species can also be absent because of their specialized diet as aphids' honeydew (*Lasius flavus*, *Lasius emarginatus*) or seeds (*Messor capitatus*) (Agosti *et al.*, 2000; Ellison *et al.*, 2007). Therefore, these species with traits differing from the CWM are likely responsible for higher Rao's quadratic entropy and FD in pitfall traps. Lastly, some species exclusive of pitfall traps are considered uncommon or rare (Blatrix *et al.*, 2013) (e.g. *Aphaenogaster gibbosa*, *Hypoponera eduardi*, *Plagiolepis pallescens*, *Ponera coarctata* or *Tetramorium atratulum*) which might lower the probability to contact them using baits traps, and could also contribute to the observed pattern. Another explanation could come from the degradation states that, due to the ongoing restorations, may have increased the relative abundance of the common and numerous species that might have monopolized baits (Agosti *et al.*, 2000). Our third assumption for the North-South gradient was validated for the richness that was higher in the southern location. This result is consistent with already reported patterns of diversity at larger spatial scales (Majer & Beeston, 1996). Surprisingly, even under at relatively small spatial scale, this N-S difference was found in functional metrics, as it was also found at larger spatial scales (e.g. in Europe: Boet *et al.*, 2020).

Our results overall suggest not using bait trapping for and assemblage survey in open temperate habitats as it is basically redundant with pitfall trapping for all metrics of diversity considered. Similar conclusions were drawn by Mahon *et al.* (2017) who stated that multiple technics were always necessary in temperate environments, especially in studies not aiming at full inventory of ants' diversity. Only active collection appears an interesting option to complete species inventory by pitfalls traps (Agosti *et al.*, 2000), but only if conducted by people with highly specialized skills to be effective (Romero & Jaffe, 2014).

Acknowledgements: This work was supported by the 'Fondation de France' (grant number 1531). We thank Jérôme Sawtschuk and Maxime Leroy for initiating the monitoring, Timothée Scherer for his help in identifying ants and sorting samples, and "Bretagne Vivante" and "Communauté de communes de Belle-île-en-Mer" for continuous support during fieldwork.

Author contribution: Conceptualization, J.P.; field work, A.H.; taxonomic identification, A.H. and C.G.; data analyses, A.H., writing – Original Draft Preparation, A.H.; Writing – Review & Editing, A.H., C.G., W.T. and J.P.; Supervision, J.P.

Conflict of interest: The authors declare no conflict of interest.

Appendix A. headcount by method and traits of the encountered species.

Species	**Headcount**		**Size**	**Dominance**	**Trophic guild**	**Dispersal**	**Colony size**	**Foraging distance (in meter)**	**stratum**
	pitfall	bait							
Aphaenogaster gibbosa (Latreille, 1798)	21	0	large	0	omnivore	independant	6,48	2	epigaeic
Aphaenogaster subterranea (Latreille, 1798)	4	0	medium	0	omnivore	independant	7,6	2	epigaeic
Formica cunicularia (Latreille, 1798)	93	42	large	0	omnivore	independant	7,24	20	epigaeic
Formica pratensis (Retzius, 1783)	1960	75	large	1	omnivore	independant	11	100	epigaeic
Hypoponera eduardi (Forel, 1894)	6	0	small	0	predator	mixed	7,31	2	hypogaeic
Lasius alienus (Foerster, 1850)	110	778	medium	1	omnivore	independant	9,47	10	epigaeic
Lasius emarginatus (Olivier, 1792)	1	0	medium	1	omnivore	independant	9,21	10	epigaeic
Lasius flavus (Fabricius, 1782)	8	0	medium	0	nectarivorous	independant	9,21	2	hypogaeic
Lasius niger (Linnaeus, 1758)	962	498	medium	1	nectarivorous	independant	9,21	10	epigaeic
Lasius platythorax (Seifer, 1992)	30	17	medium	1	nectarivorous	independant	9,21	5	epigaeic
Lasius psammophilus (Seifer, 1992)	66	36	medium	0	nectarivorous	independant	10,43	5	epigaeic
Messor capitatus (Latreille, 1798)	7	0	large	1	seed feeder	independant	8,29	20	epigaeic
Myrmecina graminicola (Latreille, 1802)	5	0	medium	0	predator	independant	4,61	2	hypogaeic
Myrmica ruginodis (Nylander, 1846)	29	0	large	0	omnivore	mixed	7,6	2	epigaeic
Myrmica sabuleti (Meinert, 1861)	45	44	large	0	omnivore	mixed	8,01	2	epigaeic
Myrmica scabrinodis (Nylander, 1846)	530	50	large	0	omnivore	mixed	7,31	2	epigaeic
Plagiolepis pallescens (Forel, 1889)	8	0	small	0	omnivore	mixed	6,68	5	epigaeic
Ponera coarctata (Latreille, 1802)	1	0	medium	0	predator	dependent	4,61	2	hypogaeic
Solenopsis fugax (Latreille, 1798)	2	0	small	NA	omnivore	mixed	NA	2	hypogaeic
Tapinoma erraticum (Latreille, 1798)	176	88	small	1	omnivore	mixed	8,16	10	epigaeic
Temnothorax unifasciatus (Latreille, 1798)	1	0	small	0	predator	independant	5,78	2	epigaeic
Tetramorium atratulum (Latreille, 1802)	1	0	small	0	parasitic	parasitic	0	NA	NA
Tetramorium gr. caespitum-impurum	910	2791	small	1	omnivore	independant	9,21	10	epigaeic

Appendix B. Functional traits used and their descriptions

Trait	Data type	States	References
Size	categorical	Worker body size from the tip of mandibles to tip of the gaster (mm): small < 3mm Medium [3mm ; 4mm] large >4mm	Arnan *et al.*, 2015 Blatrix *et al.*, 2013
Dominance	Binary	0 : Subordinate 1 : Dominant 1: strictly diurnal	Arnan *et al.*, 2015
Trophic guild	Categorical	Omnivore Predator Seed feeder Nectarivorous parasitic	Arnan *et al.*, 2015 Blatrix *et al.*, 2013 Comm. Pers. Dekoninck
Dispersal	Categorical	Independent Dependent Mixed Parasitic	Arnan *et al.*, 2015 Blatrix *et al.*, 2013 Comm. Pers. Dekoninck
Colony size	Numerical	ln of mean of number of worker per colony	Arnan *et al.*, 2015
Foraging distance	Numerical	Distance in meters from the nest while foraging	Lazaro-Gonzales *et al.*, 2013 Epps & Pennick, 2017 Schlick & Steiner, 2006 Domisch *et al.*, 2011 Plowes *et al.*, 2013 Puissauve Renaud, 2007 Fokulh *et al.*, 2012 Comm. Pers., Gouraud
Stratum	Categorical	Epigaeic Hypogaeic	Schlick & steiner, 2006 Comm. Pers. Gouraud

References:

Adis, J. (1979) Problems for interpreting arthropod sampling with pitfall traps. *Zool. Anziger Jena.*, **202**, 177–184.

Agosti, D., Majer, J., Alonso, L.E. & Schultz, T. (2000) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press.

Andersen, A.N. & Majer, J.D. (2004) Ants show the way Down Under : invertebrates as bioindicators in land management. *Front. Ecol. Environ.*, **2(6)**, 291–298.

Arnan, X., Cerdá, X. & Retana, J. (2015) Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. *PeerJ.*, **3**, e1241.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J. & Leprieur, F. (2018) betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1. https ://CRAN.R-project.org/package=betap art

Bioret, F., Bouzillé, J.B., de Foucault, B., Géhu, J.M. & Godeau, M. (1988) Le système thermo-atlantique pelouses-landes-fourrés des falaises des îles sud-armoricaines (Groix, Belle-Ile, Yeu). *Documents phytosociologiques*, **11**, 513-531.

Blatrix, R., Galkowski, C., Lebas, C. & Wegnez, P. (2013) Guide des fourmis de France. Delachaux et Niestlé.

Boet, O., Arnan, X. & Retana, J. (2020) The role of environmental vs. biotic filtering in the structure of European ant communities: A matter of trait type and spatial scale. *PloS one*, **15(2)**, e0228625.

Chao, A. (1984) Nonparametric estimation of the number of classes in a population. *Scand. J. Stat*, **11**, 265–270.

Chao, A. (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, **43**, 783–791.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.*, **84**, 45–67.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **345(1311)**, 101-118.

Dekoninck, W (Royal Belgian Institute of Natural Sciences, Brussels, Belgium). Personal communication, 2020.

De Souza, J.L.P., Baccaro, F.B., Landeiro, V.L., Franklin, E. & Magnusson, W.E. (2012) Trade-offs between complementarity and redundancy in the use of different sampling techniques for ground-dwelling ant assemblages. *Appl. Soil Ecol.*, **56**, 63-73.

Domisch, T., Neuvonen, S., Sundström, L., Punttila, P., Finér, L., Kilpeläinen, J., ... & Jurgensen, M.F. (2011) Sources of variation in the incidence of ant–aphid mutualism in boreal forests. *Agric. For. Entomol.*, **13(3)**, 239-245.

Ellison, A.M., Record, S., Arguello, A. & Gotelli, N.J. (2007) Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. *Environ. Entomol.*, **36(4)**, 766-775.

Ellison, A.M., (2012) Out of Oz: opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. *Myrmecol. News*., **17**, 105-119.

Epps, M.J. & Penick, C.A. (2017) Facultative mushroom feeding by common woodland ants (Formicidae, Aphaenogaster spp.). *Food webs*, **14**, 9-13.

Fokuhl, G., Heinze, J. & Poschlod, P. (2012) Myrmecochory by small ants–Beneficial effects through elaiosome nutrition and seed dispersal. *Acta. Oecol.*, **38**, 71-76.

Fourcassié, V.J., Schatz, B. & Beugnon, G. (1999) Temporal information in social insects. In Information Processing in Social Insects (pp. 261-275). Birkhäuser, Basel.

Gerlash, J., Samways, M. & Pryke, J. (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *J. Insect Conserv.*, **17(4)**, 831-850. https://doi.org/10.1007/s10841-013-9565-9.

Gouraud, C (University of Rennes1, Rennes, France). Personal communication, 2020.

Gotelli, N.J., Ellison, A.M., Dunn, R.R. & Sanders, N.J. (2011) Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Myrmecol. News.*, **15**, 13-19.

Groc, S., Delabie, J.H., Céréghino, R., Orivel, J., Jaladeau, F., Grangier, J., ... & Dejean, A. (2007) Ant species diversity in the 'Grands Causses' (Aveyron, France): In search of sampling methods adapted to temperate climates. *C. R. Biol.*, **330(12)**, 913-922.

Hacala, A., Leroy, M., Sawtschuk, J. & Pétillon, J., (2020) Comparative responses of spiders and plants to maritime heathland restoration. *Biodivers. Conserv.*, **29(1)**, 229-249.

Higgins, R.J. & Lindgren, B.S. (2012) An evaluation of methods for sampling ants (Hymenoptera: Formicidae) in British Columbia. *Canada. Can. Entomol.*, **144(3)**, 491-507.

Kaspari, M., Ward, P.S. & Yuan, M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, **140,** 407–413. https://doi.org/10.1007/s00442-004-1607-2.

King, J.R. & Porter, S. D. (2005) Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. *Environ. Entomol.*, **34(6)**, 1566-1578.

Lach, L., Parr, C. & Abbott, K. (Eds.). (2010) Ant ecology. Oxford university press.

Laliberté, E., Legendre, P., Shipley, B. & Laliberté, M.E. (2015) Package 'FD'. Measuring functional diversity from multiple traits, and other tools for functional ecology. https://mran.microsoft.com/snapshot/2014-11-17/web/packages/FD/FD.pdf

Lang, A. (2000) The pitfalls of pitfalls: a comparison of pitfalls trap catches and absolute density estimates of epigeal invertebrate predators in arable land. *J. Pest. Sci.*, **73(4)**, 99–106.

Lázaro-González, A., Arnan, X., Boulay, R., Cerdá, X. & Rodrigo, A. (2013) Short-term ecological and behavioural responses of Mediterranean ant species Aphaenogaster gibbosa (L atr. 1798) to wildfire. *Insect Conserv. and Divers.*, **6(5)**, 627-638.

Lessard, J. P., Dunn, R.R. & Sanders, N. J. (2009) Temperature-mediated coexistence in temperate forest ant communities. *Insectes Soc.*, **56(2)**, 149-156.

Lopes, C.T. & Vasconcelos, H.L. (2008). Evaluation of three methods for sampling ground-dwelling ants in the Brazilian Cerrado. *Neotrop. Entomol.*, **37(4)**, 399-405.

Luff, M.L. (1975) Some features influencing the efficiency of pitfall traps. *Oecologia,* **19(4)**, 345-357.

Majer, J.D. (1997) The use of pitfall traps for sampling ants–a critique. *Mem. Mus. Vic.*, **56(2)**, 323-329.

Majer, J.D. & Beeston, G. (1996) The Biodiversity Integrity Index : An Illustration Using Ants in Western Australia. *Conserv. Biol.*, **10(1)**, 65–73.

Menke, S.B. & Vachter, N. (2018) A comparison of the effectiveness of pitfall traps and winkler litter samples for characterization of terrestrial ant (Formicidae) communities in temperate savannas. *The Great Lakes Entomologist*, **47(3 & 4)**, 4.

O'hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods Ecol. Evol.*, **1(2)**, 118-122.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M.A.S.S. (2007) The vegan package. *Community ecology package*, **10**, 631-637.

Plowes, N.J., Johnson, R.A. & Hoelldobler, B. (2013) Foraging behavior in the ant genus Messor (Hymenoptera: Formicidae: Myrmicinae). *Myrmecol. News.*, **18**, 33-49.

Puissauve, R. (2007) Gestion d'une population de M. arion sur l'Éperon Murat – État des lieux. Objectif: évaluer la population de M. arion et de ses différents hôtes (origan et Myrmica sabuleti) en vue de lancer un plan de gestion conservatoire sur le site (Université François Rabelais de Tours, Conservatoire du patrimoine naturel de la région Centre, UMR-CNRS 6035 Sociobiologie des Fourmis).

Ricotta, C. & Moretti, M. (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, **167(1)**, 181-188.

Romero, H. & Jaffe, K. (2014) A comparison of methods for sampling ants (Hymenoptera: Formicidae) in Savannas. *Biotropica*, **21(4)**, 348-352.

Rosenberg, D.M., Danks, H.V. & Lehmkulh, D.M. (1986) Importance of Insects in Environmental Impact Assessment. *Environ. Manage.*, **10(6)**, 773–783.

Samways, M.J., McGeoch, M.A. & New, T.R. (2010) Insect conservation: a handbook of approaches and methods. Oxford University press, Oxford.

Schlick-Steiner, B.C., Steiner, F.M., Moder, K., Bruckner, A., Fiedler, K. & Christian, E. (2006) Assessing ant assemblages: pitfall trapping versus nest counting (Hymenoptera, Formicidae). *Insectes Soc*., **53(3)**, 274-281.

Seifert, B. & Schultz, R. (2009) A taxonomic revision of the Formica rufibarbis FABRICIUS, 1793 group (Hymenoptera: Formicidae). *Myrmecol. News*., **12**, 255-272.

Seifert, B. (2018) The ants of Central and North Europe. lutra Verlags-und Vertriebsgesellschaft. Tauer, Germany.

Seifert, B. (2020) A taxonomic revision of the Palaearctic members of the subgenus Lasius s.str. (Hymenoptera, Formicidae). *Soil Org*., **92(1)**, 15–86. https://doi.org/10.25674/so92iss1pp15.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.D., Vogt, J. & Wöllauer, S. (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, **574(7780)**, 671-674.

Sheikh, A.H., Ganaie, G.A., Thomas, M., Bhandari, R. & Rather, Y.A. (2018) Ant pitfall trap sampling: An overview. *J. Entomol. Res*., **42(3)**, 421-436.

Steiner, F.M., Schlick-Steiner, B.C., Moder, K., Bruckner, A. & Christian, E. (2005) Congruence of data from different trapping periods of ant pitfall catches (Hymenoptera: Formicidae). *Sociobiology*, **46(1)**, 105-116.

Tavares, A.A., Bispo, P.C. & Zanzini, A. C. (2008) Effect of collect time on communities of epigaeic ants (Hymenoptera: Formicidae) in areas of Eucalyptus cloeziana and cerrado. *Neotrop. Entomol*., **37(2)**, 126-130.

Topping, C.J. & Sunderland, K.D. (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *J. Appl. Ecol*., **29(2)**, 485–491.

Véle, A., Holuša, J. & Frouz, J. (2009) Sampling for ants in different-aged spruce forests: a comparison of methods. *Eur. J. Soil Biol*., **45(4)**, 301-305.

Wang, C., Strazanac, J. & Butler, L. (2001) A comparison of pitfall traps with bait traps for studying leaf litter ant communities. *J. Econ. Entomol*., **94(3)**, 761-765.

Ward, D.F., New, T.R. & Yen, A.L. (2001) Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *J. Insect Conserv*., **5(1)**, 47-53.