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A new transplantation protocol for harvester ant queens *Messor barbarus* (Hymenoptera: Formicidae) to improve the restoration of species-rich plant communities

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Abstract

We present a protocol for the transplantation of founding queens of the harvester ant *Messor barbarus* (LINNAEUS, 1767), monitoring their survival at six months, one year and 18 months. Once established, these ants are expected to have a positive impact on vegetation restoration via their ability to disperse seeds harvested by workers, thus accelerating the rehabilitation and restoration already undertaken using conventional civil engineering. The transplantations were performed on two sites currently undergoing ecological restoration, one previously degraded by intensive fruit growing (AOA) and the other destroyed by an industrial accident (OLA), and compared with natural colonisation on a reference steppe site. Founding-queen transplantation was also performed at the reference steppe site. We report here the first steps of the protocol, with results on transplantation success and on natural colonisation.

Short-term rates of survival of the transplanted founding queens are encouraging: 15% at the AOA site (after one and a half years) and 35% at the OLA site (after one year). It will take a few years longer to assess any significant impact on composition, species richness and distribution of the different plant populations characteristic of the steppe. However, we demonstrate that the density of natural nests is significantly lower at the degraded site (AOA) than at the reference steppe. It also appears that natural recolonisation by *Messor barbarus* at the destroyed site (OLA) would be difficult without the creation of a favourable habitat. These two results attest to the value of transplantation operations and confirm our hypothesis that for successful establishment the suitability of host habitats for founding queens is a more limiting factor than dispersal during the nuptial flight.

Key words: *Messor barbarus*, transplantation, ecological engineering, founding queen, steppe.

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Introduction

The transplantation of animals is defined as the intentional displacement of living individuals, either wild or bred in captivity, from one place to another (for a survey, see FISHER & LINDENMAYER 2000). The main aim of this practice is to attempt to establish, re-establish or increase the number of individuals in a population.

Animal transplantations are usually performed within the framework of conservation biology (GRIFFITH & al. 1989, FISHER & LINDENMAYER 2000), to reinforce populations of rare species or to reintroduce species that have disappeared. The main aim is generally to reduce the risk of extinction by establishing more populations of the endangered species (SHERLEY 1998). Some transplantations are reportedly undertaken to deal with problems animals may be causing for man, for example by displacing carnivorous mammals that have come too close to cities (LINNEL & al. 1997, FISHER & LINDENMAYER 2000). Other projects are focussed on conserving leisure activities such as hunting and fishing by increasing the stock of game or fish (GRIFFITH & al. 1989, BELL & al. 2006, CATALÁN & al. 2008).

Most animal transplantation programmes concern vertebrates. According to FISHER & LINDENMAYER (2000), 93% concern mammals and birds, while only 7% concern amphibians, reptiles or invertebrates. As for arthropods, examples of Lepidoptera transplantations (MARTILAA & al. 1997, WILLIAMS 1995) and, to a lesser extent, Orthoptera transplantations (SHERLEY 1998, BERGGREN & al. 2001, HOCHKIRCH & al. 2007), have also been cited in the literature.

Research on transplantations of Hymenoptera has rarely been directed at ants, and then mainly in relation to conservation biology (BRADLEY 1972, BOX 1987), biological pest control (PAVAN 1961) and the study of their ecology

(PONTIN 1969, ELMES 1971). Yet, in terms of their species-richness and above all their mechanical and chemical actions, ants play a major role in the functioning of ecosystems (FOLGARAIT 1998, DEL TORO & al. 2012). Through their ability to move through soil and to build biogenic structures (anthills, galleries, etc.), ants have a major impact on the hydraulic properties of soil (altering aggregation and porosity) and on the availability of organic matter for microorganisms (LAVELLE & al. 1997, BARROS & al. 2001). This results in changes in the organic and mineral nature of soil which may therefore alter the composition and abundance of plant species at the soil surface (WOODELL 1974, HORVITZ & SCHEMSKE 1986), and sometimes increase their species-richness (FOLGARAIT 1998, BOULTON & AMBERMAN 2006). Ants are thus considered as important soil engineers, for the same reasons as earthworms and termites (JOUQUET & al. 2006). They are often referred to as "ecosystem engineer" species (FOLGARAIT 1998) according to the definition of JONES & al. (1997): "… organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials". Harvester ants can also play an important role in the dispersal of seeds by myrmecochory (WILSON 1992). This involves the transportation, discarding, loss and / or ejection of some of the seeds subject to predation (RISSING 1986). It is all the more effective when mutualistic interaction occurs between the ants and the seeds, as in the case of seeds bearing elaiosomes (BEATTIE & HUGHES 2002). These "ecosystem engineer" species thus potentially constitute a sustainable tool for ecological engineering, which involves "… the design of sustainable systems, consistent with ecological principles, which integrate human society with its natural environment for the benefit of both" (MITSCH 1996 adapted by BERGEN & al. 2001). This encompasses ecological restoration, in turn defined by the Society for Ecological Restoration (SER 2004) as "the process which initiates or accelerates the self-repair of an ecosystem which has been degraded, damaged or destroyed, while conserving its health, integrity and sustainable management".

While ants are often used as bio-indicators of the quality of a habitat, they have never been used in an ecological engineering project as agents of ecological restoration. Yet many studies have already demonstrated that ant communities are highly sensitive to impacts on their environment, and in particular to changes that affect their species-richness, diversity and species composition (MAJER 1983, ANDERSEN 1997, SAMWAYS & al. 1997, PECK & al. 1998, LOBRY DE BRUYN 1999, ANDERSEN & al. 2002, CASTRACANI & MORI 2006, LUQUE & al. 2007, MAJER & al. 2007, ELLISON 2012). Thus, for ecosystems where the resilience of ant communities is weak, transplantation may represent a way of encouraging the return of species that can play key roles.

Our long-term aim was, for the first time, to use the harvester ant *Messor barbarus* as a tool to boost the rehabilitation and / or ecological restoration of plant communities, either by introducing it where absent or by reinforcing its natural recolonisation. As it has been already demonstrated, *M. barbarus* plays a positive role on the transport, storage and redistribution of seeds (CERDAN & al. 1990, DETRAIN & al. 1996, DETRAIN & TASSE 2000, DETRAIN & al. 2000, SÁNCHEZ & al. 2006, AZCÁRATE & PECO 2003, AZCÁRATE & al. 2005, AZCÁRATE & PECO 2007, PLOWES & al. 2013). Then, we hypothesize that they can help to restore the spatial plant community structure of herbaceous vegetation dominated by annual species. The restoration of this spatial plant community structure has been never reached with other restoration methods using civil engineering such as hay transfer, soil transfer etc. (JAUNATRE 2012). Until now, no previous experiment using ants as ecological engineers to restore the spatial plant community structure has been realised, ants were just used as bioindicators for the evaluation of restoration success (VAN HAMBERG & al. 2004, OTTONETTI & al. 2006, FAGAN & al. 2008). Over a longer period than considered here, we expect this transplantation to lead to complementarity which will accelerate the processes of ecological restoration, notably the restoration of the composition and structuring of the plant community via the supply of seeds and their redistribution by the new, artificially implanted colonies of *M. barbarus*. We tested the efficiency of this tool at two different sites, one degraded (with surviving ant nests) and the other completely destroyed (no surviving ant nests), but chose sites geographically close enough to ensure that climatic conditions did not cause interference (minimum distance 1 km). The site histories were, however, completely different, as were the ecological restoration operations being undertaken.

At each of the sites, as well as monitoring natural recolonisation, we tested a protocol for the transplantation of founding queens of *Messor barbarus* (LINNAEUS, 1767) and report on its success here. We formulate the hypothesis that the suitability of host habitats for founding queens is a more limiting factor than dispersal during the nuptial flight. We therefore compare transplantation success to natural colonisation success, addressing the following questions: Is our transplantation method able to ensure the transplantation success of this species? What is the proof of successful transplantation? Does transplantation improve the establishment of the species in restored areas? Is this operation justified? Will initial restoration type have an impact on transplantation success?

Materials and methods

The plain of La Crau

The study was carried out at the plain of La Crau in the South East of France (Bouches-du-Rhône) (Fig. 1a). This plain lies where the ancient stony delta of the Durance River was formed by deposits from the river, when it flowed directly into the Mediterranean Sea during the Pleistocene period (RAINAUD 1893, COLOMB & ROUX 1978, DEVAUX & al. 1983). The Mediterranean climate is dry and windy, with strong sunshine throughout the year. The topography is very flat with siliceous pebbles covering on average 50% of the soil surface. At 40 - 60 cm depth, an impermeable calcareous conglomerate (pudding pebble) prevents the roots of plants from reaching the water table, contributing to soil drought (RAINAUD 1893, COLOMB & ROUX 1978). Plant cover ranges from between 50% to 80% of the soil surface. On average, 30 to 40 plant species per square metre (with a maximum of 70 plant species per square metre) can be observed (RÖMERMANN & al. 2005). *Brachypodium retusum* (PERS.) P. BEAUV. is the dominant species. The other plant species most characteristic of this steppe are *Thymus vulgaris* L., *Asphodelus ayardii* JAHAND &

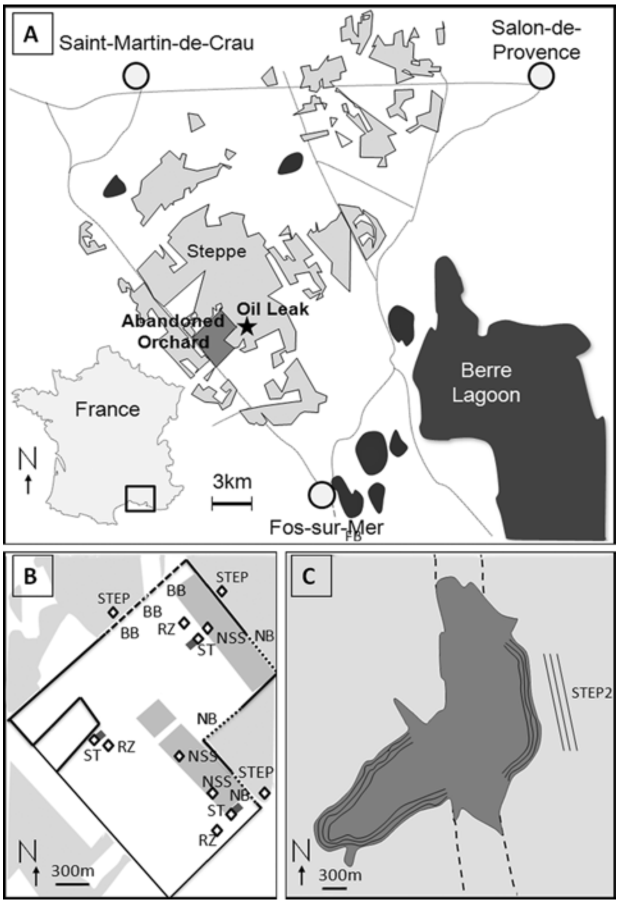

Fig. 1: (A) Situation of the plain of La Crau in France, the abandoned orchard area (AOA site) and the oil leak area (OLA site). (B) Situation of plots where the founding queens were transplanted in the abandoned orchard under different ecological restoration treatments (RZ: rehabilitated zone, NSS: nurse species seeding, ST: soil transfer), on the boundaries (BB: broad boundary, NB: narrow boundary) and in the steppe reference (STEP). (C) Situation of lines where the founding queens were transplanted on the rehabilitated area of the former oil leak and in the reference steppe (STEP2).

MAIRE, *Linum gallicum* L. or *Stipa capillata* L., but stress-tolerant annual species predominate among the flora (MOLINIER & TALLON 1950, DEVAUX & al. 1983). There are no trees. In fact, the plain of La Crau is the result of interaction between the soil, the climate and centuries of itinerant sheep grazing (DEVAUX & al. 1983, CHEREL 1988, BADAN & al. 1995, HENRY & al. 2009), thus forming a typical "steppe" type ecosystem unique in Western Europe. However, in recent decades it has undergone severe degradations and destructions (BUISSON & al. 2006).

Study sites

We undertook the transplantation of ants at two sites where an ecological restoration is in progress: the abandoned orchard area (AOA), degraded by a phase of intensive fruit growing, and the oil leak area (OLA), destroyed by an industrial accident. *Messor barbarus* was identified using the key of BLATRIX & al. (2013).

Abandoned orchard area (AOA). This first site is an abandoned former industrial orchard (peaches, nectarines, apricots) (AOA, Fig. 1b) with a surface area of 357 ha (43° 31' 36.78" N, 4° 51' 31.47" E). The orchard was in use from 1987 to 2006. The steppe (STEP), which is an integral part of a National Nature Reserve, almost entirely surrounds the former orchard and represents our reference ecosystem (Fig. 1). Boundaries separate the steppe from the former orchard: a broad boundary (BB) to the north-north-east and north-east of the site (path, ditch and embankment) and a narrow boundary (NB) to the north-west of the site (embankment and ditch). The width of the boundaries (10 metres) is much less than the maximum length of the foraging columns of *Messor barbarus* workers (around 30 m).

Ecological rehabilitation operations to restore a herbaceous steppe-like habitat for steppe birds (DUTOIT & al. 2013) started in 2009 with the uprooting of 200 000 fruit trees and 100 000 windbreak poplars (representing a total hedge line of 55 km) and with the extraction of irrigation pipes (cumulatively 5000 km). The mounds on which each row of trees was planted were levelled. The return of itinerant sheep grazing started in 2010 and constituted a means to manage the herbaceous plant communities which had settled spontaneously from the seed bank and seed rain. Different techniques of ecological restoration were then tested (JAUNATRE & al. 2012) in order to restore not only a habitat for the steppe birds but also the composition, richness, structure and dynamics of the plant communities characteristic of the steppe (DUTOIT & al. 2013). Some plots were treated by nurse species seeding (NSS), a mixture of sainfoin (*Onobrychis sativa* LAM.), ray-grass (*Lolium perenne* L.) and fescue (*Festuca arundinacea* SCHREB.) spread over 60 ha, making it possible to rapidly cover the soil while preventing the installation of weeds. On other plots, soil transfer (ST) was carried out directly without storage, in bulk and at a ratio of 1:3 (3 ha in all) from an intact steppe plot awaiting destruction following authorisation for a quarry extension. Only the surface layer was transferred (0 - 20 cm depth). An area referred to as the Rehabilitated Zone (RZ) occupies the remainder of the surface of the former orchard; here, no ecological restoration operation was undertaken, apart from uprooting the trees and levelling the ground (Fig. 1b).

Oil leak area (OLA). This second study site, situated in the National Nature Reserve a few hundred metres from the former orchard under restoration, is a 5.5 ha zone of steppe vegetation that was completely destroyed by an industrial accident (43° 31' 36.77" N, 4° 53' 04.50" E) (OLA) (Fig. 1c) in August 2009. An oil pipeline rupture resulted in a hydrocarbon leak of 4700 m^3; in order to depollute, the soil had to be excavated an average 40 cm down to the pudding pebble, removing 72000 t of polluted soil. This excavated area was then filled in with intact steppe soil from the quarry that was the source of the soil for the AOA site.

The operation to restore the destroyed steppe vegetation took place in spring 2011. Soil transfer was performed directly at a ratio of 1:1, without storage. The main soil layers were reconstituted in the original order. The soil surface was then compacted with a steamroller to limit soil expansion and oxidation of the organic matter contained therein. The steppe chosen as the reference ecosystem almost entirely surrounds this site too (STEP2) (Fig. 1c).

Transferred biological material

The transferred biological material is the harvester ant *Messor barbarus* (Hymenoptera: Formicidae). This species was chosen because it occurs naturally in La Crau, as it does throughout the north-western basin area of the Mediterranean. According to previous studies, this species might play a key role with regard to the abundance and the distribution of plants and the structuring and dynamics of the plant community, comparable to the action of centuries of sheep grazing (HENRY 2009, FADDA & al. 2008). This species, which is almost entirely seed-eating, transports to its nests as much as 63% of the total richness of flowering plant species seeds typical of the steppe (CERDAN & al. 1990). Some of these seeds may then be lost, discarded or ejected during transportation (DETRAIN & TASSE 2000, AZCÁRATE & PECO 2007) while conserving their capacity for germination (BONTE & al. 2003), which in certain seeds may persist for two years (MARTÍNEZ-DURO & al. 2010). The strong polymorphism of worker ants also enables them to transport seeds from 0.2 to 60 mg (DETRAIN & al. 1996) over a distance of as much as 30 metres.

Messor barbarus colonies are monogynous, with independent claustral foundations (CERDAN 1989). This means that the queen breeds the first larvae alone and remains throughout her life enclosed in a chamber that may be situated as much as 5 m deep within the nest. Nest volume in relation to size of population is thus high (CERDAN 1989). In the plain of La Crau, since the queen cannot be situated more than 40 cm deep due to the presence of hardened pudding pebble, the nests spread out as much as 25 m^2 over the surface. It is therefore impossible to transplant a nest with its queen without having a major impact on the collection and transplantation areas. This is why we chose to transplant *M. barbarus* founding queens (females impregnated after the nuptial flight), which can easily be collected in large numbers after the nuptial flight. The nuptial flight of *M. barbarus* occurs at the beginning of autumn after the first late summer storms, when environmental conditions are favourable: heavy precipitation on the day before the nuptial flight, high temperature (> 20°C), clear sky, little or no wind (CERDAN 1989, GÓMEZ & ABRIL 2012). During the nuptial flight, males and females mate and then fall to the ground, where the impregnated females (founding queens) alone tear off their wings and begin to dig.

Experimental protocol for the transplantation of *Messor barbarus* founding queens

Collection of founding queens. Founding queens were collected and stored in 12 cm-long glass tubes with a water supply. The tubes were then closed non-hermetically to prevent condensation while allowing aeration. All the founding queens were collected within the natural distribution area of this species (BERNARD 1968, CERDAN 1989). On 5th October 2010, some 600 founding queens destined for transportation to the AOA site were collected over an area of about 100 m^2 by four people in less than an hour. On 25th October 2011, 200 founding queens were collected for transplantation to the OLA site.

Transplantation of founding queens to the AOA site. The plots receiving the founding queens measured 50 m × 60 m and were replicated three times within each restoration treatment type (nurse species seeding, soil transfer, rehabilitated zone), as well as in the reference steppe (Fig. 1). On both the narrow and the broad boundaries, each plot was also replicated three times and the founding queens were transplanted along a 300 m line. The three replicates were situated some distance apart (minimum distance about 600 m) in order to avoid spatial auto-correlation. In the vicinity of each transplantation site we marked out a control site of the same surface area but without founding queen transplantation so as to study, over the longer term, the impact of the ants on the vegetation in the absence of artificial transplantation (Fig. 1). In autumn 2010, 30 founding queens per plot were placed in lines of six, at a distance of 10 m from each other; the five parallel lines were 10 m apart. In the boundary areas, 30 founding queens were placed in one 300 m line, at a distance of 10 m from each other. In the narrow boundary, the three replicate lines of queens were 20 m apart. The distance between founding queens was chosen as the minimum to ensure that new colonies, once established, would not attack each other. This distance is a compromise between the length of the columns formed by the worker ants, which may be some thirty metres long, and the size of the smallest plots, i.e., the soil transfer plots.

Fig. 2: Live transplanted founding queen with its brood under the geo-referenced pebble lifted for photography (photograph by Laurence Berville).

In the plain of La Crau, after the nuptial flight and once they have fallen to the ground, most founding queens settle beneath the pebbles that cover the soil surface. The transplanted founding queen was therefore placed in a small hole in the ground and a pebble was placed over the hole for protection from sudden variations in temperature, the pebble acting as an accumulator of heat and subsequently restoring it to the soil. Soil was piled around the edges of the pebbles to prevent the ants from escaping or predators such as Scolopendra (*Scolopendra cingulata*) or spiders (*Lycosa narbonensis*), abundant in pseudo-steppe, from entering. Each pebble was then geo-referenced and numbered.

Transplantation of founding queens to the OLA site. In autumn 2011, 169 founding queens were similarly transplanted in three lines at a distance of 5 m, 15 m and 25 m from the reference steppe, and 60 queens likewise in the reference steppe (Fig. 1c). In contrast to the AOA site, since this was carried out in April 2011 the vegetation was at a very early stage of development: it was very short and sparse, with large stretches of bare ground; moreover, there

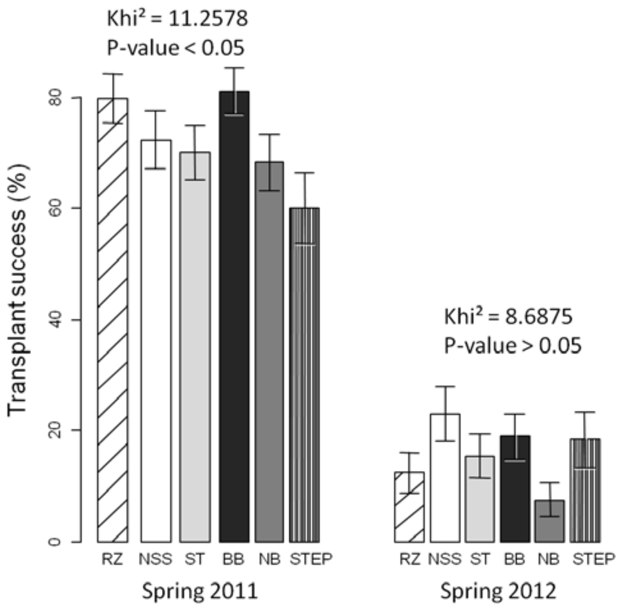

Fig. 3: Successful transplantations of founding queens in spring 2011 and spring 2012 on the AOA site, on the boundaries and in the reference steppe. Nurse species seeding (NSS, white), rehabilitated zone (RZ, oblique stripes 45°), soil transfer (ST, light gray), broad boundary (BB, dark grey), narrow boundary (NB, grey); reference steppe (STEP, vertical stripes). The percentage of successful transplantations is based on the number of founding queens still alive in each zone. The chi-square of Kruskal-Wallis test and its p-value are indicated above each graph. The p-value is adjusted according to the Benjamini-Hochberg method. Error bars represent standard errors.

were very few pebbles visible at the surface because of soil compacting carried out during the restoration.

Assessment of the artificial implantations. In order to check whether the transplanted founding queens had survived, monitoring was carried out in spring 2011 and spring 2012 at the AOA site, and in spring 2012 and autumn 2012 at the OLA site. The numbered pebbles were inventoried, lifted and quickly but carefully replaced in order to avoid disturbing and altering the microclimate within the nest. The presence of a vertical tunnel dug at the bottom of a small chamber excavated by the founding queen beneath the pebble was considered a sign of successful transplantation. The possible presence within each nest of brood, larvae, worker ants and / or a midden was also systematically recorded (Fig. 2).

Founding queen transplantations can be considered a success if the establishment rate is at least as high as that of natural colonisation, but preferably higher.

Monitoring of natural recolonisation

AOA site. An inventory of the nests of *Messor barbarus* already naturally present was carried out in spring 2011 by visually surveying the different transplantation plots and the control plots without transplantation. These nests were either newly installed or were not destroyed by the fruit-growing phase and during the ecological rehabilitation / restoration operations. We located the nests by means of the foraging trails followed by the worker ants loaded with seeds. Wherever we found disturbed soil, traces of foraging tracks without worker ants or heaps of seed detritus, we lifted pebbles to confirm the presence of a nest. This monitoring took about two hours for each plot (50 m wide and 60 m long, or 0.3 ha), with or without transplantation, with two observers placed along transects five metres apart until the site had been completely covered. Along the boundaries, observers were positioned on either side of the boundary (300 m long and 5 m wide, or 0.15 ha).

OLA site. In autumn 2011, before the artificial transplantation, we undertook an initial state survey to determine whether natural recolonisation by *Messor barbarus* had taken place, without systematic measurement. In autumn 2012, after the nuptial flight, natural recolonisation was measured as follows: Three observers surveyed the entire surface area of the restoration site for one day, randomly lifting pebbles on the soil surface (total 1107) and pebbles buried in the soil (total 137) to identify the possible presence of naturally established founding queens. Their number and location were then recorded.

Statistical analyses

All statistical analyses were performed using R software version 2.15.2. When the data did not follow a normal distribution (Shapiro-Wilk test), we used the Kruskal-Wallis non-parametric test. This test was performed to identify any significant differences in survival rate after transplantation between the different treatment types and control periods, as well as any significant differences in the survival rates of naturally established colonies (or founding queens). In the case of significant differences, we used the Mann-Whitney-Wilcoxon non-parametric test to compare the means two by two (p-value adjusted according to the method of Benjamini-Hochberg).

Results

Assessment of successful transplantation of founding queens

AOA site. In spring 2011, six months after the transplantation of the founding queens, the overall establishment success rate was 72.6% (348 founding queens alive for 479 pebbles found). In all, we transplanted 540 founding queens, but 61 pebbles marking founding queens were not found (11.3% of pebbles not found). Transplantation success rates differed for the reference steppe (63.0%), the narrow and broad boundaries (81.1% and 68.3%), and the three ecological treatment areas: rehabilitated zone (79.8%), nurse species seeding (72.4%) and soil transfer (70.1%) (Kruskal-Wallis test, chi-square = 11.2578, df = 6, p-value = 0.049). However, none of the differences were significant (Fig. 3).

In spring 2012, one and a half years after the founding queen transplantations, the success rate was only 15.7% (74 founding queens alive for 470 pebbles found at the degraded site and in the reference steppe) (Fig. 3). Pebbles not found represented 13.0%. No significant difference was recorded among the different transplant zones (Test of Kruskal-Wallis, chi-square = 8.6875, df = 6, p-value > 0.05). However, 22.0% of the founding queens found in spring 2011 to have been successfully transplanted were still alive.

Broods, worker ants and/or middens beneath pebbles were found at three transplantation locations in the refer-

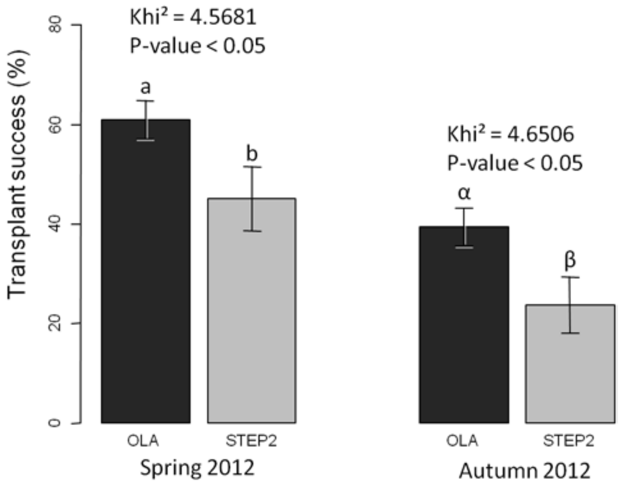

Fig. 4: Successful transplantations of founding queens in spring 2012 and in autumn 2012 on the OLA site and in the reference steppe STEP2, light grey). Percentage of successful transplantations is based on the number of founding queens still alive in each zone. The chi-square of Kruskal-Wallis test and its p-value are indicated above each graph. Error bars represent standard errors. Bars with a different letter (a and b, α and β) are significantly different ($p < 0.05$).

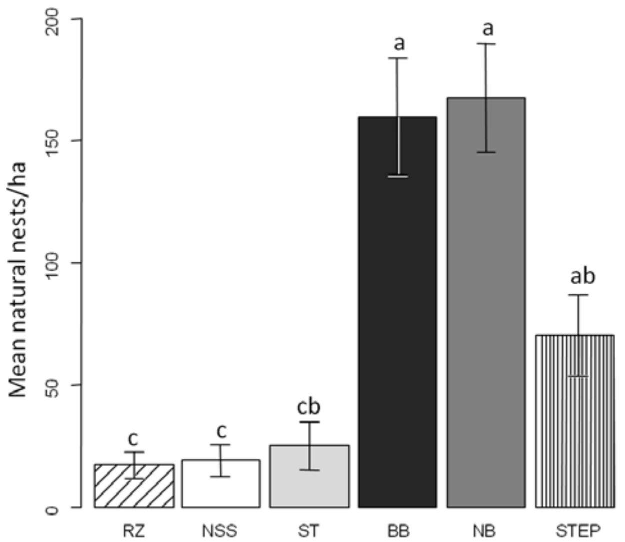

Fig. 5: Mean natural nests (per hectare) of *Messor barbarus* already present at the site degraded by intensive arboriculture (AOA: NSS, RZ, ST, on the boundaries (BB, NB) and in the reference steppe (STEP). Nurse species seeding (NSS, white), rehabilitated zone (RZ, oblique stripes 45°), soil transfer (ST, light grey), broad boundary (BB, dark grey), narrow boundary (NB, grey); reference steppe (STEP, vertical stripes). The chi-square of Kruskal-Wallis test and its p-value are indicated above each graph. Error bars represent standard errors. Bars with a different letter are significantly different ($p < 0.05$). (Comparison by Mann-Whitney-Wilcoxon tests with p-value adjusted according to the Benjamini-Hochberg method; $p < 0.05$).

ence steppe, at six in the boundaries (one in a narrow boundary and five in broad boundaries) and at ten in the AOA site (five in nurse species seeding areas, four in soil transfer areas and one in a rehabilitated zone) (Fig. 2).

OLA site. In spring 2012, six months after the founding queen transplantations, the survival rate for the transplanted founding queens was 56.3% (129 founding queens alive for 229 pebbles found). Here, all the pebbles were found. The transplantation success rate was significantly higher at the OLA study site than at the reference steppe, respectively, 60.9% and 43.3% (Kruskal-Wallis test, chi-square = 4.57, df = 1, $p < 0.05$) (Fig. 4).

In autumn 2012, one year after transplantation of the founding queens, the transplantation success rate had decreased to only 35.3% (79 founding queens alive for 224 pebbles found). Pebbles not found represented only 2.1% of the total. The transplantation success rate was again significantly higher at the restored site than at the reference steppe (respectively 39.9% and 23.7%) (Kruskal-Wallis test, chi-square = 4.65, df = 1, p-value < 0.05) (Fig. 4).

65.9% of founding queens found in spring 2012 to have been successfully transplanted were still alive in autumn 2012 (64% at the study site and 54% at the reference steppe).

We observed the presence of broods, worker ants and/or middens at only 21 transplantation locations.

Monitoring of natural recolonisation

AOA site. Spring 2011 was particularly hot and dry from April to the end of May and the *M. barbarus* worker ants therefore adapted their periods of daily summer foraging (from 7:00 am to 11:00 am and from 7:00 pm until sunset).

The mean number of natural nests recorded was significantly higher at the narrow and broad boundaries (on average 151.7 and 163.3 nests per hectare) and in the reference steppe (on average 70 nests per hectare) than in the rehabilitated zone (average 16.7 nests per hectare) and the nurse species seeding area (average 20 nests per hectare) (Kruskal-Wallis test, chi-square = 22.90, df = 6, p-value < 0.05). The mean number of natural nests also differed significantly between the boundary areas (both narrow and broad) and the soil transfer area (average 26.7 nests per hectare). The mean number of nests was higher in the reference steppe than in the soil transfer area but no significant difference was detected by the Mann-Whitney-Wilcoxon multiple comparison tests (Fig. 5).

OLA site. In autumn 2011, no new establishment of *Messor barbarus* was observed at this site. In autumn 2012, after the nuptial flight, a first natural recolonisation occurred. We counted 46 new founding queens after lifting 1107 pebbles (970 pebbles placed on the surface and 137 pebbles buried in the soil). These founding queens were all found under pebbles placed on the surface. We had removed them from the ground during the transplantation operations: 4.75% of the pebbles removed from the ground had thus been chosen naturally by founding queens. No new establishment was detected where there were no pebbles on the ground, or when pebbles had been buried by prior soil compacting operations during rehabilitation of the site.

Discussion

We transplanted *Messor barbarus* founding queens onto these two sites to test the hypothesis that the behaviour patterns of a harvesting ant could be useful for sustainable ecological restoration following major ecological restoration operations, primarily civil engineering. We hypothesized that this ant could in future play a role not only in the dispersal of characteristic seeds of the reference plant community, but also in the restoration of the spatial composition and pattern of this vegetation. With its foraging columns that can stretch as far as thirty metres, a mean number of 8000 worker ants per nest and the polymorphism of the worker ants, this species is capable of transporting and thus potentially of losing, discarding and / or ejecting a wide range of seeds.

The literature mainly reports the transportation of fragments of ant nests via sampling from the central mass with the main brood chambers, worker ants and one or several queens (PAVAN 1961, PONTIN 1969, ELMES 1971, BRADLEY 1972, BOX 1987). This transplantation technique is generally quite successful for at least a few subsequent years. However, as well as being lengthy and fastidious, the transplantation of nests may also have a serious impact on the environment, since it requires excavating the soil in the donor area in order to collect the nest and in the host area to install it (PONTIN 1969, ELMES 1971). In addition, collecting what amounts to whole nests reduces nest density in the donor area. Furthermore, it is difficult to ensure that the founding queen located deep down, namely around five metres for *Messor barbarus*, can be found and collected undamaged.

We therefore chose to transplant the founding queens alone, as this technique would appear to be sustainable and realisable at a large scale. As well as being quick and easy to achieve, the transplantation of the founding queens alone also minimises impact on the environment since no excavation of the soil is involved. Collecting these founding queens, an insignificant proportion of the numbers resulting from the nuptial flight (CERDAN 1989), has no impact on the donor site. At the time of the nuptial flight, the founding queens may land on habitats that are unsuitable for them to settle in, e.g., car parks, car windscreens or water, and / or fall victim to heavy predation (birds, lizards, spiders, scolopendra, ants) (personal observations; WHITCOMB & al. 1973). This means that, of the thousands of founding queens involved in the nuptial flight, very few survive: myrmecologists generally agree on a figure of one out of 1000. By transplanting founding queens, we enable them to get through the dispersal filter and settle in favourable micro-habitats. Nevertheless, the first year of the founding queen's life is the most vulnerable stage in the ant's life (BARONI URBANI 1968, HÖLLDOBLER & WILSON 1990, TSCHINKEL 1992 a, b, HERBERS 1993). As an example, 80% of nests of *Solenopsis invicta* perish before the workers have even started to work (TSCHINKEL 1987). Moreover, once installed in their tunnel, the founding queens may still be exposed to severe predation by ants, whether conspecific or not (EDWARDS & al. 1974, NICKERSON & al. 1975, NICHOLS & SITES 1991, KAWECKI 1992), and by other organisms (scolopendra, spiders) (WHITCOMB & al. 1973). In addition, excessive dryness or humidity can also prove fatal (JOHNSON 1998). The excessive drought that we observed during the summer of 2011 may thus be one of the reasons for the high mortality rate recorded at the AOA site. When ants have independent claustral foundation, as with *M. barbarus*, the founding queens must then succeed in laying and raising their first larvae using their own reserves (CERDAN 1989, HÖLLDOBLER & WILSON 1990).

At the OLA site, one year after transplantation, 35.3% of transplanted founding queens had survived; at the AOA site, one and a half years after transplantation, almost a quarter of transplanted founding queens were also still alive. Further proof of the success of these transplantations is that the success rate is higher at the OLA site (39.9%) than in the reference steppe (23.7%). In addition, at both sites the founding queens were observed to have raised the first worker ants six months after transplantation, and small depositories had been formed beneath the pebbles one year after transplantation.

At the AOA site, the success rate was similar throughout the transplantation areas, including the reference steppe. Within the former orchard, therefore, the various restoration operations did not have any significant influence on transplantation success in the short term. In contrast, the significantly higher success rate of the transplantations at the OLA site than at the reference steppe may be explained by greater predation in the steppe. The oil spill and the soil depollution operations totally destroyed OLA soil organisms, and thus the main predators of these ants.

At the AOA site, significant differences in density of natural nests of *Messor barbarus* were recorded: high density in boundary situations, intermediate density in the reference steppe, low density within the former orchard. These differences may be explained by the negative impact of earlier agricultural practices within the orchard between 1987 and 2006, including the use of insecticides, weeding, digging of the soil. Another explanation is the occurrence of a more positive ecotone effect in the boundary areas, an ecotone being a transition area between different elements of a landscape (ecosystem, plant communities, etc.) (VAN DER MAAREL 1990). The fact that the boundaries' soil is not compacted may also promote the establishment of new colonies.

As natural recolonisation had already taken place before the transplantation operations, the AOA habitat would appear favourable to new establishment, whether transplanted or naturally settled. For example, there is the presence of pebbles on the soil surface, without which establishment success could be compromised by predators already colonising the site.

Thus, the transplantation of founding queens can be justified where natural nest density remains low, such as within the former orchard.

At the OLA site, natural recolonisation by *Messor barbarus* only began one year after our founding queen transplantations and remains very poor, with 9.2 foundations / ha. The new natural foundations all occurred beneath pebbles that we had removed from the ground while transplanting the founding queens, showing that these artificial practices strongly influenced the natural recolonisation. The OLA site represents an unfavourable habitat for the natural return of *Messor barbarus*, since the pebbles there were buried by the compacting of the soil to encourage vegetation during site rehabilitation. Recolonisation by *Messor barbarus* thus appears to be habitat-dependent.

In contrast, the establishment success of ants at OLA could be favoured by a low rate of predation, since predators colonised the site at the same time as the new ant colonies were developing.

The transplantation of founding queens thus remains a promising method for getting past the filter of habitat conditions and the high rate of predation that occurs during natural dispersal.

Our work will continue with the monitoring of the development of the colonies and, on the longer term, the monitoring of the vegetation both close to the nests and in areas where there are no *Messor barbarus* nests, in order to measure the impact of this harvester ant on the vegetation. We hope in this way to determine whether transplanted species can have a positive influence on the restoration of a degraded ecosystem.

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