

Reduction of the Ant Mandible Gap Range After Biotic Homogenization Caused by an Ant Invasion (Hymenoptera: Formicidae)

by

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ABSTRACT

After most of the native ant species are displaced by the Argentine ant invasion, it is probable that some ecological processes carried out by natives are not replaced. In some cases this could be due to a morphological difference between the Argentine ant and the displaced native ants. The significant decrease in ant richness after the invasion (only two species detected in the invaded zones vs. 25 species in surrounding non-invaded zones) implies a drastic reduction in the ant mandible gap range (the mandible gap spectra of all the ant species in a community) in the invaded zones. This reduction could explain why some roles that were previously carried out by the displaced native species are not performed by the invasive species. This could be due to a functional inability to carry out these activities. The mandible gap was positively correlated with the ant body mass in the 26 ant species considered. The functional inability hypothesis could be applied to other invasive ants as well as to the Argentine ant.

Keywords: Argentine ant, biotic invasion, functional inability, mandible gap, resource searching.

INTRODUCTION

One well documented impact that invasive ants have on the area they invade is the competitive displacement of most of the native ant species (Hölldobler & Wilson 1990, Williams 1994, Holway *et al.* 2002). Once the invasion is complete, the invasive species is unlikely to be able to replace all the roles of the displaced native ants. Thus, due to the variety of ecological processes in which ants are implicated (Hölldobler & Wilson 1990) the disappearance of the native ant species could cause a series of cascade effects affecting the whole ecosystem. Focusing on ant-plant interactions, the differences between invasive and native ants have usually been directly or indirectly attributed to the invasive species' numerical superiority, aggressive behavior, and affinity for carbohydrate-rich food, and to a lesser extent to other biological traits

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such as temperature tolerance, daily activity patterns, colony cycles, and seasonal preferences for food types (Lach 2003). However, little attention has been given to functional traits with the aim of explaining why the roles of the displaced natives are not replaced by the invader. The present study suggests that morphological differences between the invasive ants and the displaced native ants could explain why some roles are not performed after the invasion, i.e. due to a functional inability.

In a similar way to human hands, the mandibles constitute the ants' most important tool and they are used for several vital functions. Ants use their mandibles for various robust activities like catching prey, fighting, digging, cutting leaves, cracking seeds or scraping wood, and simultaneously for delicate activities such as grooming, brood care, carrying nestmates, transporting liquids, and even for communication among nestmates (Hölldobler & Wilson 1990). The most studied mandible functional traits are the power and velocity of the mandible closing movement (Gronenberg *et al.* 1997, Paul 2001). However, the mandible gap is another important morphological trait limiting the functionality of these tools, as ants are unable to grasp objects that are larger than their maximum mandible opening.

In a well constituted ant community we can find a wide variety of mandible types, adapted to the particular requirements of each ant species. Moreover, in an ant community we can find a wide range of different mandible gaps related to the variety of ant body sizes. Therefore, the displacement of native ant species after the invasion could cause an alteration of the ant mandible gap range in the invaded areas. This morphological change may imply that resources are used differently due to a functional inability of the invasive ants, and may alter some ecological processes.

The present study is focused on a well known invasive ant species, the Argentine ant *Linepithema humile* (Mayr). It is native to the south of the Parana River in Argentina (Tsutsui *et al.* 2001), but the Argentine ant has been introduced in various zones of the world due to human commercial activities (Hölldobler & Wilson 1990, Suarez *et al.* 2001). Its distribution range now includes areas with Mediterranean-type climates throughout the world (Passera 1994, Suarez *et al.* 1998). Although its rapid expansion in invaded zones has been facilitated by human habitat alteration (Suarez *et al.* 1998), there is increasing evidence of its ability to occupy non-altered habitats (Cole *et al.* 1992, Human & Gordon 1996, Holway 1998a, Gómez *et al.* 2003). The competitive displacement of native ants is a widely reported effect of this species in the invaded areas (Cammell *et al.* 1996, Human & Gordon

1997, 1999, Suarez *et al.* 1998, Holway 1998b, 1999, Gómez & Oliveras 2003). Thus, the invaded areas suffer a dramatic impoverishment and homogenization of the ant community, which becomes almost completely monopolized by *L. humile*.

In the present study the alteration of the ants' mandible gap range after the Argentine ant invasion is evaluated, and the potential ecological implications are analyzed.

MATERIALS AND METHODS

Study site

The study was carried out in the southern edge of the Gavarres Massif (NE Spain). The climate of this region is Mediterranean sub-humid, with 627 mm of annual rainfall, a minimum monthly average temperature in January of 7.2°C and a maximum in July of 22.6°C. In this area the zones invaded by the Argentine ant and the non-invaded zones are in close proximity. The Argentine ant distribution in the study area is concentrated mainly in the zones next to the Mediterranean coast and urbanized areas from where its access and subsequent expansion to less-altered areas began. Ants were collected from two different sources: from zones invaded by the Argentine ant and from surrounding non-invaded zones. Sampling zones consist of open cork oak secondary forests dominated by *Quercus suber* (L.), *Quercus ilex* (L.), *Erica arborea* (L.), *Cistus monspeliensis* (L.), *Cistus salviifolius* (L.) and *Arbutus unedo* (L.). The relative proximity, as well as the similar environmental characteristics of the sampling zones allows us to assume that the composition of the native ant community in the non-invaded zones is very similar to what it was in the invaded zone before the invasion. Therefore, the two ant sources considered (invaded vs. non-invaded) could represent two successive time stages, previous and posterior to invasion.

Ant species and mandible gap

Ants were collected in the field by visiting the study zones several times during spring and summer 2004 at different daily periods to find the maximum species richness present. The mandible gap of the ant species was measured from live ant workers. This was done using metallic sheets of different gauge widths. The mandible gap was measured by holding a worker by its thorax (or leg in smaller species) with soft forceps and offering it sheet gauges of increasing widths (± 0.05 mm) until the ant could not grasp it. Thus, each measurement corresponds to the maximum mandible gap of the measured ant. This was carried out under a binocular microscope. A total of 50 workers of

Table 1. Mandible gap of the ant species found and their presence in the invaded and the non-invaded zones. Ant species are arranged by mean mandible gap, from largest to smallest.

Ant species	n	Mandible gap (mm)		Species presence	
		Mean (SE)	Range	Non-invaded zone	Invaded zone
<i>Camponotus cruentatus</i>	50	2.276 (0.060)	1.60–3.30	×	
<i>Camponotus aethiops</i>	7	1.800 (0.098)	1.50–2.20	×	
<i>Aphaenogaster senilis</i>	50	1.742 (0.013)	1.50–1.90	×	
<i>Cataglyphis piliscapus</i>	50	1.706 (0.026)	1.35–2.00	×	
<i>Camponotus pilicornis</i>	40	1.683 (0.051)	1.30–2.80	×	
<i>Messor barbarus</i>	50	1.635 (0.071)	0.80–2.80	×	
<i>Messor structor</i>	50	1.604 (0.042)	1.05–2.25	×	
<i>Messor bouvieri</i>	50	1.374 (0.027)	0.95–1.70	×	
<i>Camponotus ligniperdus</i>	1	1.300 (0.000)	1.30–1.30	×	
<i>Camponotus vagus</i>	3	1.233 (0.033)	1.20–1.30	×	
<i>Myrmica sabuleti</i>	4	1.225 (0.043)	1.10–1.30	×	
<i>Formica cunicularia</i>	50	1.217 (0.015)	1.00–1.50	×	
<i>Formica fusca</i>	6	1.208 (0.042)	1.10–1.40	×	
<i>Camponotus piceus</i>	1	1.100 (0.000)	1.10–1.10	×	
<i>Camponotus lateralis</i>	50	1.050 (0.020)	0.80–1.25	×	
<i>Aphaenogaster subterranea</i>	50	1.007 (0.014)	0.80–1.20	×	
<i>Tapinoma nigerrimum</i>	50	0.919 (0.017)	0.70–1.20	×	
<i>Crematogaster scutellaris</i>	50	0.904 (0.011)	0.65–1.10	×	
<i>Tetramorium caespitum</i>	50	0.888 (0.008)	0.75–1.00	×	
<i>Tetramorium ruginode</i>	50	0.888 (0.011)	0.70–1.00	×	
<i>Lasius lasioides</i>	50	0.878 (0.009)	0.70–1.00	×	
<i>Pheidole pallidula</i>	50	0.646 (0.006)	0.60–0.70	×	
<i>Camponotus truncatus</i>	1	0.600 (0.000)	0.60–0.60	×	
<i>Linepithema humile</i>	50	0.597 (0.008)	0.50–0.70		×
<i>Temnothorax racovitzai</i>	8	0.463 (0.018)	0.40–0.55	×	
<i>Plagiolepis pygmaea</i>	50	0.333 (0.006)	0.25–0.40	×	×

each ant species were measured (a lower number of ants were measured for less common species which were only found sometimes, (see Table 1)).

The correlation between the mean mandible gap and the mean ant body mass was evaluated to assess whether this characteristic is representative of the ant body size. To measure the biomass we used the data provided in the biomass database for Iberian ants generated by Gómez and Espadaler (2000). They followed a two-step process to estimate the ant species biomass: (1) the head length (HL) of workers was directly measured under a stereoscopic microscope to the next 0.006 mm for the smallest ants (up to 1.3 mm HL; $n = 110$ species) or to the next 0.013 mm for bigger ants ($n = 32$ species); in 95 species HL was taken directly from published information; (2) dry body mass was then obtained by applying the transformation for each subfamily proposed by Kaspari and Weiser (1999) (but the transformation of

Espadaler and Gómez (2001) for the Formicidae). In polymorphic species, the minimum and maximum were taken and the mean used. Correlations were measured on \log_{10} -transformed data with the Pearson's correlation coefficient using the SPSS statistical package for Windows version 12.0.1 (SPSS Inc).

RESULTS

Ant species and mandible gap

Only two ant species were found in the invaded zone, the invasive *Linepithema humile* and the native *Plagiolepis pygmaea* (Latreille). In the non-invaded zones 25 native ant species were detected (Table 1). The mandible gap of the invasive *L. humile* was shorter than most of the native ant species (Table 1). Only two native species had shorter mandible gaps than the Argentine ant: *Temnothorax racovitzai* (Bondroit) and *Plagiolepis pygmaea*. As a consequence, the overall ant mandible gap, which ranged from 0.25 mm (*Plagiolepis pygmaea* minimum observed gap) up to 3.30 mm (*Camponotus cruentatus* (Latreille) maximum observed gap) in the non-invaded zone, was reduced to 0.25 mm (*P. pygmaea* minimum observed gap) up to 0.70 mm (*L. humile* maximum observed gap) in the invaded zone.

Significant positive correlation between the mean ant mandible gap and the mean ant body mass (both \log_{10} -transformed) was obtained for the 26 ant species considered (Pearson correlation coefficient: $r = 0.889$, $P < 0.001$) (Fig. 1).

DISCUSSION

The widely reported reduction in the native ant diversity after the Argentine ant invasion is currently taking place here. As previously detected in the same study area (Oliveras *et al.* 2005) the tiny *Plagiolepis pygmaea* is apparently the only native epigaeic species capable to coexist with the invasive *L. humile*. In the invaded zones, the Argentine ant is unlikely to be able to replace all the roles or functions of the displaced native ants. We propose that in some cases it could be due to its inability to carry out the same functions (functional inability). The smaller mandible gap of *L. humile* compared with most of the native ant species could be one cause of this functional inability. In the present study, the wide range of mandible gaps found in the non-invaded zone (up to 3.30 mm) becomes more than four times smaller in the invaded zone (up to 0.70 mm). In practical terms, a single ant's ability to manipulate indivisible objects will be seriously affected after the invasion, and thereafter several roles carried out by native ants are unlikely to be replaced in the invaded zones due this reduced ability.

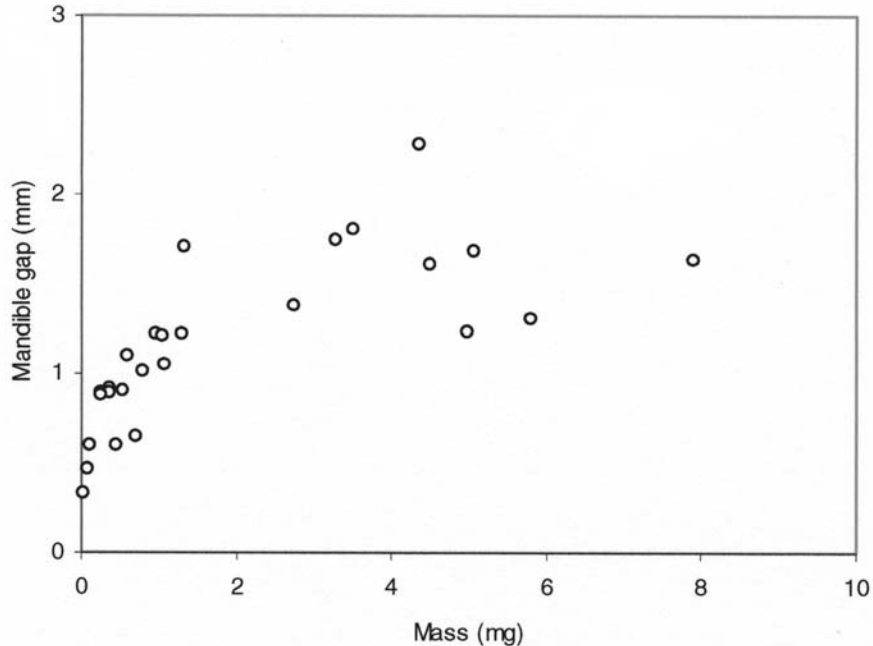


Fig. 1. Bivariate plot of mean ant species body mass and mean mandible gap in ant species found in the invaded and the non-invaded study zones.

The level of impact due to this kind of functional inability to manipulate indivisible items depends on size and morphology. Thus, only the objects with all their parts larger than the maximum mandible gap of the Argentine ant would be affected by this functional characteristic.

Myrmecochory, the seed dispersal carried out by non-granivorous ants, could be one process altered by this characteristic. Although in many cases the ants can break up large food resources into smaller pieces that are easier to transport to the nest, other resources, like myrmecochorous seeds, are normally collected intact. Once in the ants nest, the lipid rich elaiosome attached to the seed, which is the attractive part for the ants, is eaten and the seed is discarded. Thus, the ant mandible gap could be the decisive factor that determines whether the ant successfully transports the seed. The Argentine ant has usually been considered a bad or null seed disperser (Bond & Slingsby 1984, Christian 2001, Carney *et al.* 2003, Gómez *et al.* 2003), but the reasons why this species fail in transporting seeds have not been investigated. Although in some cases it could be because the seed is not attractive for *L. humile*, some works demonstrate that the Argentine ants are at-

tracted to different myrmecochorous seeds (Midgley & Bond 1995, Quilichini & Debussche 2000, Carney *et al.* 2003, Gómez & Oliveras 2003). In these cases the reasons why they do not disperse seeds could be explained by a functional inability of the ant that prevents them transporting the seeds. In some species the excessive seed mass could prevent *L. humile* from transporting it. But in other cases a morphological incompatibility between the ant and the seed, such as a seed-shape with each part larger than the ants' mandible gap, could be the reason for their inability to transport the seed. In field experiments performed in the invaded study zone we observed *L. humile* workers transporting the large myrmecochorous seeds of the Compositae *Silybum marianum* (L.) (mean \pm SE seed mass = 26.204 ± 0.228 mg, $n = 150$) (Oliveras unpublished data), but frequently failing after several attempts to transport lighter seeds (see Gómez & Oliveras 2003) due to the ants' inability to grasp them efficiently. This could also be valid for some of the myrmecochorous seeds with a mass that is unlikely to be limiting but with a documented null dispersal in the Argentine ant invaded areas (*i.e.* *Rhamnus alaternus* (9.14 ± 2.13 mg, $n = 678$, unpublished) (Gómez *et al.* 2003); *Dendromecon rigida* (16 mg) (Carney *et al.* 2003); *Diastella divaricata* (26.18 ± 10.39 mg), *Serruria phyllicoides* (9.02 ± 2.21 mg), *Serruria rubricaulis* (7.85 ± 1.93 mg), *Spatalla racemosa* (4.31 ± 0.65 mg) and *Serruria inconspicua* (4.04 ± 1.27 mg) (Christian 2003)). Thus, the functional inability due to the reduced mandible gap could explain the Argentine ant's poor or null performance in the seed dispersal process previously carried out by some ant adapted seed species.

In a similar way, catching prey could be another altered process, and the size range of prey could be reduced according to the mandible gap reduction after invasion.

There are also other processes of environment transformation that could be altered by this functional inability. Ants are one of the major agents of soil bioturbation in semi-arid environments (Lobry de Bruyn & Conacher 1994a). Thus, as ants are size-selective in the material they excavate (Lobry de Bruyn & Conacher 1994a), the reduction of the mandible gap range could affect soil bioturbation and influence the formation of texture-contrast soils. Moreover, the size of ant biopores could also be altered, having important consequences on water infiltration and on soil erosion caused by water flowing overland (Lobry de Bruyn & Conacher 1994b).

Due to the small body size of *L. humile*, like most invader ants (McGlynn 1999), the roles of the bigger native species with a larger mandible gap are probably the less replaced activities due to this

functional inability. On the other hand, roles of native species with a similar or smaller body size (and hence mandible gap) than *L. humile* are unlikely to be non-replaced after the invasion due to this functional characteristic.

Furthermore, the correlation between mandible gap and body size in ants suggests that, as most of non-native ants are smaller than native ants (McGlynn 1999), the reduction in the ant mandible gap range could be the rule in most ant invasions after the native ants are displaced.

Other functional traits concerning ant mandibles, such as power and to a lesser extent velocity of the mandible closing movement, which are probably very diverse in an ant community, are unlikely to be entirely replaced but are very likely to be reduced after the invasion. These functional incapacities could also be a reason why various roles of native species are not replaced. Along the same lines, differences in other morphological and physiological body traits could imply other functional incapacities which could explain why some processes carried out by the displaced native species are not replaced by the invader.

The functional inability hypothesis, as an explanation for why the roles of displaced native species are not taken over by the invasive Argentine ant, could be applied to other invasive ants, and could help us understand some consequences of these invasions.

ACKNOWLEDGEMENTS

We thank S. Abril for assistance in collecting the ants. X. Espadaler provided useful comments that greatly improved a previous version of the manuscript. This study has been financed by the Spanish Ministry of Education and Science (CGL2004-05240-C02-02/BOS).

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