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Review

Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: A global survey

Szabolcs Lengyel[a,b,*], Aaron D. Gove[c], Andrew M. Latimer[d], Jonathan D. Majer[c], Robert R. Dunn[a,c]

[a] *Department of Biology, North Carolina State University, USA*
[b] *Department of Ecology, University of Debrecen, Hungary*
[b] *Centre for Ecosystem Diversity and Dynamics, Curtin University of Technology, Australia*
[d] *Department of Plant Sciences, University of California, Davis, USA*

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ABSTRACT

Seed dispersal is a fundamental life history trait in plants. Although the recent surge of interest in seed dispersal by ants (myrmecochory) has added greatly to knowledge on the ecology of seed dispersal and ant–plant mutualisms, myrmecochory also represents a unique opportunity to examine the links between seed dispersal and evolution in flowering plants. Here we review the taxonomic, phylogenetic and biogeographic distribution of myrmecochory in flowering plants. Myrmecochory is mediated by elaiosomes, i.e., lipid-rich seed appendages that attract ants and serve as rewards for dispersal. We surveyed the literature for evidence of elaiosomes in angiosperm plants to estimate the global prevalence of myrmecochory. We then searched the literature for phylogenetic reconstructions to identify myrmecochorous lineages and to estimate the minimum number of independent evolutionary origins of myrmecochory. We found that myrmecochory is present in at least 11 000 species or 4.5% of all species, in 334 genera or 2.5% of all genera and in 77 families or 17% of all families of angiosperm plants. We identified at least 101, but possibly up to 147, independent origins of myrmecochory. We estimated three or more origins in 13 families and found that at least half the genera are myrmecochorous in 10 families. Most myrmecochorous lineages were Australian, South African or northern temperate (Holarctic). A mapping of families containing myrmecochorous genera on a dated angiosperm supertree showed that myrmecochory has evolved in most of the major angiosperm lineages and that it is more frequent in younger families (crown group age <80 million years) than in older ones. We suggest that the relatively low physiological and energetic costs of producing an elaiosome and the consistent selective benefits of myrmecochory (dispersal, protection from seed predators and fire, safe and nutrient-rich microsites) explain the numerous evolutionary and developmental origins of myrmecochory in angiosperm plants, and we propose that elaiosomes thus provide one of the most dramatic examples of convergent evolution in biology.

Contents

Introduction

Seed dispersal is central to plant reproduction, recruitment, population genetics and ecology because it determines the movement of plant genes in space and, in many cases, in time. Seed dispersal links the usually sessile individuals to ecological

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[*] Corresponding author at. Department of Ecology, University of Debrecen, Egyetem tér 1., Debrecen 4032, Hungary. Tel.: +36 52 512 900/62357;
fax: +36 52 512 941.
E-mail address: szabolcslengyel@yahoo.com (S. Lengyel).

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processes operating at larger geographic scales such as long-distance dispersal, colonization, range expansion, isolation and speciation (Bullock and Nathan, 2008). Even subtle changes in traits that influence seed dispersal can therefore have far-reaching consequences on fitness and a multitude of other biological traits, and, thus, dispersal mode is one of the most fundamental life history traits in plants. Seed dispersal modes are usually classified into five broad types ('syndromes'): unaided (passive, ballistic, etc.), by wind (anemochory), by water (hydrochory), by vertebrates externally (e.g. on fur: exozoochory) or internally (passing through the gut: endozoochory), and by ants (myrmecochory) (van der Pijl, 1982; Vittoz and Engler, 2007). Although it is recognized that these modes differ dramatically in their benefits (and costs) to plants, the number of origins and global significance of different modes of seed dispersal remain poorly understood.

Myrmecochory is probably the least studied of the main seed dispersal syndromes (Bronstein et al., 2006). The signal adaptation for myrmecochory is the elaiosome, a lipid-rich appendage of the seed. 'Elaiosome' is a collective functional term (Warburg, 1892; Sernander, 1906) encompassing appendages or seed surface structures that are anatomically described more accurately as arils, arillodes, caruncles, funicles, strophioles, or sarcotesta. Elaiosomes develop in a multitude of pathways either from various seed tissues such as the chalaza, funiculus, hilum, mycropyle, and raphe–antiraphe (or some combination of these), or, less frequently, from fruit tissues such as the exocarp, receptacle, flower tube or bracts, perigonium, style or the spicule (Gorb and Gorb, 2003). The various tissue origins and developmental pathways apparently all serve the same main function (attracting ants, see below), suggesting that the various seed appendages termed elaiosomes have evolved convergently (Bronstein et al., 2006). These unusually diverse developmental origins, spread widely across angiosperm lineages, make elaiosomes a dramatic example of convergent evolution.

In all cases studied to date, the primary function of elaiosomes is to attract ants and elicit the transport of the seed to the nest by the ants. In the nest, ants consume the elaiosome or, more often, feed it to their larvae. The seeds are then deposited in garbage piles in the nest or outside the nest. Elaiosomes thus function as rewards for ants (Beattie, 1985; Edwards et al., 2006) in much the same way as fruits or berries serve as rewards for vertebrate dispersers. The first comprehensive treatment of myrmecochory was an elegant monograph by Sernander (1906). Work on myrmecochory was relatively slow until the 1970s, when the first Australian review was published by Berg (1975). A similar overview for South Africa was provided by Bond and Slingsby (1983). In his reviews focusing primarily on temperate North America and Eurasia, Beattie (1983, 1985) estimated that myrmecochory is globally present in at least 3000 plant species in 70 plant families. Interest in the ecology and evolution of myrmecochory has increased considerably since the early 1990s, with many studies focusing on the various benefits of the mutualism to plants and ants (reviewed in Gorb and Gorb, 2003; Giladi, 2006; Rico-Gray and Oliveira, 2007). Although the most recent estimates suggest that myrmecochory is present in more than 80 families (Giladi, 2006), there has been no systematic evaluation of the taxonomic, biogeographic and phylogenetic distribution of myrmecochory in angiosperm plants. Most of the frequently cited lists of ant-dispersed plants were published before the recent surge of interest or are restricted to certain biogeographic regions. There has been no global treatment of myrmecochory to date. General texts on seed dispersal, e.g., van der Pijl (1982), mention only exemplary taxa for dispersal syndromes. As a result, our knowledge on the taxonomic, geographic and phylogenetic distribution of myrmecochorous plants is fragmentary. It is conceivable that myrmecochory is far more restricted, or alternatively, has arisen many more times than suggested in previous taxonomic or regional accounts.

Here we present an updated, referenced, global list of myrmecochorous plant genera to evaluate the taxonomic, geographic and phylogenetic distribution and global significance of myrmecochory in angiosperm plants. Our goal is to estimate a minimum number of angiosperm species, genera and families of plants in which seeds are dispersed by ants, and a minimum number of evolutionary origins of myrmecochory. We then analyse the biogeographic and phylogenetic distribution of myrmecochory in angiosperm families.

Methods

We searched for information on myrmecochorous species and genera from reference books, regional floras, reviews, primary literature and other sources (e.g., studies of ant-mediated seed dispersal, taxonomic revisions; references are given in Table 1). We identified plants as myrmecochorous if their seeds had elaiosomes. In plants where elaiosome-bearing seeds are dispersed in two phases (diplochory; Vander Wall and Longland, 2004), we included those in which seeds are first dispersed unaided (e.g., passively or ballistically), but excluded those in which seeds are dispersed primarily by vertebrates and only secondarily by ants (e.g. genera *Carduus* and *Cirsium*). Although our dataset is not (and cannot be) exhaustive as dispersal mode is not documented for many plant species and genera, the literature sources included cover a large part of the seed dispersal literature, and we believe our original list of myrmecochorous genera is unlikely to increase dramatically. We estimate that our dataset contains information on at least 90% of the genera in which elaiosome-bearing seeds have been reported to date (at least 350 genera).

We next identified independent evolutionary origins of myrmecochory using recent phylogenetic reconstructions. We searched for phylogenetic trees based on molecular data for each myrmecochorous genus on our list. We used well-sampled trees with a resolution that was adequate to designate origins, i.e., family-level trees for smaller families and tribe-level trees for genera in larger families. For a few large genera, we also used section-level subgeneric trees. References to the phylogenies used are given in Table 1.

Due to a lack of a comprehensive genus-level angiosperm supertree detailed enough for our purposes, it was not possible to map myrmecochory directly onto one phylogenetic tree to identify independent origins. Instead, we used information on the sister group and the next higher node on the trees for each myrmecochorous genus. We identified an independent origin of myrmecochory when (i) the sister group of the myrmecochorous genus/lineage was not reported in the literature sources as myrmecochorous, and (ii) the outgroup for the monophyletic group that included the myrmecochorous genus and its sister group was also not reported as myrmecochorous. This method was appropriate for estimating origins, especially in cases when myrmecochory was found only in one genus within a wider lineage, which involved 66% of the origins found ($n = 147$). In a few cases, it was also possible to identify origins within a genus (i.e., among species of *Erythronium*, *Globba*, *Gossypium*, Table 1).

In ambiguous cases, especially in large genera/lineages, we made special efforts to avoid overestimating the number of origins. For some large genera in which myrmecochory has been reported, dispersal mode was not known for most species or no well-resolved genus-level or subgeneric phylogeny could be found. In these cases, it was not possible to precisely identify origins and we identified only one evolutionary origin for

Table 1
Myrmecochorous genera in monophyletic lineages, with biogeographic distribution and diversity. Boldface type indicates lineages in which more than 50% of all species are myrmecochorous ($n = 101$ lineages).

No	Family	Genera with myrmecochory	Myrmecochory reference	Geographic distribution[a]	No. species[b]	Phylogeny reference
1	Achariaceae	*Acharia*	Steyn et al. (2002)	PT	1	N/A
2	**Aizoaceae**	***Gunniopsis***	Hassan et al. (2005)	**AU**	**15**	Klak et al. (2003)
3	**Aizoaceae**	***Sesuvium*, *Trianthema***	Hassan et al. (2005)	**WW**	**29**	Klak et al. (2003)
4	Amaranthaceae	*Sclerolaena*, *Dissocarpus*, *Maireana*	Berg (1975), Davidson and Morton, (1981)	AU	125	Kadereit et al. (2003)
5	**Amaryllidaceae**	***Leucojum*, *Galanthus*, *Narcissus*, *Sternbergia*, *Vagaria*, *Lapiedra*, *Hannonia*, *Pancratium***	Berg (1975), van der Pijl (1982), Dahlgren et al. (1985)	**HA**	**289**	Meerow et al. (2006)
6	**Apiaceae**	***Platysace*, *Xanthosia*, *Actinotus***	Berg (1975), Westoby et al. (1990)	**AU**	**68**	Chandler and Plunkett (2004)
7	Apocynaceae	*Hoya*, *Dischidia*, *Absolmsia*, *Micholitzia*, *Madangia*	Beattie (1983)	IM	284	Wanntorp et al. (2006)
8	Araceae	*Philodendron*, *Anthurium*	Beattie (1983)	NT	1524	N/A
9	**Aristolochiaceae**	***Asarum*, *Saruma***	Berg (1975), Beattie and Culver (1981), Gonzalez and Rudall (2003), Gorb and Gorb (2003)	**PA**	**86**	Kelly (1998), Neinhuis et al. (2005)
10	**Asteraceae**	***Amberboa*, *Volutaria*, *Mantisalca*, *Cyanopsis*, *Goniocaulon*, *Plagiobasis*, *Karvandarina*, *Russowia*, *Tricholepis***	Beattie (1983)	**PA**	**107**	Petit (1997), Garcia-Jacas et al. (2001), Martins and Hellwig (2005)
11	Asteraceae	*Carduus*	Beattie (1983), Andersen (1993)	PA	90	N/A
12	**Asteraceae**	***Centaurea***	van der Pijl (1982), Beattie (1983), Andersen (1993), Wagenitz and Hellwig (1996), Melendo et al. (2003)	**PA**	**383**	Garcia-Jacas et al. (2001)
13	**Asteraceae**	***Chrysogonum***	Beattie (1983)	**NA**	**18**	Clevinger and Panero (2000)
14	Asteraceae	*Cirsium*	Beattie (1983), Andersen (1993)	WW	250	Garcia-Jacas et al. (2002)
15	**Asteraceae**	***Cullumia***	Bond and Slingsby (1983)	**PT**	**26**	Karis (2006)
16	**Asteraceae**	***Dymondia***	Bond and Slingsby (1983)	**PT**	**1**	McKenzie et al. (2006)
17	**Asteraceae**	***Euryops***	Bond and Slingsby (1983)	**PT**	**100**	Knox and Palmer (1995)
18	**Asteraceae**	***Galactites***	Beattie (1983)	**PA**	**12**	Garcia-Jacas et al. (2002)
19	**Asteraceae**	***Osmitopsis***	Bond and Slingsby (1983)	**PT**	**11**	Watson et al. (2000)
20	**Asteraceae**	***Osteospermum***	Bond and Slingsby (1983)	**OW**	**153**	Watson et al. (2000)
21	**Asteraceae**	***Wedelia***	Nesom (1981), Bond and Slingsby (1983)	**NA**	**100**	Panero et al. (1999)
22	Balanophoraceae	*Mystropetalon*	Takhtadzian, (1997)	PT	1	N/A
23	**Berberidaceae**	***Epimedium*, *Vancouveria*, *Bongardia***	Stebbins (1971), Berg (1972), Mabberley (2008)	**HA**	**67**	Liu et al. (2002), Kim et al. (2004)
24	**Berberidaceae**	***Gymnospermium***	Beattie (1983)	**PA**	**12**	Kim and Jansen (1998), Liu et al. (2002), Kim et al. (2004)
25	**Boraginaceae**	***Nemophila***	Stebbins (1971), van der Pijl (1982), Beattie (1983), Chuang and Constance (1992)	**NA**	**11**	Ferguson (1998)
26	Boraginaceae	*Omphalodes*	Gorb and Gorb (2003)	HA	30	Langstrom and Chase (2002)
27	Boraginaceae	*Pentaglottis*, *Borago*, *Symphytum*, *Nonea*, *Elizaldia*, *Paraskevia*, *Pulmonaria*, *Brunnera*, *Trachystemon*, *Phyllocara*, *Hormuziaka*, *Anchusa*	Beattie (1983), Bacchetta et al. (2008)	OW	170	Langstrom and Chase (2002), Hilger et al. (2004)
28	Bromeliaceae	*Aechmea*	Beattie (1983)	NT	185	Bremer (2002)
29	Bromeliaceae	*Nidularium*	Beattie (1983)	NT	50	Givnish et al. (2005)
30	**Bruniaceae**	***Audouinia capitata***	Bond and Slingsby (1983)	**PT**	**1**	Quint and Classen-Bockhoff, (2006)
31	**Bruniaceae**	***Lonchostoma***	Bond and Slingsby (1983)	**PT**	**10**	Quint and Classen-Bockhoff (2006)
32	**Buxaceae**	***Buxus*, *Notobuxus***	Beattie (1983), Kohler (2007)	**WW**	**90**	von Balthazar et al. (2000)
33	**Cactaceae**	***Aztekium***	Van Rheede and Rooyen (1999)	**NA**	**2**	Nyffeler (2002)
34	Cactaceae	*Blossfeldia*, *Frailea*, *Setiechinopsis*	Beattie (1983), Mabberley, (2008)	NT	11	Nyffeler (2002)
35	**Cactaceae**	***Gymnocalycium***	Van Rheede and Rooyen (1999)	**NA**	**70**	Nyffeler (2002)
36	Campanulaceae	*Phyteuma*	Beattie (1983)	PA	40	Roquet et al. (2008)
37	**Caricaceae**	***Carica***	Beattie (1983)	**NT**	**23**	Rodman et al. (1996)
38	Caryophyllaceae	*Arenaria*	van der Pijl (1982)	HA	215	Fior et al. (2006)
39	**Caryophyllaceae**	***Moehringia***	van der Pijl (1982), Beattie (1983), Minuto et al. (2006)	**PA**	**31**	Fior and Karis (2007)
40	Celastraceae	*Psammomoya*	Berg (1975)	AU	2	N/A
41	Cleomaceae	*Cleome*, *Podandrogyne*	Steentoft (1988)	HT	276	N/A
42	**Colchicaceae**	***Colchicum*, *Androcymbium*, *Merendera*, *Bulbocodium*, *Hexacyrtis*, *Ornithoglossum*, *Sandersonia*, *Gloriosa*,**	Berg (1975), Westoby et al. (1990), Nordenstam (1998), Gorb and Gorb (2003),	**WW**	**245**	Vinnersten and Reeves (2003)

Table 1 (*continued*)

No	Family	Genera with myrmecochory	Myrmecochory reference	Geographic distribution[a]	No. species[b]	Phylogeny reference
		Baeometra, ***Neodregea***, ***Wurmbea***, ***Camptorrhiza***, ***Iphigenia***, ***Schelhammera***, ***Tripladenia***, ***Disporum***, ***Uvularia***, ***Kuntheria***, ***Burchardia***	Membrives et al. (2003), Dunn et al. (2007)			
43	Costaceae	*Monocostus, Dimerocostus, Tapeinochilos, Cheilocostus, Costus, Paracostus, Chamaecostus*	Specht and Stevenson (2006)	PnT	73	Kress et al. (2001)
44	Cyperaceae	*Lepidosperma, Dichromena, Carex*	Beattie (1983), Westoby et al. (1990), Gorb and Gorb (2003), Mabberley (2008)	PT	57	N/A
45	**Dasypogonaceae**	***Dasypogon***	Dunn et al. (2007)	**AU**	**4**	Givnish et al. (2005)
46	**Dilleniaceae**	***Hibbertia***, ***Adrastaea***, ***Pachynema***	Berg (1975), Westoby et al. (1990)	**AU**	**124**	Horn (2006)
47	**Dipsacaceae**	***Knautia***	Sernander (1906), Mayer and Svoma (1998), Gorb and Gorb (2003), Mabberley (2008)	**PA**	**60**	Caputo et al. (2004)
48	**Dipsacaceae**	***Scabiosa***	Beattie (1983)	**PA**	**80**	Caputo et al. (2004)
49	**Elaeocarpaceae**	***Tetratheca***	Berg (1975), Westoby et al. (1990), Harrington and Driver, 1995), Boesewinkel (1999)	**AU**	**39**	Boesewinkel (1999), Crayn et al. (2006)
50	Ericaceae	*Leucopogon, Brachyloma, Monotoca*	Beattie (1983), Westoby et al. (1990)	IM	246	N/A
51	Euphorbiaceae	*Acalypha*	Berg (1975), Beattie (1983), Westoby et al. (1990)	PnT	430	N/A
52	**Euphorbiaceae**	***Crotonsubg.Astraea***	Berry et al. (2005)	**NT**	**10**	Berry et al. (2005)
53	**Euphorbiaceae**	***Bertya***, ***Beyeria***, ***Ricinocarpos***	Berg (1975), Beattie (1983), Westoby et al. (1990)	**AU**	**45**	Wurdack et al. (2005)
54	**Euphorbiaceae**	***Claoxylon***	Westoby et al. (1990)	**OW**	**75**	Wurdack et al. (2005), Kabouw et al. (2008)
55	**Euphorbiaceae**	***Conceveiba***	Tokuoka and Tobe (2003)	**NT**	**18**	Wurdack et al. (2005)
56	**Euphorbiaceae**	***Euphorbia***, ***Chamaesyce***, ***Synadenium***, ***Monadenium***, ***Pedilanthus***, ***Neoguillauminia***, ***Calycopeplus***, ***Anthosterna***, ***Dichostemma***	Berg (1975), van der Pijl (1982), Webster (1994), Tokuoka and Tobe (2002)	**WW**	**1846**	Wurdack et al. (2005)
57	Euphorbiaceae	*Jatropha*	Berg (1975)	NT	175	N/A
58	Euphorbiaceae	*Mercurialis*	Gorb and Gorb (2003), Mabberley (2008)	PA	8	Wurdack et al. (2005)
59	**Euphorbiaceae**	***Monotaxis***, ***Adriana***, ***Amperea***	Berg (1975), Tokuoka and Tobe (2003)	**PT**	**31**	Wurdack et al. (2005)
60	**Euphorbiaceae**	***Pera***, ***Clutia***, ***Chaetocarpus***	Bond and Slingsby (1983), Tokuoka and Tobe (2003), Wurdack et al. (2005)	**PnT**	**108**	Wurdack et al. (2005)
61	**Euphorbiaceae**	***Seidelia***	Tokuoka and Tobe (2003)	**PT**	**4**	Wurdack et al. (2005)
62	Fabaceae	*Acacia*	Berg (1975), Davidson and Morton (1984)	HT	1450	N/A
63	**Fabaceae**	***Cytisus***	Pemberton and Irving (1990), Cristofolini and Troia (2006)	**PA**	**60**	Cubas et al. (2002), Pardo et al. (2004)
64	**Fabaceae**	***Daviesia***, ***Viminaria***, ***Erichsenia***, ***Goodia***, ***Bossiaea***, ***Platylobium***, ***Muelleranthus***, ***Ptychosema***, ***Aenictophyton***	Berg (1975), Westoby et al. (1990), de Kok and West (2002)	**AU**	**287**	Orthia et al. (2005)
65	**Fabaceae**	***Hardenbergia***, ***Kennedia***	Berg, (1975), Milewski and Bond (1982), Hughes and Westoby, (1992)	**AU**	**59**	Kajita et al. (2001)
66	**Fabaceae**	***Hovea***, ***Templetonia***, ***Lamprolobium***	Berg (1975), Westoby et al. (1990)	**AU**	**52**	Thompson et al. (2001)
67	Fabaceae	*Petalostylis*	Berg (1975)	AU	2	N/A
68	**Fabaceae**	***Pultenaea***(=***Mirbelia s.l.***)	Berg (1975), Westoby et al. (1990)	**AU**	**470**	Crisp et al. (2004), Orthia et al. (2005)
69	**Fabaceae**	***Ulex***, ***Stauracanthus***	Sernander (1906), van der Pijl (1982), Melendo et al. (2003)	**PA**	**21**	Pardo et al. (2004)
70	**Gesneriaceae**	***Chrysothemis***	Lu and Mesler (1981), Mabberley (2008)	**NT**	**12**	Zimmer et al. (2002)
71	**Gesneriaceae**	***Codonanthe***	Beattie (1983)	**NT**	**34**	Zimmer et al. (2002)
72	**Goodeniaceae**	***Dampiera***	Berg (1975), Westoby et al. (1990)	**AU**	**66**	Gustafsson et al. (1996
73	**Goodeniaceae**	***Goodenia***, ***Scaevola***, ***Verreauxia***, ***Velleia***, ***Coopernookia***	Berg (1975), Milewski and Bond (1982), Westoby et al. (1990)	**AU**	**350**	Gustafsson et al. (1996
74	**Gyrostemonaceae**	***Gyrostemon***, ***Codonocarpus***, ***Walteranthus***, ***Tersonia***	Berg (1975)	**AU**	**18**	Hufford (1996), Rodman et al. (1996)
75	**Hemerocallidaceae**	***Caesia***, ***Hensmania***, ***Johnsonia***, ***Arnocrinum***	Berg, (1975), Dahlgren et al. (1985), Westoby et al. (1990)	**AU**	**58**	Givnish et al. (2005)

Table 1 (*continued*)

No	Family	Genera with myrmecochory	Myrmecochory reference	Geographic distribution[a]	No. species[b]	Phylogeny reference
76	**Hyacinthaceae**	***Lachenalia***	Beattie (1983)	**PT**	**110**	Pfosser et al. (2003)
77	Hyacinthaceae	*Ornithogalum*	Gorb and Gorb (2003)	OW	200	Pfosser and Speta (1999)
78	Hyacinthaceae	*Puschkinia*	Gorb and Gorb (2003)	PA	4	Pfosser and Speta (1999)
79	**Hyacinthaceae**	***Scilla*, *Chionodoxa***	van der Pijl (1982)	**PA**	**40**	Pfosser and Speta (1999)
80	Hypoxidaceae	*Curculigo*	Dahlgren et al. (1985)	HT	20	N/A
81	Iridaceae	*Iris*	Goldblatt et al. (1998), Wilson (2004), Davies et al. (2005)	PA	280	N/A
82	Iridaceae	*Patersonia*	Westoby et al. (1990)	AU	22	N/A
83	**Iridaceae**	***Witsenia*, *Klattia***	Manning and Goldblatt (1991)	**PT**	**4**	Chase et al. (2000), Davies et al. (2004b)
84	**Juncaceae**	***Luzula***	Berg (1975), Beattie and Culver (1981), Andersen (1993)	**WW**	**115**	Bremer (2002)
85	**Lamiaceae**	***Ajuga***	Berg (1975), Hsi-wen and Hedge (1994)	**OW**	**50**	Wagstaff et al. (1998)
86	Lamiaceae	*Ballota*	Bresinsky (1963)	PA	30	N/A
87	**Lamiaceae**	***Lamium***	van der Pijl (1982 (Beattie (1983)	**HA**	**190**	Wagstaff et al. (1998)
88	**Lamiaceae**	***Rosmarinus***	Beattie (1983) (Hsi-wen and Hedge (1994)	**PA**	**22**	Walker et al. (2004)
89	**Lamiaceae**	***Teucrium***	Beattie (1983)	**WW**	**250**	Wagstaff et al. (1998)
90	Laxmanniaceae	*Lomandra*	Berg (1975) (Westoby et al. (1990)	AU	50	N/A
91	**Liliaceae**	***Erythroniumspp.* - Eurasian + Eastern North American lineage**	Dahlgren et al. (1985) (Patterson and Givnish (2002), Guitian et al. (2003)	**HA**	**8**	Allen et al. (2003)
92	**Liliaceae**	***Gagea***	Dahlgren et al. (1985), Patterson and Givnish (2002)	**PA**	**91**	Patterson and Givnish (2002), Peterson et al. (2004), Givnish et al. (2005)
93	**Liliaceae**	***Scoliopus***	Beattie (1983), Utech (1992), Patterson and Givnish (2002)	**NA**	**5**	Patterson and Givnish (2002)
94	**Limeaceae**	***Macarthuria***	Berg (1975), Steyn et al. (2002)	**AU**	**12**	Stevens (2008)
95	**Malvaceae**	***Gossypium sect. Grandicalyx* (‘genome K’lineage)**	Berg (1975), Westoby et al. (1990)	**AU**	**12**	Seelanan et al. (1999), Liu et al. (2001)
96	**Malvaceae**	***Lasiopetalum*, *Hannafordia*, *Maxwellia*, *Thomasia*, *Guichenotia*, *Commersonia*, *Rulingia*, *Keraudrenia*, *Seringia***	Berg (1975), Westoby et al. (1990)	**AU**	**167**	Whitlock et al. (2001)
97	Malvaceae	*Sterculia*	Gorb and Gorb (2003)	PnT	150	Wilkie et al. (2006)
98	Marantaceae	*Calathea*	Horvitz and Beattie (1980), Beattie (1983)	NT	257	N/A
99	**Melanthiaceae**	***Trillium***	Beattie and Culver (1981), Beattie (1983), Dahlgren et al. (1985)	**HA**	**38**	Farmer and Schilling (2002)
100	Menyanthaceae	*Villarsia*	Mabberley (2008)	AU	14	N/A
101	Myrtaceae	*Myrtus*	Ciccarelli et al. (2005)	PA	2	N/A
102	**Papaveraceae**	***Corydalis*, *Dicentra*, *Adlumia*, *Dactylocapnos*, *Rupicapnos*, *Pseudofumaria*, *Cysticapnos***	Beattie and Culver (1981), Bond and Slingsby (1983)	**HA**	**384**	Liden et al. (1997)
103	Papaveraceae	*Dendromecon*	Beattie (1983)	NA	2	N/A
104	**Papaveraceae**	***Sanguinaria*, *Chelidonium*, *Eomecon*, *Macleaya*, *Bocconia*, *Hylomecon*, *Stylophorum***	Beattie and Culver (1981), van der Pijl (1982), Beattie (1983), Gorb and Gorb (2003)	**HA**	**99**	Blattner and Kadereit (1999)
105	**Penaeaceae**	***Penaea*, *Brachysiphon*, *Endonema*, *Saltera*, *Stylapterus***	Bond and Slingsby (1983)	**PT**	**23**	Rutschmann et al. (2004), Sytsma et al. (2004), Rutschmann et al. (2007)
106	**Phyllanthaceae**	***Breynia***	Berg (1975), Westoby et al. (1990)	**IM**	**35**	Kathriarachchi et al. (2006)
107	**Picrodendraceae**	***Picrodendron*, *Micrantheum*, *Oldfieldia*, *Stachystemon*, *Aristogeitonia*, *Scagea***	Berg (1975), Westoby et al. (1990), Webster (1994), Wurdack et al. (2005), Sutter et al. (2006)	**OW**	**82**	Tokuoka and Tobe (2006), **Wurdack unpubl. from**Wurdack et al. (2005)
108	Piperaceae	*Peperomia*	Beattie (1983)	PnT	1600	
109	**Poaceae**	***Chionachne***	Mabberley (2008)	**IM**	**9**	Mathews et al. (2002)
110	Poaceae	*Cryptochloa*, *Rottboelia*, *Sieglingia*, *Triodia*	Beattie (1983), Mabberley (2008)	PnT	79	N/A
111	**Poaceae**	***Melica***	Stebbins (1971), van der Pijl (1982), Beattie (1983)	**HA**	**80**	Barker et al. (2001)
112	**Polygalaceae**	***Polygala*, *Bredemeyera*, *Muraltia*, *Nylandtia*, *Heterosamara*, *Salomonia*, *Comesperma*, *Monnina*, *Securidaca***	Berg (1975), Beattie (1983), Westoby et al. (1990), Forest et al. (2007)	**WW**	**910**	Forest et al. (2007)
113	**Portulacaceae**	***Claytonia*, *Montia***	Beattie and Culver (1981), Beattie (1983), Mabberley (2008)	**NA**	**41**	Applequist and Wallace (2001), Nyffeler (2007)
114	**Primulaceae**	***Cyclamen***	Beattie (1983), Mabberley (2008)	**PA**	**20**	Anderberg et al. (2000)

Table 1 (*continued*)

No	Family	Genera with myrmecochory	Myrmecochory reference	Geographic distribution[a]	No. species[b]	Phylogeny reference
115	Primulaceae	*Primula*	Stebbins (1971), van der Pijl (1982), Beattie (1983)	HA	430	N/A
116	**Proteaceae**	***Grevillea***	Berg (1975), Westoby et al. (1990), Auld and Denham (1999)	**AU**	**260**	Hoot and Douglas (1998), Barker et al. (2007)
117	**Proteaceae**	***Mimetes*, *Orothamnus*, *Leucospermum*, *Diastella*, *Sorocephalus*, *Spatalla*, *Paranomus*, *Vexatorella*, *Serruria*, *Leucadendron*, *Adenanthos***	Berg (1975), Protea Atlas Project (2007)	**PT**	**308**	Hoot and Douglas (1998), Barker et al. (2002), Barker et al. (2007)
118	**Ranunculaceae**	***Anemone***	Beattie and Culver (1981), van der Pijl (1982), Beattie (1983)	**HA**	**120**	Johansson and Jansen (1993)
119	**Ranunculaceae**	***Delphinium***	Beattie (1983)	**HA**	**250**	Johansson and Jansen (1993)
120	**Ranunculaceae**	***Ficaria***	Weiss (1908), Gorb and Gorb (2003)	**PA**	**5**	Paun et al. (2005)
121	**Ranunculaceae**	***Helleborus***	van der Pijl (1982), Beattie (1983), Manzaneda et al. (2007), Mabberley (2008)	**HA**	**20**	Johansson and Jansen (1993)
122	Ranunculaceae	*Hepatica*	Beattie and Culver (1981), van der Pijl (1982), Beattie (1983)	HA	20	N/A
123	**Ranunculaceae**	***Trollius*, *Adonis***	Beattie (1983)	**HA**	**55**	Johansson and Jansen (1993)
124	Resedaceae	*Reseda*	Berg (1975), Peters et al. (2003)	OW	65	Martin-Bravo et al. (2007)
125	**Restionaceae**	***Restio***	Berg (1975), Westoby et al. (1990)	**PT**	**88**	Bremer (2002), Moline and Linder (2005)
126	**Rhamnaceae**	***Phylica*, *Trichocephalus***	Bond and Slingsby (1983)	**PT**	**151**	Richardson et al. (2004)
127	**Rhamnaceae**	***Pomaderris*, *Spyridium*, *Trymalium*, *Siegfriedia*, *Cryptandra*, *Stenanthemum***	Berg (1975), Milewski and Bond (1982), Westoby et al. (1990; Boesewinkel (1999)	**AU**	**172**	Richardson et al. (2004)
128	Rosaceae	*Aremonia*	Mabberley (2008)	PA	1	N/A
129	Rosaceae	*Potentilla*	Gorb and Gorb (2003), Guillen et al. (2005)	HA	330	N/A
130	**Rubiaceae**	***Opercularia*, *Pomax***	Westoby et al. (1990)	**AU**	**19**	Andersson and Rova (1999), Anderson et al. (2001)
131	Rubiaceae	*Theligonium*	Mabberley (2008)	PA	4	N/A
132	**Rutaceae**	***Asterolasia***	Auld (2001)	**AU**	**21**	Mole et al. (2004)
133	Rutaceae	*Brombya*	Mabberley (2008)	AU	2	N/A
134	Rutaceae	*Medicosma*	Mabberley (2008)	AU	25	N/A
135	**Rutaceae**	***Phebalium*, *Microcybe***	Berg (1975), Westoby et al. (1990), Auld (2001)	**AU**	**31**	Mole et al. (2004)
136	**Santalaceae**	***Thesium*, *Osyridicarpos***	Sernander (1906), Pilger (1935)	**OW**	**177**	Der and Nickrent (2008)
137	**Sapindaceae**	***Cardiospermum***	Reynolds (1981)	**NT**	**61**	Harrington et al. (2005)
138	**Sapindaceae**	***Dodonaea***	Berg (1975), Hughes and Westoby (1990), Jurado et al. (1991)	**PnT**	**70**	Harrington et al. (2005)
139	**Scrophulariaceae**	***Melampyrum***	Weiss (1908), Stebbins (1971), van der Pijl (1982), Beattie (1983), Fischer (2004)	**PA**	**35**	Wolfe et al. (2005), Bennett and Mathews (2006)
140	**Scrophulariaceae**	***Pedicularis***	Stebbins (1971), van der Pijl (1982), Beattie (1983), Fischer (2004)	**HA**	**350**	Wolfe et al. (2005), Bennett and Mathews (2006)
141	**Solanaceae**	***Datura***	Beattie (1983)	**NA**	**11**	Olmstead et al. (2008)
142	Solanaceae	*Markea*	Beattie (1983)	NT	42	Olmstead et al. (2008)
143	Stemonaceae	*Stemona*, *Pentastemona*, *Croomia*, *Stichoneuron*	Dahlgren et al. (1985), Gorb and Gorb (2003), Rudall and Bateman (2006)	IM	27	Caddick et al. (2002)
144	**Tecophilaeaceae**	***Cyanastrum***	Beattie (1983)	**PT**	**7**	Chase et al. (2000)
145	**Turneraceae**	***Turnera***	Schappert and Shore (2000), Cuautle et al. (2005)	**NT**	**100**	Truyens et al. (2005)
146	**Urticaceae**	***Parietaria***	Gorb and Gorb (2003), Mabberley (2008)	**WW**	**10**	Sytsma et al. (2002)
147	**Valerianaceae**	***Fedia***	Beattie (1983)	**PA**	**3**	Hidalgo et al. (2004)
148	Violaceae	*Rinorea*	Gorb and Gorb (2003)	PnT	165	N/A
149	**Violaceae**	***Viola*, *Hybanthus***	Berg (1975), Beattie and Culver (1981)), van der Pijl (1982)	**WW**	**400**	Tokuoka (2008)
150	Zingiberaceae	*Globba sect. Globba*, *Sempervirens*, *Nudae*	Pfeiffer et al. (2004), Zhou et al. (2007)	IM	80	N/A
151	Zingiberaceae	*Roscoea*, *Renealmia*	Nordhagen (1932), Mabberley (2008)	PnT	92	N/A
152	**Zygophyllaceae**	***Zygophyllum*, *Augea*, *Fagonia***	Bond and Slingsby (1983)	**WW**	**120**	Sheahan and Chase (2000), Beier et al. (2003)

[a] Biogeographic distribution types: AU—Australian, IM—Indo-Malayan, NA—Nearctic, NT—Neotropical, PA—Palearctic, PT—Paleotropical/Ethiopian (African, mostly Cape Floristic Region); complex distribution types: HA—Holarctic (NA+PA), NW—New World (NA+NT), OW—Old World (PT+PA+AU), PnT—Pan-tropical (mostly PT+NT+IM+AU), HT—Holotropical (PT+NT+AU), WW—Worldwide.

[b] Number of all species in the lineage.

Table 2
Plant families (n=22) in which myrmecochory has been reported in at least 20% of all genera or is estimated in at least 50% of all species.

Family	Myrmecochory			Number of all[a]		Myrmecochory (%)	
	Origins	Genera	Species	Genera	Species	Genera	Species
Aristolochiaceae	1	2	86	4	480	50	18
Berberidaceae	2	4	79	14	701	29	11
Buxaceae	1	2	90	4	120	50	75
Caricaceae	1	1	23	5	34	20	68
Cleomaceae	1	2	276	10	300	20	92
Colchicaceae	1	19	245	19	245	100	100
Costaceae	1	7	73	7	110	100	66
Dasypogonaceae	1	1	4	4	16	25	25
Dilleniaceae	1	3	124	12	300	25	41
Goodeniaceae	2	6	416	12	440	50	95
Gyrostemonaceae	1	5	18	5	18	100	100
Hemerocallidaceae	1	4	58	19	85	21	68
Laxmanniaceae	1	1	50	5	65	20	77
Limeaceae	1	1	12	2	23	50	52
Papaveraceae	3	15	485	41	760	37	64
Penaeaceae	1	7	23	7	23	100	100
Picrodendraceae	1	7	82	27	85	26	96
Polygalaceae	1	9	910	18	1045	50	87
Primulaceae	2	2	450	9	900	22	50
Resedaceae	1	1	65	3	85	33	76
Stemonaceae	1	4	27	4	27	100	100
Violaceae	2	2	565	20	800	10	71

[a] Data are from Stevens (2008).

myrmecochory per genus or lineage (given that myrmecochory was not present in the sister group or the outgroup). When phylogenetic trees were not available for one or more myrmecochorous genus in a family, we assumed one independent origin of myrmecochory for each family, regardless of the number of myrmecochorous genera. In four cases, the position of a genus on a tree could not be reliably resolved, and we did not count origins for these genera.

Data on the number of species in genera were taken primarily from the phylogenetic studies. When these data were not available, we used information from the Angiosperm Phylogeny Group website (APG, version 9; Stevens, 2008) or from Mabberley (2008). We took two measures to avoid overestimating the number of myrmecochorous species. First, when data on species numbers from the different sources differed considerably (> 10%), we took the minimum number to estimate the number of species. Second, we included diversity data in our estimate only from those genera in which more than 50% of the species for which mode of seed dispersal was known were myrmecochorous. Similarly, we included lineages comprising of several genera only when all genera within the lineage were myrmecochorous based on the 50% rule. Better documentation of the seeds of species within poorly studied genera may shift some genera above or below this cut-off. However, such changes seem unlikely to have a systematic bias because in most genera, all species of known dispersal mode were myrmecochorous.

Data on the geographical distribution of genera were collected primarily from the phylogenetic studies, from the Angiosperm Phylogeny Group website (Stevens, 2008) or from Mabberley (2008). To classify groups into biogeographical distribution types, we primarily used Wallace's six biogeographical regions (Palearctic, Nearctic, Paleotropical, Neotropical, Indo-Malayan, Australian) but designated other categories to better characterise more complex distributions (Holarctic, Holotropical, Old World, New World, Pan-tropical, Worldwide).

We used a dated phylogenetic supertree of angiosperm families (Davies et al., 2004a) to study the phylogenetic distribution of families with myrmecochorous genera. The consensus tree was downloaded from the Phylomatic Project website (www.phylodiversity.net/phylomatic) and was re-drawn with highlighting families containing myrmecochorous genera using software Mesquite (Maddison and Maddison, 2008). The branch lengths in this tree represent maximum ages for the terminals (families); therefore, they should be interpreted as the age of the crown group for each family.

Results

Overall, we found evidence of myrmecochory in 334 genera in 77 families (Table 1). The number of species in genera in which all or most (> 50%) species are myrmecochorous (indicated in bold in Table 1) is estimated at 11 532, distributed in 101 independent origins of myrmecochory in 55 angiosperm families. When all genera in which myrmecochory has been reported are considered (all lineages from Table 1), the number of species is 23 030, and the minimum number of origins is 147.

Families with more than three independent origins were Asteraceae (12), Euphorbiaceae (10), Fabaceae (7), Ranunculaceae (6), Hyacinthaceae and Lamiaceae (4 each). Seven families had three origins (Cactaceae, Iridaceae, Liliaceae, Malvaceae, Papaveraceae, Poaceae, Rutaceae). Two origins were found in 19 of the families and one origin was found in 45 of the families.

In several families, myrmecochorous seed dispersal appears to be the norm. Myrmecochorous species are found in all or nearly all the genera of Colchicaceae (total 19 genera), Costaceae and Penaeaceae (7 each), Gyrostemonaceae (5) and Stemonaceae (4) (Table 2). Approximately half of the genera are myrmecochorous in Polygalaceae (18), Goodeniaceae (12), Aristolochiaceae and Buxaceae (4 each), and Limeaceae (2). Besides these families, the estimated proportion of myrmecochorous species is also high (> 70%) in Cleomaceae, Laxmanniaceae, Picrodendraceae, Resedaceae and Violaceae.

The families containing myrmecochorous genera are represented in all major lineages in the angiosperm phylogeny (Fig. 1). Although myrmecochory is present in several families that

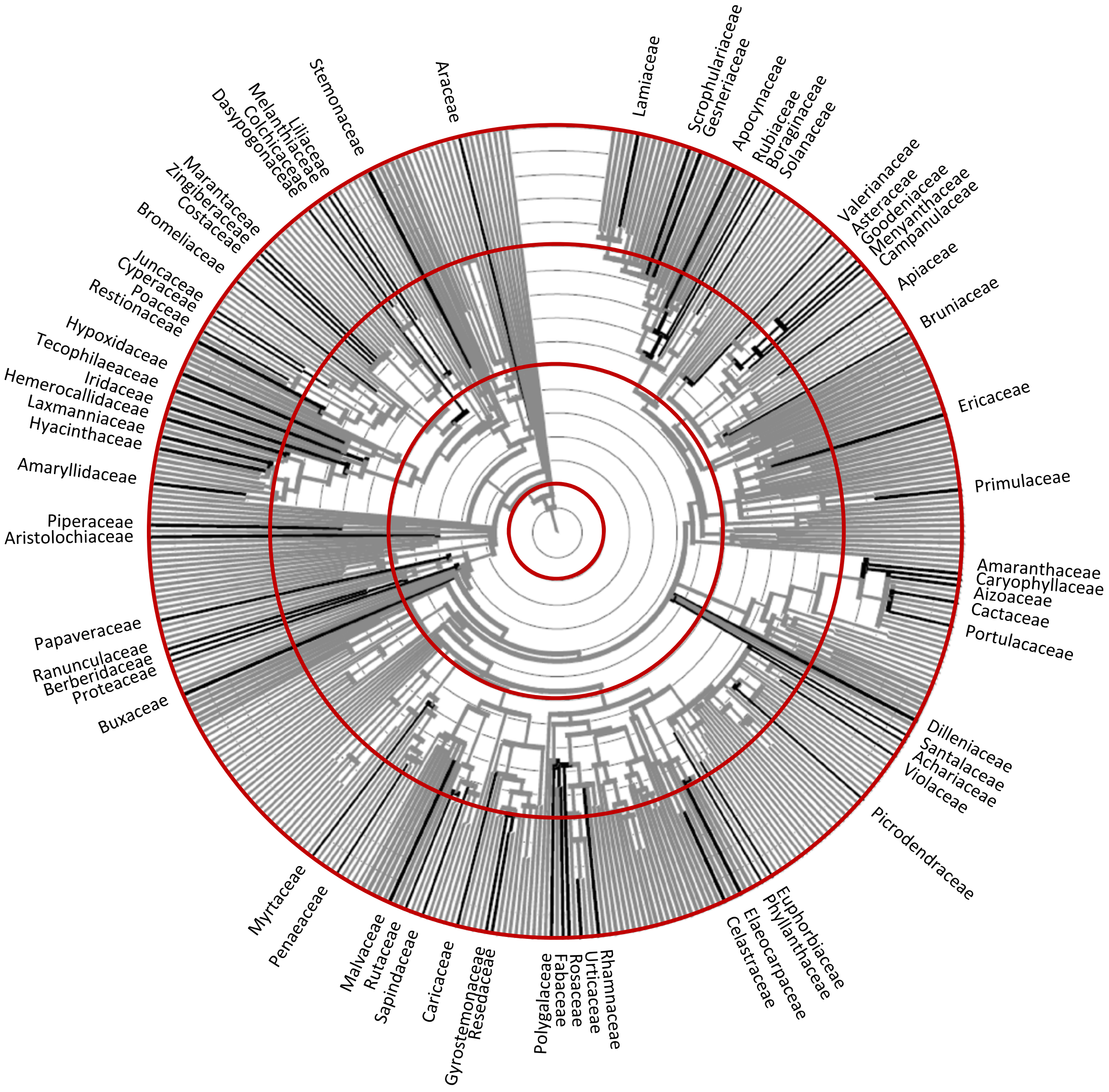

Fig. 1. A phylogeny of 410 angiosperm families using the dated topology of Davies et al. (2004a), re-drawn using program Mesquite (Maddison and Maddison, 2008). Families containing one or more myrmecochorous genera (n=71 families) are marked in black and shown by name (names of other families are omitted for clarity). Six families with myrmecochorous genera are omitted due to their unresolved position in the phylogeny. Time intervals are 10 million years (thin circles) and 50 million years (thick circles).

diverged early (ca. 100 million years ago, MYA) in angiosperm phylogeny, most families in which myrmecochory is found originated at or after 70–80 MYA (Fig. 1). It is important to emphasize that these time periods do not necessarily represent the dates of the evolutionary transitions to myrmecochory. Rather, the time periods indicate the maximum ages of families in which myrmecochory has later evolved in at least one genus.

The Australian and the Palearctic/Nearctic biogeographic regions emerged as main centers of myrmecochory (Australian: 29 origins and 78 genera, Holarctic combined: 48/86) (Fig. 2). A third center is the Cape Floristic Region (CFR) of South Africa in which the Paleotropical origins and genera are concentrated (16/34). Tropical/subtropical regions had relatively fewer origins and genera (Neotropical, Indo-Malayan, Holotropical and Pantropical combined: 34/59). Myrmecochorous lineages did not appear to be restricted in their geographical distribution as 42% of the genera (n=334) were present in more than one biogeographic region.

Origins in individual families tended to cluster in specific biogeographic regions. In Australia, more than one origin was found in Fabaceae (5), Rutaceae (4), and Euphorbiaceae, Goodeniaceae and Malvaceae (2 each), while in the Holarctic, many origins were from Asteraceae (6), Ranunculaceae (all 6 origins), Papaveraceae (all 3), and Hyacinthaceae and Dipsacaceae (2 each). More than one origin was found in the Paleotropical region (mainly CFR) from Asteraceae (4) and Bruniaceae (2). In the Neotropical region, several origins were from Euphorbiaceae (3), Cactaceae (3), and Bromeliaceae and Gesneriaceae (2 each). Each of the relatively few origins from the Indo-Malayan region (6) were from separate families.

Within the subset of families present in at least four biogeographic regions (n=4), most origins in Euphorbiaceae were from tropical regions (3 Neotropical, 2 Pan-tropical, 1 Paleotropical and 1 Old World) and Australia (2). Myrmecochory in Fabaceae evolved primarily in Australia (at least 5 origins), and one origin each was Palearctic, Holarctic and Holotropical. Origins in Asteraceae were mostly from the northern hemisphere (4 Palearctic, 2 Nearctic) or from the Paleotropical region (4). A similar pattern was found for Lamiaceae, with one origin each from the Palearctic, Holarctic, Old World and Worldwide categories. These patterns largely corresponded with the biogeographic distribution of each family, although Australian origins appear overrepresented in Fabaceae and Euphorbiaceae.

Discussion

Myrmecochory is estimated here to be present in at least 11 000 species or ca. 4.5% of all species (n=250 000 total), in 334 genera or 2.5% of all genera (n=13 208 total), and in 77 families or 17% of all families (n=445 total) of angiosperm plants (totals are from Stevens, 2008). These numbers suggest that seed dispersal by ants has evolved many more times and that it constitutes a larger proportion of angiosperm diversity than was previously appreciated.

Our estimates raise the number of myrmecochorous species from 3000 (Beattie, 1983) to above 11 000, indicating that myrmecochorous plants are a globally significant portion of plant diversity. This number, however, still underestimates the real prevalence of myrmecochory. First, this number excludes all of the c. 12 000 species that are in lineages in which myrmecochory occurs, but for which either the exact number of myrmecochorous species or their phylogenetic relationships are not yet known (lineages not in boldface type in Table 1). Clearly some unknown, potentially a large number of the species in these lineages are myrmecochorous, which would increase the real number of myrmecochorous species far above that estimated here. Second, we provide evidence for myrmecochory in 77 families. This number is smaller than the 80+ families mentioned in the literature (e.g. in Giladi, 2006; based on estimates in Berg, 1975; Bond and Slingsby, 1983; Beattie, 1985), principally because of changes in family-level systematics. However, our data support previous claims that the real number of families containing myrmecochorous genera is likely to be above 80. Finally, we infer myrmecochory primarily based on diaspore morphology. However, seeds without elaiosomes may also attract ants with volatile chemical cues that may or may not function as rewards (e.g., Youngsteadt et al., 2008). Our study, which focuses only on elaisomes, is likely to exclude several such ant–plant mutualisms, and thus provides a conservative estimate of the prevalence of myrmecochory in angiosperms.

The number of origins is also likely to be underestimated in this study. First, our method to establish evolutionary origins was highly conservative (see section "Methods"). Second, elaiosomes of different tissue origins or development types are present in several families (e.g., Polygalaceae; Forest et al., 2007), indicating that elaiosomes likely have evolved multiple times in such families (e.g. six times in Polygalaceae, whereas only one origin was counted in our study). Future developments such as mapping origins on a (currently unavailable) genus-level angiosperm supertree will be useful to provide a more accurate estimate of the number of independent origins.

Our world survey confirmed the three 'hotspots' for myrmecochory suggested previously (Berg, 1975; Beattie, 1983; Dunn et al., 2007). These hotspots encompass relatively open dry habitats of mediterranean climate in Australia and the CFR of South Africa and similar habitats and temperate forests of the northern hemisphere (Holarctic). Although we found evidence of myrmecochory on all continents except Antarctica and in many different ecosystems, there were relatively fewer reports of myrmecochory from tropical areas. While targeted studies did find evidence for myrmecochory in several lineages of tropical forest plants (Horvitz and Beattie, 1980; Pfeiffer et al., 2004; see also e.g., Marini-Filho, 1999; Kaufmann and Maschwitz, 2006 for epiphytes), these records still come primarily from just a handful of genera such as *Calathea* and *Globba*, and from related families. At present it is difficult to say whether the relative rarity of tropical myrmecochores is a reflection of a real pattern or of a lack of adequate sampling.

Myrmecochory provides one of the best examples to date for convergent evolution in general and for the repeated evolution of plant–animal mutualisms more specifically. The presence of myrmecochory in a wide range of genera and families suggests that the selection pressures acting on it have been strong and/or that elaiosomes are physiologically and energetically cheap to produce and relatively easy to evolve, either in terms of genetic architecture or development. In terms of the relevant selection pressures, myrmecochory is associated with several benefits to plants in addition to the general advantages of dispersal: exploitation of new sites and reduced competition with kin. These additional benefits do not typically exist in other dispersal syndromes. Myrmecochory provides the seed with protection from seed predators, a safe place for seed survival during unfavourable periods such as fires and/or a microsite rich in nutrients (see detailed reviews of these benefits in Beattie, 1983; Gorb and Gorb, 2003; Giladi, 2006; and Rico-Gray and Oliveira, 2007). The physiological and energetic costs of developing elaiosomes are likely to be much smaller than developing fleshy fruits, so they are cheap to make (Goldblatt, 1997). That their costs are low is supported by the observations that myrmecochorous plants are more frequent on infertile soils than on fertile soils (Milewski, 1983; Westoby et al., 1990), whereas the relationship is the opposite for fleshy-fruited, bird-dispersed species (French and Westoby, 1992). Despite this correlative evidence, at present, we can only speculate about the relative ease of evolving an elaiosome (compared with other morphological traits), and future research on the genetic basis of elaiosome development will certainly be very revealing.

One hypothesis for the evolution of myrmecochory suggests that seed dispersal by ants has evolved from antagonistic interactions between seeds and ants that could both disperse and predate seeds (Levey and Byrne, 1993). Ants need to be abundant at levels that guarantees that seeds will be picked up and the seed traits need to directly influence the subsequent fate of seeds. Under such conditions, a seed structure that has small physiological/energetic costs to produce but can manipulate ants into retrieving, dispersing and discarding the seed to a microsite suitable for germination and growth (rather than milling the seed) could increase plant fitness. Selection for elaiosome production is expected to be particularly strong when the abundance of ants is sufficiently high to make them a reliable dispersal agent. Previous results on the timing of elaiosome evolution are consistent with this explanation. Although both monocot angiosperms and ants have evolved at least 120 MYA, Dunn et al. (2007) showed that the origins of myrmecochory in monocots are almost exclusively from the last 50 MYA, when ant abundance was many times greater than before. More specifically, the number of origins of elaiosomes was strongly correlated with the relative abundance of ants in compression fossil and amber deposits (Dunn et al., 2007). Our mapping of myrmecochory on the angiosperm family tree (Fig. 1) also shows that myrmecochory is more frequently found in younger ($<$70 MY) as opposed to older families. These observations support the hypothesis that elaisomes began to provide consistent benefits to plants after ants became superabundant. These properties of myrmecochory can explain the unexpectedly high proportion of myrmecochorous plants in several distant parts of the angiosperm phylogenetic tree.

More research is required to explore the conditions under which the overall benefits of myrmecochory exceed those in other seed dispersal syndromes. Data from a related study using sister-group comparisons to test whether myrmecochory is associated with higher diversification rates (Lengyel et al. 2009) suggest that myrmecochory was roughly equally likely to have evolved from unaided dispersal (30%), wind dispersal (32%) and vertebrate

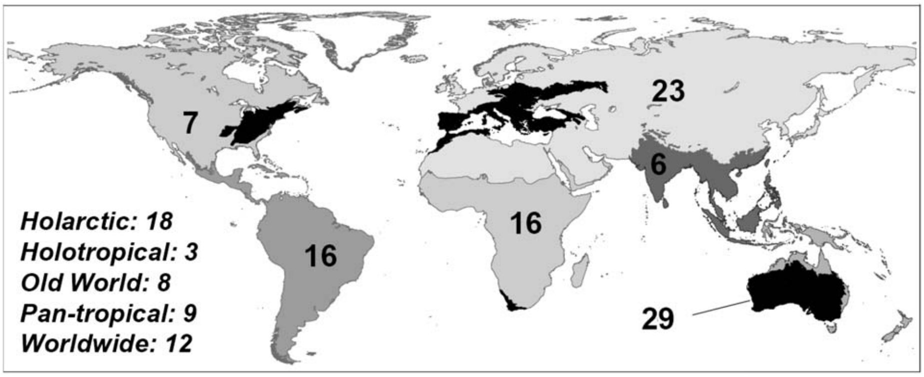

Fig. 2. Biogeographical distribution of myrmecochory. The number of evolutionary origins (total $n=147$) is given for each major biogeographic region (in shades of gray) and more complex distributions (inset). Myrmecochore diversity hotspots are shown in black. Please see section "Methods" for the logic of estimating origins and assigning genera to biogeographic regions.

dispersal (exo- and endozoochory combined, 30%) ($n=101$ origins). It is relatively straightforward to understand the benefits of myrmecochory as a cheap, easy and reliable mode of seed dispersal once ants became abundant enough in cases when myrmecochory evolved from the presumably more primitive abiotic dispersal types (unaided or wind). However, it is much less straightforward to understand how myrmecochory (and the elaiosome) has evolved from vertebrate dispersal (and the fleshy fruit), which appears a more complex and more costly mode of seed dispersal. One hypothesis for such transitions can be that myrmecochory enabled plants to colonise new environments or habitat types in which the lack of abundant vertebrate dispersers or the high costs of producing fleshy fruits precluded the maintenance of vertebrate dispersal. For example, myrmecochory may be favoured by selection in more open, drier or less predictable habitats than in closed, wetter and more stable habitats due either to the higher availability of ants as opposed to vertebrates as dispersers or to the lower costs of developing a reward for dispersal (a relatively cheap elaiosome as opposed to a costly fleshy fruit). It will require further studies to test whether the evolutionary transitions to myrmecochory were associated with the ability of plant lineages to colonise new environments or habitat types. This scenario appears possible because myrmecochorous lineages have diversified on average more than twice as fast as their sister groups did (Lengyel et al. 2009), and higher diversification rates are often associated with the ability of plants to colonise new environments or habitats.

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