Sphericity and smaller pollen-size are better represented in introduced rather than native plant species

Esfericidad y menor tamaño de polen están mejor representados en plantas introducidas que nativas

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RESUMEN

Mayor esfericidad y menor tamaño son dos de los principales rasgos presentes en granos de polen sugeridos para aumentar la dispersión por viento y polinizadores. Considerando el aumento en la pérdida de hábitat y la deforestación, cualquier rasgo que mejore la dispersión del polen podría ayudar a mantener y aumentar los límites de distribución de las poblaciones vegetales. En este estudio se muestra que las especies introducidas presentan significativamente granos de polen de menor tamaño y más esféricos que especies nativas, lo cual podría aumentar su éxito de dispersión.

Pollination is defined as the process by which pollen is transferred from the anther to the receptive part of the carpel with or without biotic assistance (Faegri & Van der Pijl 1979). Pollen is dispersed both by wind and insects (Mesquida *et al.* 1988), but the relative contribution of each to transport and pollination is yet unresolved (Cresswell & Osborne 2004, Walklate *et al*. 2004). There is some agreement that insects carry pollen over short distances within fields while wind can carry pollen for longer distances.

In recent times some climatic variations have been shown at a global scale. This phenomenon is known as global change (IPCC 2007). Fragmentation, habitat loss and land-use change are important components of this global change (Parmesan & Galbraith 2004), and causing in turn a decrease in pollination success due to an increase in the distance between patches or plant populations. Nonetheless, some external traits present in pollen grains could maintain an adequate –or higher– pollination success, due to long-distance dispersal by wind or higher amounts of pollen carried by pollinators (Vonhof & Harder 1995, Jackson & Lyford 1999). For instance, biological invasion success has been a major target to assess the importance of such “key traits” on dispersal and establishment success worldwide (Rejmanek & Richardson 1996, Sans *et al*. 2004).

The shape and size of pollen grains are two of the main traits suggested to enhance dispersal (Cruzan 1990, Jackson & Lyford 1999, Ackerman 2002). First, more spherical particles can be dispersed with higher velocity and for longer distances than those with a greater deviation from sphericity, since there is lower friction force in the former (Jackson & Lyford 1999, Ackerman 2002). Second, it has been indicated that pollen of smaller size is dispersed farther by wind in nature, and pollen size is negatively correlated with the number of pollen grains that each pollinator can carry (Vonhof & Harder 1995), affecting the plant´s fitness. For example, Cruzan (1990) showed that the total number of seeds produced by a fruit was decreased when different donors carried large pollen grains, apparently due to increased post-fertilization abortion. On the other hand, the physical forces required to remove pollen grains from the anther also highlight the role of wind gusts and turbulent conditions in pollen dispersal. A pollen-sized particle at rest on a surface will resist movement by simple gravitational forces; this resistance increases with particle size, deviation from sphericity, and surface roughness (Grace & Collins 1976, Niklas 1985).

In the present study we compared some “key traits” which could improve dispersal and hence pollination success in plant populations. Specifically, we assessed the sphericity and size of the pollen grains in native and introduced plant species.

We characterized a subset of the Chilean flora with respect to pollen size by selecting 95 species (52 and 43 species for native and introduced, respectively) both from the “Guía de Polen” (Arredondo-Núñez 2010) and some plant species growing in the city of Santiago (Table I, Supplementary Material). All species were separated into native and introduced categories for analysis. To test the hypothesis that active dispersal strategies aid in the success of introduced species, we compared by one-way ANOVA the maximum pollen-size and sphericity index for all species. The sphericity index was calculated according to the following equation (Jou *et al.* 1995):

$$\phi = \frac{\sqrt{a \cdot b^2} \cdot 2^3}{a + \frac{b^2}{\sqrt{a^2 - b^2}} \ln\left(\frac{a + \sqrt{a^2 - b^2}}{b}\right)}$$

Where "a" is the major semi-axis and "b" is the minor semi-axis.

Overall, introduced plant species showed significantly smaller pollen-size ($F_{1,93}=3.96$; $p=0.048$) than native species (Fig. 1A). Similarly, those plant species corresponding to introduced status showed significantly ($F_{1,93} = 7.55$; $p = 0.007$) more spherical pollen grains than natives (Fig. 1B). Ecologists have long been fascinated by the question of which species traits can predict their potential for dispersal and colonization of a new environment. Elton (1958) hypothesized that species able to establish themselves in new communities possessed abilities or traits that allowed them to use resources or tolerate stresses in ways that native species cannot. Following the same logic we can suggest that those plant species that are able to improve their pollen dispersal either by wind or pollinators could maintain their population size or spread their distributional ranges.

Several physical and biotic features act, at least potentially, as "filters or barriers" to invasion (Kruger *et al*. 1986). The success of many invaders can also be ascribed, at least partly, to the beneficial effects of various abiotic features in the target systems. Many invasions, therefore, rely on inherent properties of the invaded system for their success. For example, wind is often a very important vector of dispersal for seeds or pollen grains of incipient invaders. On the other hand, mutualisms involving animal-mediated pollination and pollen dispersal often facilitate invasions (Richardson *et al.* 2000). The spread of many alien plants, particularly woody ones, depends on pollinator mutualisms (Simberloff 2006). Most alien plants are well served by generalist pollinators (insects and birds), and pollinator limitation does not appear to be a major barrier for the spread of introduced plants. Thus, pollen grains with smaller size and more sphericity could have a greater advantage, as could those from introduced plant species. Additionally, presence of exine ornamentation could be other trait that difficult the dispersal of pollen grains, and in our study we found this structure mainly in natives than introduced with 67% and 16%, respectively (Table I, Supplementary Material).

Nevertheless, an increase in the distance between patches or between plant populations could result in reduced pollination success because pollination service would become less efficient, making wind dispersal more important. Currently, habitat loss and land-use change are arising as components of global change, resulting in more distanced plant populations (Parmesan & Galbraith 2004). Thus, plant species showing "key traits" in their pollen grains will maintain efficient dispersal and hence higher pollination success.

Ecological studies have shown that in many cases terrestrial plants have responded to climate changes by migrating rather than evolving to adapt to them (Graham & Grimm 1990). Given the extreme climate changes predicted and increasing rates of habitat loss and fragmentation, long-distance dispersal will be essential to allow species to move across fragmented landscapes (Thomas *et al*. 2004). For species with obvious adaptations for long-distance dispersal (*e.g.*, introduced species), "key traits" that improve the capacity for dispersal either by wind or pollinators might play a pivotal role in the future. Thus, a better understanding of dispersal in general, and pollen dispersal traits in particular, become essential to understanding the responses of plants to habitat loss and fragmentation under a future scenario of global change.

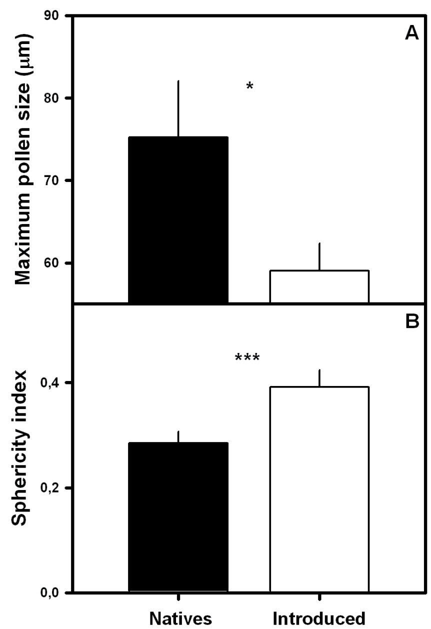

Figure 1. Maximum size (A) and sphericity index (B) of pollen grains of native (filled bars) and introduced (empty bars) plan species. Are showed ± 2EE. Asterisks indicate significant differences.

Figura 1. Tamaño máximo (A) e índice de esfericidad (B) de granos de polen pertenecientes a especies de plantas nativas (barras llenas) e introducidas (barras vacías). Se muestran ± 2EE. Asteriscos indican diferencias significativas.

TABLE I. Family, origin, maximum size (µm), sphericity index and presence of exine ornamentation (x) of the species used in this study.

TABLA I. Familia, origen, tamaño máximo (µm), índice de esfericidad y presencia de ornamentación de la exina (x) de las especies utilizadas en el presente estudio.

Species	Family	Origin	Maximum size	Sphericity Index	Ornamentation
Abutilon indicum	Malvaceae	Introduced	90.26	0.37	
Acanthus mollis	Acanthaceae	Introduced	74.65	0.15	
Alstroemeria ligtu	Alstroemeriaceae	Native	101.40	0.14	x
Alstroemeria revoluta	Alstroemeriaceae	Native	123.86	0.13	x
Anagallis alternifolia	Primulaceae	Native	38.08	0.27	
Anagallis arvensis	Primulaceae	Introduced	49.52	0.22	
Antirrhinum majus	Plantaginacea	Introduced	38.24	0.40	
Aristotelia chilensis	Elaeocarpaceae	Native	26.53	0.46	
Baccharis sagittalis	Asteraceae	Native	108.36	0.16	
Bellis perennis	Asteraceae	Introduced	40.55	0.44	
Bergenia crassiflora	Saxifragaceae	Introduced	64.13	0.49	
Bomarea salsilla	Alstroemeriaceae	Native	92.20	0.14	x
Calceolaria integrifolia	Calceolariaceae	Native	35.27	0.32	
Calendula arvensis	Asteraceae	Introduced	38.24	0.56	x
Centaurium cachanlahuen	Gentianaceae	Native	52.33	0.42	
Chloraea chrysantha	Orchidaceae	Native	126.23	0.17	x
Chloraea longipetala	Orchidaceae	Native	129.34	0.15	x
Cirsium vulgare	Asteraceae	Introduced	84.66	0.26	x
Citrus limonum	Rutaceae	Introduced	40.50	0.43	
Colletia hystrix	Rhamnaceae	Native	43.27	0.28	
Colliguaja dombeyana	Euphorbiaceae	Native	103.51	0.24	x
Convolvulus arvensis	Convolvulaceae	Introduced	56.88	0.29	
Crassula arborescens	Crassulaceae	Introduced	25.98	0.40	
Cydonia oblonga	Rosaceae	Introduced	60.67	0.94	
Cynoglossum creticum	Boraginaceae	Introduced	32.63	0.19	
Cytisus scoparius	Fabaceae	Introduced	50.06	0.37	
Datura stramonium	Solanaceae	Introduced	120.17	0.87	x
Desfontainia fulgens	Desfontainiaceae	Native	120.31	0.24	x
Digitalis purpurea	Plantaginaceae	Introduced	50.52	0.29	x
Dioscorea brachybothrya	Dioscoreaceae	Native	52.94	0.17	x
Drimys winteri	Winteraceae	Native	59.04	0.21	
Escallonia pulverulenta	Escalloniaceae	Native	32.74	0.69	
Escallonia revoluta	Escalloniaceae	Native	32.57	0.21	
Fabiana imbricata	Solanaceae	Native	48.27	0.19	
Francoa appendiculata	Francoaceae	Native	39.29	0.18	
Fuchsia magellanica	Onagraceae	Native	78.61	0.16	x
Gamochaeta spicata	Asteraceae	Native	23.71	0.44	x
Gamochaeta stachydifolia	Asteraceae	Native	51.33	0.29	x
Gaultheria insana	Ericaceae	Native	69.82	0.30	x
Geranium berteroanum	Geraniaceae	Native	52.73	0.87	x
Gevuina avellana	Proteaceae	Native	73.98	0.31	x
Gochnatia foliolosa	Asteraceae	Native	130.85	0.30	x
Hebertia lahue	Iridaceae	Native	92.64	0.16	x
Hypericum caespitosum	Hyperaceae	Native	330.53	0.20	x
Iris spurea subsp. *ochroleuca*	Iridaceae	Introduced	75.89	0.19	
Lampranthus spectabilis	Aizoaceae	Introduced	56.56	0.34	

Species	Family	Origin	Maximum size	Sphericity Index	Ornamentation
Lapageria rosea	Philesiaceae	Native	102.56	0.15	x
Leontodon taraxacoides	Asteraceae	Introduced	56.78	0.18	x
Lepechinia chamaedryoides	Lamiaceae	Native	86.05	0.19	x
Libertia sessiliflora	Iridaceae	Native	52.95	0.17	x
Ligustrum vulgare	Oleaceae	Introduced	48.29	0.40	
Lilium sp.	Liliaceae	Introduced	156.52	0.12	
Lithrea caustica	Anacardiaceae	Native	54.96	0.30	x
Lobelia tupa	Campanulaceae	Native	55.48	0.29	x
Lotus corniculatus	Fabaceae	Introduced	22.00	0.95	
Lythrum hyssopifolia	Lythraceae	Introduced	57.37	0.46	x
Malva sylvestris	Malvaceae	Introduced	71.97	0.31	
Mentha pulegium	Lamiaceae	Introduced	72.51	0.34	x
Muehlenbeckia hastulata	Polygonaceae	Native	29.66	0.45	x
Mutisia ilicifolia	Asteraceae	Native	134.18	0.14	x
Myrceugenia pinifolia	Myrtaceae	Native	54.67	0.12	
Narcissus tazetta	Amaryllidaceae	Introduced	25.98	0.16	
Nicotiana acuminata	Solanaceae	Native	65.85	0.29	
Osteospermum fruticosum	Asteraceae	Introduced	52.17	0.39	
Oxalis articulata	Oxalidaceae	Native	53.79	0.36	
Oxalis pes-caprae	Oxalidaceae	Introduced	54.78	0.44	
Papaver setigerum	Papaveraceae	Introduced	29.34	0.25	
Pelargonium peltatum	Geraniaceae	Introduced	76.53	0.31	
Platanus orientalis	Platanaceae	Introduced	33.98	0.28	
Podanthus ovatifolius	Asteraceae	Native	38.50	0.25	x
Prunus domestica	Rosaceae	Introduced	60.27	0.27	
Punica granatum	Lythraceae	Introduced	52.63	0.32	
Puya berteroniana	Bromeliaceae	Native	64.04	0.21	x
Quinchamalium chilense	Santalaceae	Native	40.75	0.20	
Rosa canina	Rosaceae	Introduced	102.13	0.56	
Rosa rubiginosa	Rosaceae	Introduced	48.45	0.78	
Rosa sp.	Rosaceae	Introduced	60.91	0.28	
Rubus ulmifolius	Rosaceae	Introduced	62.52	0.29	
Rumex acetosella	Polygonaceae	Native	87.36	0.23	x
Senecio vulgaris	Asteraceae	Introduced	82.37	0.26	x
Senna stipulacea	Fabaceae	Native	52.33	0.21	
Silybum marianum	Asteraceae	Introduced	85.14	0.31	
Sophora macrocarpa	Fabaceae	Native	39.61	0.28	x
Stachys grandidentata	Lamiaceae	Native	55.00	0.53	x
Taraxacum officinale	Asteraceae	Introduced	52.18	0.39	
Teline monspessulana	Fabaceae	Introduced	47.38	0.37	
Teucrium bicolor	Lamiaceae	Native	108.03	0.16	x
Trifolium repens	Fabaceae	Introduced	52.05	0.98	
Tristerix corymbosus	Loranthaceae	Native	53.05	0.23	x
Tulipa sp.	Liliaceae	Introduced	95.14	0.20	
Ugni molinae	Myrtaceae	Native	24.78	0.73	
Uncinia phleoides	Cyperaceae	Native	108.06	0.52	x
Valeriana aff. *stricta*	Valerianaceae	Native	59.89	0.57	x
Viola portalesia	Violaceae	Native	63.54	0.30	x
Zantedeschia aethiopica	Araceae	Introduced	87.02	0.15	

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REFERENCES

Ackerman, J.D. 2002. Diffusivity in a marine macrophyte canopy: implications for submarine pollination and dispersal. American Journal of Botany 89: 1119-1127.

Arredondo-Núñez, A. 2010. Guía de Polen Reserva Nacional Los Ruiles. Alvimpress, Santiago. 69 pp.

Cresswell, J.E. & J.L. Osborne. 2004. The effect of patch size and separateness on bumblebee foraging in oilseed rape (*Brassica napus*): implications for gene flow. Journal of Applied Ecology 41: 539-546.

Cruzan, M.B. 1990. Variation in pollen size, fertilization ability, and postfertilization siring ability in *Erythronium grandiflorum*. Evolution 44: 843-856.

Elton, C. 1958. The ecology of invasions by animals and plants. Methuen & Co. Ltd., London. 181 pp.

Faegri, K. & L. van der Pijl. 1979. The principles of pollination ecology. Pergamon Press, New York. 224 pp.

Grace, J. & M. A. Collins. 1976. Spore liberation from leaves by wind. In: C.H. Dickinsonb & T.F. Preece (eds), pp. 185-198. Microbiology of aerial plant surfaces. Academic Press, London.

Graham, R.W. & E.C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology & Evolution 5: 289-292.

IPCC. 2007. Intergovernmental panel on climate change. http://www.ipcc.ch

Jackson, S.T. & M.E. Lyford. 1999. Pollen dispersal models in quaternary plant ecology: assumptions, parameters, and prescriptions. Botanical Review 65: 39-75.

Jou, D., J.E. Llebot & C. Pérez-García. 1995. Física para ciencias de la vida. Editorial Reverté, Barcelona. 526 pp.

Kruger, F.J., D.M. Richardson & B.W. van Wilgen. 1986. Processes of invasion by alien plants. In: I.A.W. Macdonald, F.J. Kruger & A.A. Ferrar (eds), pp. 145-155. The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town.

Mesquida, J., M. Renard & J.S. Pierre. 1988. Rapeseed (*Brassica napus* L.) productivity: the effect of honeybees (*Apis mellifera* L.) and different pollination conditions in cage and field tests. Apidologie 19: 51-72.

Niklas, K.J. 1985. The aerodynamics of wind pollination. Botanical Review 51: 328-386.

Parmesan, C. & H. Galbraith. 2004. Observed impacts of global climate change in the U.S. Pew Center on Global Climate Change, Arlington. 55 pp.

Rejmánek, M. & D.M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77: 1655-1661.

Richardson, D.M., N. Allsopp, C.M. D´Antonio, S.J. Milton & M. Rajmánek. 2000. The plant invasions – the role of mutualisms. Biological Review 75: 65-93.

Sans, F.X., H. García-Serrano & I. Afán. 2004. Life-history traits of alien and native *Senecio* species in the Mediterranean region. Acta Oecologica 26: 167-178.

Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecology Letters 9: 912-919.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A. Townsend Peterson, O.L. Phillips & S.E. Williams. 2004. Extinction risk from climate change. Nature 427: 145-148.

Vonhof, M.J. & L.D. Harder. 1995. Size-number trade-offs and pollen production by papilionaceous legumes. American Journal of Botany 82: 230-238.

Walklate, P.J., J.C.R. Hunt, H.L. Higson & J.B. Sweet. 2004. A model of pollen-mediated gene flow for oilseed rape. Proceedings of the Royal Society of London B, 271: 441-449.

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