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# Wild boars as seed dispersal agents of exotic plants from agricultural lands to conservation areas

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ABSTRACT

Some large omnivorous mammals serve as effective dispersal vectors of plant seeds that are adapted for dispersal through endozoochory or epizoochory. Seed dispersal by native wild boars (*Sus scrofa lybicus*) was investigated at Ramat-Hanadiv Park in central Israel by controlled germination, in a greenhouse, of dung, pellets, and brushed hair samples. Many seedlings emerged from the dung and hair samples but pellets did not contain any viable seeds. Forty-one percent of the species and 91% of the seedlings dispersed by endozoochory were exotic species. Eighteen percent of the species and 59% of the seedlings, dispersed by epizoochory were exotic species. Some of these species are ruderal plants which grow along roads and disturbed sites in the park, but only one has established in the park core. The large numbers of exotic seeds illustrate the potential impact of the omnivorous wild boar as effective vector dispersing exotic plant species from agricultural and urban areas into protected natural ecosystems. However, the establishment was only minor yet probably due to summer drought and high resistance of the Mediterranean maquis to invading plants.



## 1. Introduction

Long-range seed dispersal is often accomplished by large mammals via endozoochory or epizoochory (Couvreur et al., 2004, 2005; Manzano and Malo, 2006). The endozoochory seed dispersal mechanism is mostly relevant for fleshy fruits that contain seeds that are well protected against mechanical and chemical damage caused by the chewing and the digestive processes (Howe and Smallwood, 1982; Van der Pijl, 1982; Herrera, 1995). Recent studies have shown that seeds of plants without fleshy fruits can also be dispersed by endozoochory (Pakeman et al., 2002; Couvreur et al., 2005); these plants produce small, round seeds with a hard seed coat, which animals consume together with green leaves or shoots (Pakeman et al., 2002; Couvreur et al., 2005). The epizoochory seed dispersal mechanism involves dispersal units with various adherence mechanisms such as hooks, spikes, or adhesives (Howe and Smallwood, 1982; Van der Pijl, 1982; Sorensen, 1986). Other seeds may lack any specific adaptation, and are dispersed randomly by endozoochorous or epizoochorous agents.

Exotic invasive species pose a threat to biodiversity in natural ecosystems (Pimm et al., 1995; Meyer and Florence, 1996; Wilcove et al., 1998). Seed dispersal is crucial for the success and spread of such invasive plants (Calvino-Cancela, 2011). The importance of seed-dispersing and the activity of ground-disturbing species in facilitating the spread and establishment of invasive species has been thoroughly discussed by Schiffman (1997). The dispersal of exotic plants by native vertebrate species was described recently (Myers et al., 2004; Vavra et al., 2007; Brochet et al., 2009; Calvino-Cancela, 2011) as well as the dispersal of native endemic plants by alien herbivores (Castro et al., 2008). Herrera (1989) addressed frugivory and dispersal of native plant seeds by medium-size carnivores. However, the potential role of large omnivores as principal dispersal agents of exotic invasive plants has not been addressed in the literature.

Wild boars are large omnivore mammals, commonly found in a wide variety of habitats and climatic conditions. The subspecies *Sus scrofa lybicus* originally extends from south Caucasus through the Levant to the Nile Delta (Groves, 2007) and maintains stable native populations in Israel. Wild boars consume a wide variety of food, which varies in time and space; they forage on plants and animal-derived foods at similar frequencies, but the proportion of

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plants is always much higher than animals in their diet (Schley and Roper, 2003; Herrero et al., 2006; Pinna et al., 2007). In winter and early spring wild boars consume large amounts of herbaceous plants and feed on their sugar-containing sap that is rich in proteins and vitamins. To extract plant-sap they chew large amounts of grass, which they spit out later as 'pellets' (Rosenfeld, 1998). In many cases wild boars feed on human products such as agricultural crops and organic waste, which often form their entire diet (Schley and Roper, 2003).

Wild boars thrive in human-modified areas such as agricultural fields, planted forests, riparian canals, and they even invade human neighborhoods (Cahill et al., 2003; Herrero et al., 2006). Because of the small extent of protected natural areas in Israel and their proximity to agricultural lands and urban areas, wild boars often use the dense natural vegetation as shelter, but feed on nearby agricultural crops, human waste and in gardens where they cause severe damage (Rosenfeld, 1998).

Several studies conducted in western Europe depicted wild boars as important epizoochorecal (Schmidt et al., 2004; Heinken et al., 2006) and endozoochorecal seed dispersers (Heinken and Raudnitschka, 2002; Heinken et al., 2006). Wild boars carry large quantities of seeds of large numbers of native species over large distances and across diverse habitats; in contrast to deers, for example, which drop dung many times during the day, wild boars drop it two or three times a day (Rosenfeld, 1998). In a single night they can forage up to 5 km while (Canaani, 1988) and therefore they may act as effective long-range endozoochorous seed dispersal agents (Schupp, 1993). Additionally, their thick winter fur, and their scratching and wallowing habits, make them also efficient agents of epizoochorous seed dispersal. Animal seed dispersal can be directed to disturbed habitats, such as wallowing points, trampled areas, or attractive feeding pastures (Couvreur et al., 2005), which are often preferred sites for establishment of invasive species.

The objective of the present research was to study the role of the wild boar, a common and notorious large omnivore, as an endozoochorecal and epizoochorecal seed disperser from agricultural lands and urban areas into neighboring protected dry Mediterranean maquis. Specifically, we aimed to answer the following questions. (1) Which plant species are dispersed by wild boars through endozoochory or epizoochory? (2) What are the characteristics of the species dispersed via each mode? (3) What is the potential contribution of wild boars to the spread of exotic seeds into a protected natural area dominated by Mediterranean vegetation?

## 2. Methods

### 2.1. Study area

The study area is in the Ramat-Hanadiv Park Israel (500 ha), located on the southern end of Mt. Carmel (32°30′N, 34°57′E) at an altitude of 120 m above sea level. The landscape is a plateau with dry stream beds cutting westward down to the coastal plain. The soil is mostly typical Mediterranean Terra Rossa developed on limestone (Kaplan, 1988). The climate is Mediterranean, with mean annual precipitation of 540 mm falling mainly between December and February. The typical vegetation in Ramat-Hanadiv is Mediterranean shrubland (maquis) dominated by *Phillyrea latifolia*, *Pistacia lentiscus*, *Calicotome villosa*, *Sarcopoterium spinosum*, and a few scattered trees – *Ceratonia siliqua* and *Quercus ithaburensis*. Highly diverse annual herbaceous vegetation occupies the open spaces among the shrubs (Hadar et al., 1999). Planted coniferous forest of *Pinus halepensis*, *Pinus brutia*, *Pinus canariensis* and *Cupressus sempervirens* cover some parts of the park. The Ramat-Hanadiv Park is surrounded mostly by grazing lands, croplands, urban neighborhoods and public gardens.

### 2.2. Endozoochory

To examine the role of wild boars as endozoochorous seed dispersal agents, we collected fresh dung, from May 2007 through April 2008. Samples were collected from seven fixed locations representing the park core area. Once every fourteen days we collected dung samples that had been dropped during this period by several different individuals (see in Rosenfeld, 1998). Samples were dried at ambient temperature and stored in paper bags. Prior to germination, we crumbled each sample separately and used five to ten 10-g random subsamples for germination tests. This method helped to reduce variance among samples collected at the same time. During the spring of 2008 we also collected 'pellets' and treated them in a similar way.

### 2.3. Epizoochory

Fifteen wild boars were trapped in cage-traps in the park core from spring 2007 through winter 2008. The animals were anesthetized by Zoletil (Virbac, Carros, France) with darts, treated and released. We brushed the boars' fur with a coarse metal dog brush and their hooves with a fine steel brush, the treatments took place on plastic sheets for a fixed time of 8 min. Seed samples were collected from the plastic sheets and stored in paper bags pending germination test.

### 2.4. Germination

All brushed, dung, and pellet samples were germinated in a greenhouse at Ramat-Hanadiv. Samples were sown in marked standard (15 cm diameter) pots filled with sterilized light pot soil, and were covered with a 2-mm layer of pot soil. The pots were sheltered with a dense mosquito net (0.5 mm, external) to avoid contamination with seeds. Similar pots, but without seeds, were randomly scattered among the seeded pots as a control. Plants were watered to saturation three times weekly. Samples germinated in November 2007, the time of natural germination; late samples germinated in November 2008. Germination was monitored once a week for 6 months. Each germinated seedling was identified and carefully removed from the pot to reduce competition.

### 2.5. Species abundance and seed traits

Abundance data of the plant species growing in the protected core area of the Ramat-Hanadiv Park were obtained from the park's LTER database (2003–2009). The number of sampled quadrates in which a given species had been recorded was divided by the total area of monitored quadrates, as a proxy for abundance. Seed mass data were obtained from IGB database (IGB, 2011) and from Kew seed information database (Kew, 2011). Seeds were divided into three mass-classes: **1**. Miniature (seeds mass $< 2$ mg), **2**. Medium ($10$ mg $>$ seeds mass $> 2.1$ mg), **3**. Large (seeds mass $> 10.1$ mg).

### 2.6. Data analysis

We applied Chi-square tests to explore the association between seed fleshiness (or none) and species origin (native or exotic) for seeds dispersed by endozoochory, and the association between the seed adhesiveness (or none) and species origin (native or exotic) for seeds dispersed by epizoochory. Chi-square test was applied to explore the association between seed size (miniature, medium, large) and species origin (native or exotic). Statistical analysis was conducted with the SPSS for Windows software, version 14.0 (SPSS Inc, Chicago, IL, USA).

## 3. Results

### 3.1. Endozoochory

A total of 1373 seedlings, representing 31 species, germinated from wild boar-dung (Table 1), but none germinated from any of the pellet samples. Most seedlings belonged to the exotic species: *Morus* sp., *Amaranthus blitum* and *Ficus religiosa*. Of the species that were endozoochorously dispersed in wild boars' and germinated from wild boar-dung, 41% (12 species) were exotic, and these exotic species contributed 91% of all the seedlings (Fig. 1). There was a significant association between the origin of the seedlings (native or exotic) and fruit characteristics (fleshy or dry) ($\chi^2 = 1040.47$, $df = 3$, $P < 0.05$) mainly due to the high numbers of exotic species with fleshy fruits, but no such association was found at the species level ($\chi^2 = 2.58$, $df = 3$, $P = 0.46$). Ten species produced fleshy fruits, one species produced fleshy pods, one species produced fleshy leaves and stems, and the remaining 20 species produced dry fruits; although most species did not produce fleshy fruits, most of the seedlings were of plants with fleshy fruits (Table 1).

Seeds were dispersed during all months of the year. The mean (±stder) number of seedlings per unit weight of dung varied throughout the year was $10.11 \pm 5.03$ (seedlings per 10 g dung) and, at the species level, we detected seasonal differences in the numbers of seeds per unit weight of dung according to fruiting seasons of the various species.

A significant association was found between the origin of the seedlings (native or exotic) and seed mass characteristics (miniature, medium, large) ($\chi^2 = 1758.65$, $df = 5$, $P < 0.005$) mainly due to the high numbers of exotic seedlings with miniature seed, and a similar but weaker relationship was found also at the species level ($\chi^2 = 14.65$, $df = 5$, $P < 0.05$) (Fig. 1).

Eighty-eight percent of the native species that were endozoochorously dispersed has an established populations in the park core, but only one exotic species has established population in the park core (Table 1).

### 3.2. Epizoochory

Two hundred and seventeen seedlings, representing 22 species, germinated (Table 2) from 15 samples of wild boar fur-brushings. The majority of these seedlings belonged to four exotic species and the remaining 18 species were native (Fig. 1). Most seeds of the exotic species had fruits with no special adhesion mechanisms, whereas most seeds of native species bore adhesive fruits ($\chi^2 = 42.7$, $df = 3$, $P < 0.05$), and a similar relationship was found also at the species level ($\chi^2 = 9.27$, $df = 3$, $P < 0.05$). About half of the species bore fruits with adhesive characteristics. Four of the species that lacked adhesion mechanisms were typically wind-dispersed, including the most abundant species found: *Conyza* sp. that comprised 45% of all individuals.

There was a significant association between the origin of the seedlings (native or exotic) and seed mass (miniature, medium, large) ($\chi^2 = 148.16$, $df = 5$, $P < 0.05$) due to the high numbers of exotic seedlings with miniature seed, and such association found also at the species level ($\chi^2 = 25.45$, $df = 5$, $P < 0.05$).

Eighty-nine percent of the native species that were dispersed by epizoochory have established populations in the park core, but only one exotic species that were dispersed by epizoochory has an established population in the park core (Table 2).

**Table 1**
List of 31 species that germinated from wild boar-dung samples ($n = 136$) collected in Ramat-Hanadiv Park (2007–2008), Israel; number of seedlings, their origin (native or exotic), fleshy (+) or dry (−) fruit, seed mass (mg) and their relative abundance in the park (number of observation per 1000 m$^2$).

| Species | Seedlings | Origin | Fleshy fruit | Seed mass (mg) | Abundance |
|---|---|---|---|---|---|
| 1. *Morus* sp. L. | 480 | Exotic | + | 9.0 | – |
| 2. *Amaranthus blitum* L. | 466 | Exotic | − | 1> | – |
| 3. *Ficus religiosa* L. | 132 | Exotic | + | 1.0 | – |
| 4. *Opuntia* sp. | 77 | Exotic | + | 16.0 | – |
| 5. *Ficus benghalensis* L. | 72 | Exotic | + | 0.33 | – |
| 6. *Solanum lycopersicum* | 6 | Exotic | + | 1.23 | – |
| 7. *Amaranthus blitoides* S. Watson | 5 | Exotic | − | 0.9 | – |
| 8. *Euphorbia hirta* L. | 2 | Exotic | − | 0.08 | – |
| 9. *Amaranthus cruentus* L. | 2 | Exotic | − | 1> | – |
| 10. *Amaranthus spinosus* L. | 1 | Exotic | − | 0.21 | – |
| 11. *Conyza* sp. | 1 | Exotic | − | 0.03 | 4.7 |
| 12. *Acacia saligna* (Labill.) Wendl. f. | 1 | Exotic | − | 16.0 | – |
| 13. *Brachypodium distachyum* (L.) P. Beauv | 32 | Native | − | 4.6 | 1161.5 |
| 14. *Portulaca oleracea* L. | 26 | Native | + | 0.2 | – |
| 15. *Poa infirma* Kunth | 12 | Native | − | 0.25 | 12.9 |
| 16. *Aegilops geniculata* Roth | 10 | Native | − | 16.25 | 84.6 |
| 17. *Chenopodium murale* L. | 10 | Native | − | 0.6 | 2.3 |
| 18. *Ceratonia siliqua* L. | 8 | Native | + | 197.0 | 11.7 |
| 19. *Tamus* sp. | 8 | Native | + | 17.9 | 669.4 |
| 20. *Helianthemum salicifolium* (L.) Mill. | 4 | Native | + | 0.3 | 180.9 |
| 21. *Trifolium echinatum* M. Bieb. | 4 | Native | − | 1.29 | – |
| 22. *Trifolium clypeatum* L. | 3 | Native | − | 7.3 | 714 |
| 23. *Bromus lanceolatus* Roth | 2 | Native | − | 3.93 | 131.5 |
| 24. *Cynodon dactylon* (L.) Pers. | 1 | Native | − | 0.2 | 3.5 |
| 25. *Phillyrea latifolia* L. | 1 | Native | + | 16.3 | 334.7 |
| 26. *Tordylium* sp. | 1 | Native | − | 7.3 | 2.3 |
| 27. *Trifolium purpureum* Loisel. | 1 | Native | − | 1.1 | 42.3 |
| 28. *Trifolium resupinatum* L. | 1 | Native | − | 1.4 | 171.5 |
| 29. *Solanum nigrum* L. | 1 | Native | + | 0.7 | – |
| 30. *Poaceae* sp. | 2 | _ | | | |
| 31. *Asteraceae* sp. | 1 | _ | | | |

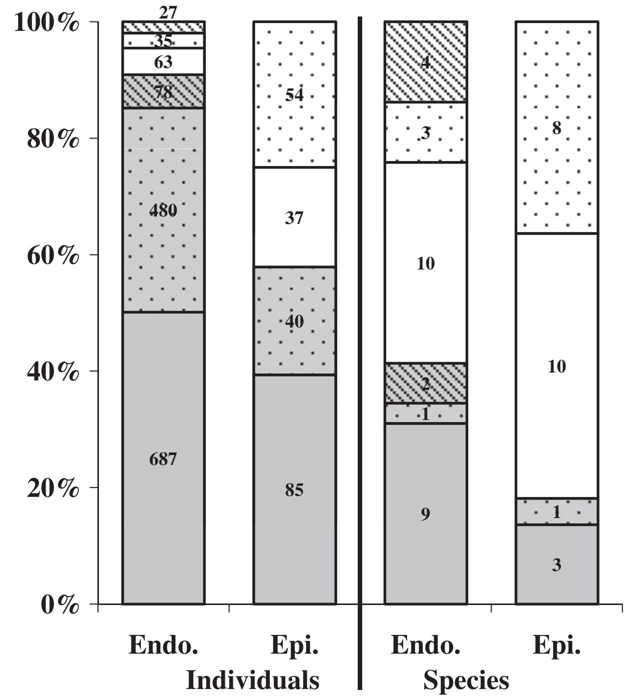


**Fig. 1.** The percentages, numbers, and seed mass of native (gray background bars) and exotic (white background bars) species and individual plants whose seeds were dispersed by wild boars via endozoochory (Endo.) or epizoochory (Epi.). Seeds were divided into three mass-classes; 1. Miniature (open bars, seeds mass $<$ 2 mg), 2. Medium (dotted bars, 10 mg $>$ seeds mass $\geq$ 2 mg), 3. Large (striped bars, seeds mass $\geq$ 10 mg). Four individuals of three species that were unidentified at the species level are absent from the Figure.

## 4. Discussion

Wild boars move between natural protected areas and human-modified areas such as agricultural fields, plantations, waste-disposal sites, and gardens, where they prefer to forage especially during the dry seasons (Rosenfeld, 1998; Cahill et al., 2003; Herrero et al., 2006). In human-modified areas they commonly feed on exotic species and collect seeds that cling to their fur and thus are dispersed into natural ecosystem. Our results demonstrate the potential of native large omnivores in general and wild boars in particular, to disperse exotic species as they forage over long distances and exploit food sources that vary in time and space. The exotic species found to be dispersed by wild boars in the present study were mostly ruderal or early succession species that are likely to establish in disturbed areas or in the margins of natural systems (Dafni and Heller, 1982; Feinbrun-Dothan and Danin, 1991). However, only one of the exotic species (*Conyza* sp.), known as invasive species (Thebaud and Abbott, 1995; Yan et al., 2001), was dispersed in large quantities by the wild boars had established populations in the park core. Although the Mediterranean flora in Israel is regarded as relatively resistant to invasive species (Har-Edom and Sternberg, 2010) compared with other Mediterranean-type ecosystems in the world (Grooves and Di Castri, 1991), the risk of invasion by exotic species, mediated by wild boars, is apparent.

In contrast to the classical vertebrate seed dispersal mechanisms (Howe and Smallwood, 1982; Sorensen, 1986), 20 out of 31 species (native and exotic) with no fleshy fruits were also dispersed by endozoochory, 10 out of 22 species (native and exotic) of plants with no adhering mechanism were dispersed by epizoochory, and six species were dispersed by both endozoochory and epizoochory. Most of these species produce many small round seeds with hard seed coats, lacking adherence mechanisms but are well adapted for endozoochory (Fig. 1). These seeds probably were eaten or adhered to the fur while the wild boars were feeding on vegetative parts of the plants; they possibly survived mouth and gut damages or did not immediately fall off the fur. These results demonstrate the dispersal advantage of small seeds, even in the absence of any special mechanism, which is definitely necessary for larger seeds (Sorensen, 1986; Corlett, 1998). The best examples are the two exotic species *A. blitum*, which have small, round dry seeds with hard coats that are dispersed by endozoochory, and *Conyza* sp., which is a classic wind-dispersed species but was dispersed by epizoochory. The fact that these two species, which are invasive in

**Table 2**
List of 23 species that germinated from seeds brushed from the fur of 15 wild boars (2007–2008) in Ramat-Hanadiv Park; number of seedlings, their origin (native or exotic), adhesive (+) or non-adhesive (−) fruit, seed mass (mg) and their relative abundance in the park (number of observation per 1000 $m^2$).

| Species | Seedlings | Origin | Adhesive fruit | Seed mass (mg) | Abundance |
|---|---|---|---|---|---|
| 1. *Conyza* sp. | 81 | Exotic | − | 0.03 | 4.7 |
| 2. *Bidens tripartita* L. | 40 | Exotic | + | 2.1 | − |
| 3. *Amaranthus blitum* L. | 3 | Exotic | − | 1> | − |
| 4. *Amaranthus blitoides* S. Watson | 1 | Exotic | − | 0.9 | − |
| 5. *Bromus madritensis* L. | 24 | Native | + | 3.33 | 69.3 |
| 6. *Brachypodium distachyum* (L.) P. Beauv. | 12 | Native | + | 4.6 | 1161.48 |
| 7. *Sonchus oleraceus* L. | 10 | Native | − | 0.3 | 501.5 |
| 8. *Andropogon distachyos* L. | 9 | Native | + | 0.86 | 281.9 |
| 9. *Senesio vernalis* Waldst. et Kit. | 7 | Native | − | 0.2 | 331.2 |
| 10. *Bromus alopecuros* Poiret | 6 | Native | + | 2.19 | 167.9 |
| 11. *Lolium rigidum* Gaudin | 5 | Native | + | 3.8 | 118.6 |
| 12. *Bromus syriacus* Boiss. and Blanche | 4 | Native | + | 3.43 | 9.4 |
| 13. *Bromus scoparius* L. | 3 | Native | + | 1.0 | 61.1 |
| 14. *Pallenis spinosa* (L.) Cass. | 3 | Native | − | 1.12 | 214.9 |
| 15. *Torilis* sp. | 1 | Native | + | 1.6 | 42.3 |
| 16. *Medicago orbicularis* (L.) Bartal | 1 | Native | − | 3.8 | 1.2 |
| 17. *Chenopodium murale* L. | 1 | Native | − | 0.6 | 2.3 |
| 18. *Atriplex rosa* L. | 1 | Native | − | 2.56 | − |
| 19. *Anagallis arvensis* L. | 1 | Native | − | 0.5 | 1021.7 |
| 20. *Piptatherum blancheanum* Boiss. | 1 | Native | + | 10.0> | 274.8 |
| 21. *Solanum nigrum* L. | 1 | Native | − | 0.7 | − |
| 22. *Silene colorata* Poiret | 1 | Native | − | 0.31 | 98.6 |
| 23. *Poaceae* sp. | 1 | _ | | | |

many ecosystems worldwide (Grooves and Di Castri, 1991; Thebaud and Abbott, 1995; Yan et al., 2001) and are noxious weeds in Israel (Dafni and Heller, 1982; Feinbrun-Dothan and Danin, 1991), have not invaded (yet) protected natural areas in large quantities is not due to lack of seed sources or dispersers, but probably because they are intolerant for summer drought or shade and thus fail to compete with native species (Har-Edom and Sternberg, 2010).

Eight of the exotic species dispersed by wild boars – *A. blitum*, *Amaranthus blitoides*, *Amaranthus cruentus*, *Amaranthus spinosus*, *Conyza* sp., *Bidens tripartite*, *Euphorbia hirta*, and *Acacia saligna* – are known as potentially invasive species in the region (Dafni and Heller, 1982; Feinbrun-Dothan and Danin, 1991; Grooves and Di Castri, 1991); the rest are potentially invasive species in parts of north America (NRCS, 2011) but established in the region only in human-altered and disturbed sites. In contrast to the large number of exotic species dispersed via endozoochory, most of the species found to be dispersed by epizoochory were native annual herbaceous species (Fig. 1), half of which have typical fur-adherence mechanisms (Table 2).

Our results show that wild boars are seed dispersal agents via endozoochory and epizoochory, these findings are consistent with the results of previous West European studies (Heinken and Raudnitschka, 2002; Schmidt et al., 2004; Heinken et al., 2006). The number of plant species dispersed by wild boars in Israel was lower than that in Europe but, on the other hand, the number of exotic plants dispersed in Israel by boars, mainly via endozoochory, was higher than that in Europe (Heinken and Raudnitschka, 2002; Schmidt et al., 2004; Heinken et al., 2006). Most of the seeds dispersed by wild boars through endozoochory were of exotic woody species, which produce large amounts of fleshy fruits during a short period (Table 1). Wild boars adapt their foraging activity to these spatial and temporal varying resources, thereby enabling them to survive the dry, food poor and long summer.

Wild boar pellets did not contain any seeds and therefore cannot be regarded as a part of wild boar seed dispersal guild. Grass-chewing is limited to winter and early spring, when most of the herbaceous plants are green, still growing and still has no seeds. In addition, the intensive chewing of the juicy green leaves might destroy the few seeds of early-fruiting species.

It is well established that long-distance seed dispersal by vertebrates is an important mechanism for preservation of fragmented and isolated plant populations, and for natural establishment of new populations (Sorensen, 1986; Couvreur et al., 2004; Clark et al., 2005; Manzano and Malo, 2006). Indeed, these are important processes in an era of rapid environmental changes worldwide. However, vertebrates that are long-distance seed dispersers do not distinguish between exotic and native species, and thus as the present paper implies, they can serve dispersal agents of new invasive species, which damage natural protected areas.

To conclude, our findings show that large omnivores can function as dispersal agents of exotic and invasive species. In the Mediterranean ecosystem of Israel wild boars are effective seed dispersers of native and exotic species with seeds that are adapted to endozoochory or epizoochory. They also disperse seeds of species with non-adapted small seeds that are dispersed in both ways. Wild boars disperse exotic seeds from human-modified lands into protected natural areas, but there is no significant establishment of these species yet.

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