

Comparing the palatability of native and non-native Mediterranean plants

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Abstract

Herbivory is thought to be an important factor in the ecology of introduced species. A lower palatability to the herbivores may contribute to the success of invasive species in their new habitat. Here we investigate the palatability (to the generalist herbivore snail *Cepaea hortensis*) of 11 non-native plant species found on Crete and compare it to that of 13 native species. These were collected from three different habitats (dunes, olive groves and shrublands), so as to be able to reconstruct a community background palatability. Our results indicate that non-natives fall into the range of palatabilities found among the natives, with no significant overall difference between these groups. In all three tested habitats, non-natives were more palatable than the native community background. Only in dunes was one non-native species, *Acacia saligna*, markedly less palatable than the community average. Palatability of the species was not related to their commonness on Crete, independent of being native or not.

Key-words

Alien species, *Cepaea hortensis*, community palatability, Crete, dune, herbivory, island, Mediterranean, olive-grove, non-native species, palatability, shrubland

Résumé

L'herbivorie est connue comme étant un facteur important intervenant dans l'écologie des espèces introduites. Une faible palatabilité vis-à-vis des herbivores est susceptible de contribuer aux succès des espèces invasives dans leur nouvel habitat. Dans ce travail, nous avons étudié la palatabilité (vis-à-vis d'un gastéropode herbivore et généraliste *Cepaea hortensis*) de 11 espèces végétales introduites en Crète et nous l'avons comparée à celle de 13 espèces végétales indigènes. Ces espèces sont issues de 3 catégories d'habitats (dunes, oliveraies et matorrals), de façon à permettre une reconstruction de la palatabilité à l'échelle de la communauté. Nos résultats indiquent que la palatabilité des espèces introduites s'insère dans la gamme de palatabilité rencontrée chez les espèces indigènes, sans différence significative globale entre les 2 groupes. Toutefois, pour chacun des 3 habitats testés, la palatabilité des espèces introduites s'est avérée plus élevée que la palatabilité moyenne à l'échelle de la communauté. Une seule espèce introduite, *Acacia saligna*, présente dans les formations dunaires, est apparue comme nettement moins appétante que la moyenne de la communauté. La palatabilité des espèces n'est pas reliée à leur abondance en Crète, que l'espèce soit indigène ou introduite.

Mots-clés

Espèces introduites, *Cepaea hortensis*, palatabilité des communautés, crête, dune, herbivorie, îles de Méditerranée, oliveraie, palatabilité, matorral

INTRODUCTION

Biological invasions of natural communities by non-native plant species is one of the most serious threats to biodiversity (Heywood, 1995), especially in Mediterranean-type ecosystems (Huenneke, 1988; Vitousek, 1988). The extent to which introduced species become established, and later become pests, differs widely (Williamson and Fitter, 1996; Williamson, 1999), and seems to be a function of both species traits (“invasiveness”) and community susceptibility (“invasibility”: Alpert *et al.*, 2000).

One of the interfaces between invasiveness and invasibility is the interaction between non-native plants and their herbivores. It has been argued that palatability differences allow non-native plant species to become invaders (Blossey and Nötzold, 1995). This would imply that grazers, browsers and plant parasites are important in controlling the invasion process (Noble, 1989).

Anti-herbivore chemistry of the non-native may be very different from that of the natives (often helped by the fact that the non-natives are recruited from families new to the community, Rejmánek, 1996). Thus, they present a novel suite of feeding deterrents to the local herbivores, which make them more effective in their defence against the consumers (it has even been argued that co-evolution between plants and their consumers is the cause of the diverse secondary metabolism found in plants, see Harborne, 1997; Hartley and Jones, 1997, for review). To a generalist herbivore, which is confronted with different defence cocktails in each plant species, such differences are probably less important, as it is far less engaged in co-evolution with its forage than a monophagous specialist.

To date, very little information on the palatability of non-native plant species compared to that of the local natives is available (Crawley *et al.*, 1996; Williamson and Fitter, 1996). More work has concentrated on related topics, such as comparing the performance of a non-native invader in its native and its new range (Callaway and Aschehoug, 2000; Bossdorf *et al.*, 2004) or the effect of herbivory on exotic and indigenous congeneric species (e.g. Schierenbeck *et al.*, 1994, e.g. Radford and Cousens, 2000). These studies however did not take account of the background palatability of native species when addressing the effect of herbivory on the establishment of a non-native.

In this study, we report on a bioassay-palatability trial comparing 11 non-native and 13 native plant species common to three habitats on the Greek island of Crete. We hypothesise that invasive introduced plant species on

Crete have a lower palatability to generalists than natives. The richness of the local flora, its many island endemics and the numerous non-native plant species present on the island make Crete an island of high invasion risk (Vitousek, 1988). Two of the selected habitats (dunes and shrublands) are important communities for rare species, while the third (recently abandoned olive groves) represents the anthropogenic habitat most commonly invaded by non-native species (Lonsdale, 1999).

METHODS

The study was performed on Crete, Greece (35.5° N 25° E) from 10 to 20 May 2002. Ten sites were selected for each of three habitat types: olive grove, coastal dune and phrygana (the arid dwarf-shrubland frequent in the eastern Mediterranean). In each site, cover of the most common plant species and all those used in this study were recorded. Non-native species occurred in none of the plots chosen for the recordings, because they usually produce monodominant stands within the investigated communities.

Sampling procedure and bioassay-palatability trial

Ca. 10 g leaf material of 13 typical common native and 11 common non-native plant species (table 1) was collected near the above sites. The five replicates for each plant species were several km apart. Within eight hours extracts were prepared following Grime *et al.* (1993): 1 g fresh leaf material was ground in 10 ml H₂O_{dist.}, filtered through Whatman #1 filter paper and then frozen until further use.

Palatability trials were run according to (Grime *et al.*, 1993): the test was a comparison between 0.18 ml extract on a 1.5 cm × 1.5 cm piece of Whatman #1 filter paper (added in three doses) and filter paper without extract. These filter papers were dried at 30 °C in a drying oven and then weighed to the nearest mg. Both filter papers were re-wetted with equal amounts of water just before offering them to the snails. Pre-trials have shown that snails eat the moist filter paper. After the trial, the filter paper was left to dry again and then re-weighed. Each sample extract was fed to two different snails (i.e. two subsamples per replicate).

As a bioassay agent for palatability, some 50 *Cepaea hortensis* garden snails were collected. Grime *et al.*

Native	Non-native
<i>Ammophila arenaria</i> , Poaceae (Aa)	<i>Acacia saligna</i> , Fabaceae (As)
<i>Calicotome villosa</i> , Fabaceae (Cv)	<i>Agave americana</i> , Agavaceae, (Ag)
<i>Ceratonia siliqua</i> , Fabaceae (Cs)	<i>Ailanthus altissima</i> , Simaroubaceae (Aia)
<i>Cupressus sempervirens</i> , Cupressaceae (Cu)	<i>Arundo donax</i> , Poaceae (Ad)
Forb mixture from the undergrowth (F)	<i>Carpobrotus acinaciformis</i> , Aizoaceae (Ca)
<i>Medicago marina</i> , Fabaceae (Mm)	<i>Nicotiana glauca</i> , Solanaceae (Ng)
<i>Olea europaea</i> , Oleaceae (Oe)	<i>Opuntia ficus-indica</i> , Cactaceae (Of)
<i>Otanthus maritimus</i> , Asteraceae (Om)	<i>Oxalis pes-caprae</i> , Oxalidaceae (Op)
<i>Pancreatium maritimum</i> , Amaryllidaceae (Pm)	<i>Phytolacca americana</i> , Phytolaccaceae (Pa)
<i>Quercus coccifera</i> , Fagaceae (Qc)	<i>Ricinus communis</i> , Euphorbiaceae (Rc)
<i>Sarcopoterium spinosum</i> , Rosaceae (Ss)	<i>Robinia pseudoacacia</i> , Fabaceae (Rp)
<i>Thymus capitatus</i> , Lamiaceae (Tc)	
<i>Urginea maritima</i> , Liliaceae (Um)	

Table 1. Native and non-native species sampled (abbreviations).

(1993) used the species *Cepaea nemoralis*, which is rare in Scotland (Kerney, 1976). We selected *C. hortensis* not only because it is an accepted generalist herbivore (Grime *et al.*, 1993), but also because all plant species tested are unknown to the snails. Thus, there was no 'native' plant species in the palatability trial from the snails' perspective. Hence, no bias with respect to coevolution was introduced. This could have led to a false representation of the general palatability of that species. Moreover, most larger snails in the cultivated areas of Crete are in fact non-native (e.g. *Helix aspera*), being imported from the mainland (Francisco Welter-Schultes, personal communication). By focussing solely on the palatability of water-soluble leaf content, we disregard the importance of leaf toughness, hairiness, etc. As dozens of different herbivores are consuming the plants (sheep, goat, different species of snails, beetles and bugs), it is impossible to test for specific palatability to all these herbivores. We therefore resorted to only investigate water-extractable leaf content, which will be consumed by all these leaf herbivores.

The individually marked snails were kept in a cage under near-natural conditions until used for the trial. For this, they were starved for 24 h, then put together with the extract and the control filter paper in a moist plastic bowl and left for 16 h overnight. After the trial snails were fed on lettuce for two days before the starving for the next trial. Each snail was used approx. five times for different plant species extracts. No snail received the same combination of plant species, and sequences of plant species were randomised. Feeding trials took place between 11th

June and 7th July 2002. Air temperature during the feeding period was recorded at half-hourly intervals.

A palatability index was calculated as the preference for extract over control per total amount eaten:

PI ranges from $\bar{D}1$ to +1, with negative values indicating rejection of extract compared to water. The nonlinear index used by Grime *et al.* (1993) = extract eaten/control eaten) is not sensible when very little of the control or extract sample has been eaten, as it produces a bias in favour of high index values (which can be cured by the taking the logarithm of the ratio Elston *et al.*, 1996). Using the same index (but calling it "acceptability index"), Dirzo (1980) had to discard those trials where the test disk has been rejected or where control disks were consumed less than half (although stating that these tests are a valid measure of acceptability). This was the case in some of our trials. However, their index is related to ours by the formula:

Species distribution data

The data for the species' distribution on Crete were taken from Turland (1992) and Turland *et al.* (1993). They mapped all species in a 8.25 km \times 8.25 km grid. We used the number of occupied cells as an index of distribution.

Statistical Analysis

Arcsin (0.1* square-root (x+1)) transformed data from the feeding trials were analysed with a mixed effect

model (function “lme” in R: Pinheiro and Bates; 2000), as subsamples were nested within replicates. ‘Status’ (native or non-native) was used as the fixed effect and ‘species’ as a random effect, since we were not interested in the specific identity, but rather in the difference between native and non-native. ‘Temperature at time of feeding’, ‘woodiness of the species’ and ‘snail weight’ (as well as all interactions) were used as additional explanatory variables, but were excluded from the final model as their contributions were far from significant ($P > 0.4$, model simplification following suggestions of Crawley 2002).

RESULTS

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Species differed widely in their palatability to snails (fig. 1). However, our hypothesis, that native and introduced species differ in their palatability to a generalist herbivore was not confirmed. They did not differ significantly in their palatability (fig. 2; $F_{1, 22} = 2.12$, $P = 0.160$; log-ratios produced the same results).

Within habitats, we compared the palatability of all non-native species to that of the natives occurring in this habitat, weighted by their abundance according to our vegetation recordings. This background palatability

had values of $PI_{olive\ grove} = \text{€}0.407$, $PI_{phrygana} = \text{€}0.499$ and $PI_{dune} = \text{€}0.265$. Apart from the dunes, non-native palatability was always higher than this background level. Only in the dunes did the PI-value of the introduced *Acacia saligna* indicate lower palatability than that of the native community (see fig. 1). Palatability and cover for native species was unrelated in all three habitats (Pearson’s correlation: $P > 0.3$ for all three habitats).

The species also differ widely in their distribution on Crete as measured by the number of occupied grid cells. This was, however, not related to their palatability (fig. 3). While non-natives were overall less common than natives ($F_{1, 21} = 11.32$, $P < 0.01$), palatability was unrelated to distribution for both types ($F_{1, 21} = 0.01$, $P = 0.93$).

DISCUSSION

In this comparison of the palatability of 13 native and 11 non-native Cretan plant species we could not detect a difference using a generalist herbivore as a bioassay. In fact, non-natives were even slightly more palatable than natives (although not significantly so: fig. 2). We therefore have to conclude that there is no *a priori* reason to believe that the ‘nativeness’ status of a species has any relevance

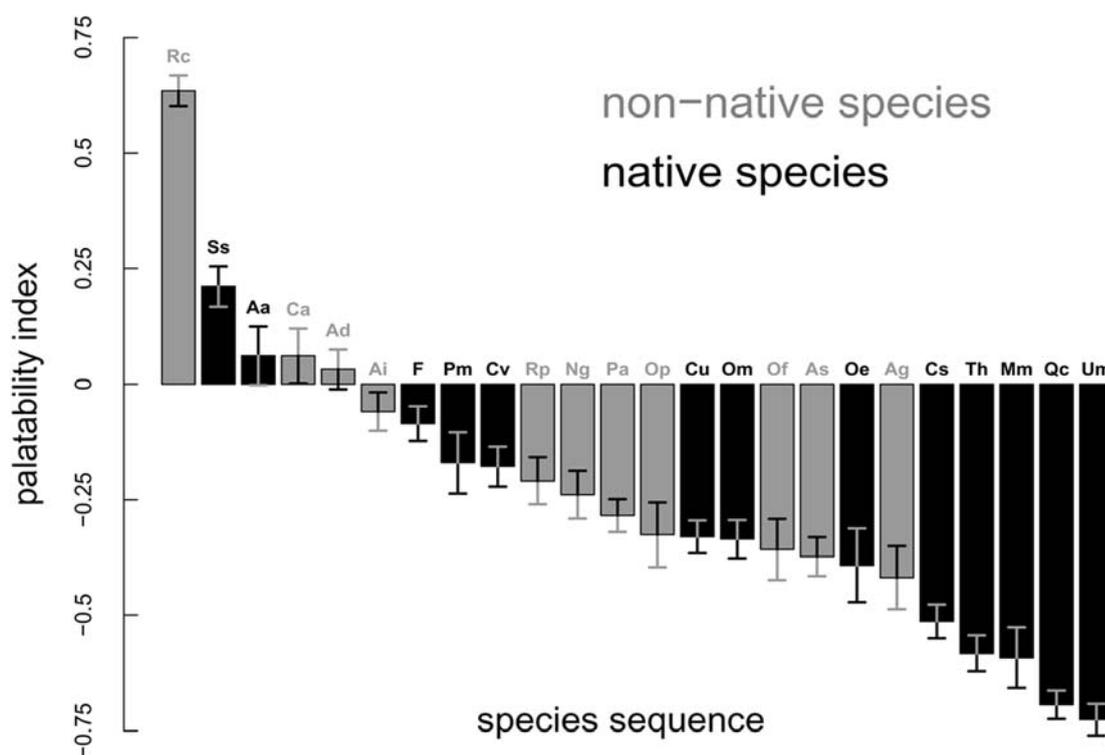


Fig. 1. Palatability sequence of the tested 24 species. Positive values indicate preference of extract over water. Abbreviations as in table 1.

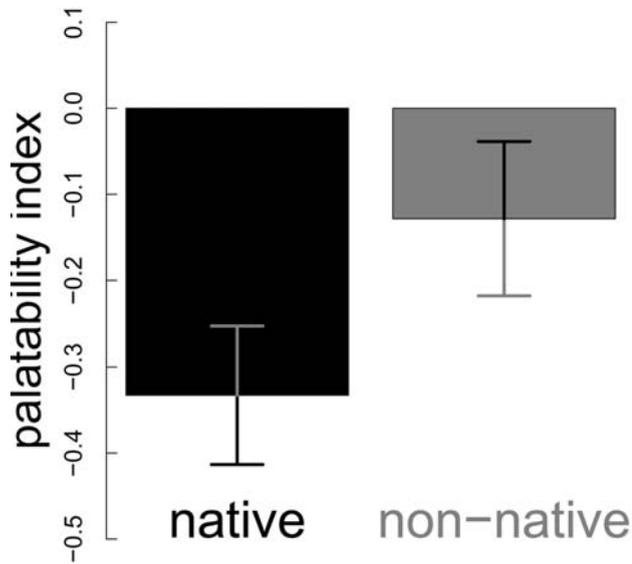


Fig. 2. Palatability of natives compared to non-natives.

for the probability of generalist herbivores limiting its success at establishment in a given habitat. Consistent with this finding, there was no relationship between palatability and distribution of the species on Crete.

Our study does not address palatability to specialist herbivores, therefore an extrapolation to the effect of herbivory *per se* on the establishment of non-native species is not possible. Possibly species that suffer heavily from a native specialist herbivore might evolve higher competitive performance in its absence (the EICA hypothesis: Blossey and Nötzold, 1995; Keane and Crawley, 2002), which is based on the ideas of Herms and Mattson (1992). A test of this coevolutionary hypothesis is beyond the scope of this study.

Palatability values measured by our experiments showed a greater variability than those given by Dirzo (1980) and Grime *et al.* (1993). In these two studies, (converted) PI values for water extracts of grasses and dicotyledons are usually in the range of 0 to 0.15 (Grime *et al.*, 1993). For plants where cell sap was known to be distasteful, PI values went down to 0.33, but clearly neither above 0 nor below 0.5, as was the case in our experiment. This is probably a consequence of their rejection of trials where only control material was consumed, biasing against low palatability. In another palatability experiment, when simultaneously offering 43 species to a snail and a cricket, consumption data show clear rejections (i.e. PI values of 1) for 24 and 10 species, respectively (Grime *et al.*, 1996). Moreover, since filter paper ranking 12th in the list, snails consumed less of 73 % of all species than of the

filter paper control. However, these trials were performed on fresh material, not extracts, and are thus not directly comparable to our situation.

Comparing the palatability of non-natives not only to that of natives, but more specifically to common native species within a given habitat has not been attempted before. Given that non-natives are slightly more palatable than natives, it is not surprising to find that the background PI-values are also generally more negative, i.e. natives are less palatable. The exception of *Acacia saligna* (syn. *Acacia cyanophylla*) in the dunes is remarkable, as this species is a pest in South Africa (Roux and Middlemiss, 1963) and became invasive more recently in western Mediterranean coastal dunes (Cronk and Fuller, 1995). Investigations into this coincidence of high community background palatability and low palatability of *Acacia saligna* may be fruitful. As for the other species, it is remarkable that the species with the highest palatability, *Ricinus communis* or Castor Oil Plant, ironically has seeds highly toxic to mammals (ricin leads to the agglutination of red blood cells). This high toxicity does not hold for leaves and snails, apparently, as none of them died in the weeks following the experiments.

Palatability is related to a plant's growth rate (Herms and Mattson, 1992). Faster growing species allocate less assimilates to anti-herbivore defense, thus being more palatable (Hartley and Jones, 1997, Jones and Hartley,

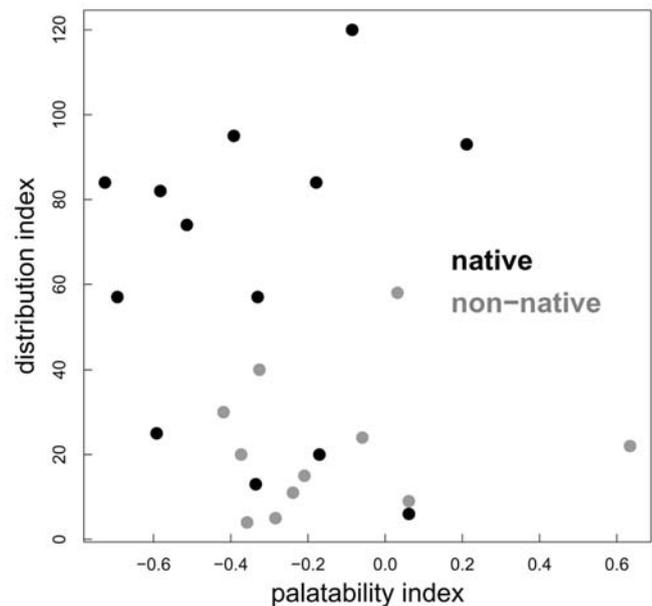


Fig. 3. Distribution of the 24 species on Crete was unrelated to palatability. Grey dots refer to non-natives, black dots to natives.

Table A1. Additional data for native and non-native species. Following species and family name is the palatability index from this study (N = 5), the nativity status (1 = native, 0 = non-native), woodiness (1 = woody, 0 = herbaceous), the distribution on Crete (max. = 120) and the average percent cover in the three vegetation types (% of all vegetation, i.e. not counting bare ground).

species	family	PI ± 1 SE	native	woody	dist.	dune/old field/phrygana
<i>Acacia saligna</i>	Fabaceae	-0.37 ± 0.042	0	1	20	
<i>Ammophila arenaria</i>	Poaceae	0.06 ± 0.063	1	0	6	47.6 / 0 / 0
<i>Agave americana</i>	Agavaceae	-0.42 ± 0.068	0	1	30	
<i>Ailanthus altissima</i>	Simaroubaceae	-0.06 ± 0.042	0	1	24	
<i>Arundo donax</i>	Poaceae	0.03 ± 0.043	0	0	58	
<i>Calicotome villosa</i>	Fabaceae	-0.18 ± 0.043	1	1	84	8 / 18.6 / 17.8
<i>Carpobrotus acinaciformis</i>	Aizoaceae	0.06 ± 0.059	0	0	9	
<i>Ceratonia siliqua</i>	Fabaceae	-0.51 ± 0.037	1	1	74	0 / 4.7 / 0
<i>Cupressus sempervirens</i>	Cupressaceae	-0.33 ± 0.036	1	1	57	0 / 0.7 / 0
Forb mixture from the undergrowth		-0.09 ± 0.038	1	0	120	22.2 / 50.2 / 14.6
<i>Medicago marina</i>	Fabaceae	-0.59 ± 0.065	1	0	25	7.1 / 0 / 0
<i>Nicotiana glauca</i>	Solanaceae	-0.24 ± 0.052	0	1	11	
<i>Olea europaea</i>	Oleaceae	-0.39 ± 0.080	1	1	95	0 / 7.8 / 5.9
<i>Opuntia ficus-indica</i>	Cactaceae	-0.23 ± 0.081	0	1	4	
<i>Otanthus maritimus</i>	Asteraceae	-0.34 ± 0.041	1	0	13	27.2 / 0 / 0
<i>Oxalis pes-caprae</i>	Oxalidaceae	-0.33 ± 0.070	0	0	40	0 / 9.9 / 0
<i>Pancreatium maritimum</i>	Amaryllidaceae	-0.17 ± 0.066	1	0	20	23 / 0 / 0
<i>Phytolacca americana</i>	Phytolaccaceae	-0.28 ± 0.036	0	0	5	
<i>Quercus coccifera</i>	Fagaceae	-0.69 ± 0.031	1	1	57	0 / 0 / 4.3
<i>Ricinus communis</i>	Euphorbiaceae	0.63 ± 0.033	0	1	22	
<i>Robinia pseudoacacia</i>	Fabaceae	-0.21 ± 0.051	0	1	15	
<i>Sarcopoterium spinosum</i>	Rosaceae	0.21 ± 0.043	1	1	93	12 / 11.6 / 52.1
<i>Thymus capitatus</i>	Lamiaceae	-0.58 ± 0.038	1	1	82	61.7 / 35.1 / 53.9
<i>Urginea maritima</i>	Liliaceae	-0.73 ± 0.034	1	0	84	0 / 5.4 / 9.9

Nomenclature follows Jahn & Schönfelder (1995).

1999). However we have no data for the species tested in this study, and a recent review found no supportive evidence for the hypothesis that non-natives have higher growth rates than natives (Daehler, 2003). Nevertheless, it may be that our specific selection of non-natives is indeed more palatable because they have a higher growth rate.

Another trait of the foliage that reduces consumption is leaf and tissue toughness. As we produced extracts, we did not test this trait, but it may play an important role in the field. Sclerophylly is very common in woody Mediterranean plant species, due to the ecophysiological constraints of the climate (Larcher, 1995) and the deterrent effect of tough leaves on herbivores (Davidson, 1993). This holds true as much for the native (*Ammophila arenaria*, *Ceratonia siliqua*, *Cupressus sempervirens*, *Olea europaea*, *Quercus coccifera* and *Thymus capitatus*) as for the non-native species in this experiment (*Acacia saligna*, *Agave americana*, *Arundo donax*, *Nicotiana glauca* and *Opuntia ficus-indica*).

The Cretan landscape has been subject to intense grazing by livestock for centuries (Rackham and Moody, 1996). Those plants now present must therefore have adapted to this situation. As additional winter feeding keeps livestock densities usually well above the population density supported by the vegetation alone, one could assume the plants are accustomed to very high levels of grazing. Hence new plant species are more likely to come from habitats with lower grazing intensity. For a generalist herbivore this could mean a higher palatability of non-natives compared to the native Cretan species. This is in fact what we found, although the slightly higher mean palatability was statistically not significant.

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APPENDIX

The table in the appendix gives data on PI, nativeness, woodiness, distribution and cover in the three vegetation types for all 24 species.

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