



Reduction of inter- and intraspecific seed mass variability along a land-use intensification gradient

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ABSTRACT

The functional response of natural patches to surrounding land-use changes is strongly related to variations in functional traits of coexisting species. To exemplify the effects on species of a general pattern of land-use intensification mountains-coastland, we investigated the variation of a key plant trait - seed mass - in small woodlots located along a land-use intensification gradient for two common species (*Asparagus albus* and *Asparagus acutifolius*) in the Mediterranean areas. Moreover, along this gradient, we also explored the relationship between seed mass variation and different environmental filters.

Along the gradient, *A. acutifolius* seed mass decreased from natural and semi-natural to urban and artificial areas (higher to lower elevation), whereas *A. albus* seed mass increased along the same gradient, with heavier seed in patches located in the urban and artificial areas than in those located in natural and semi-natural areas. At intra-specific level, *A. acutifolius* seeds were significantly different at the extremes of the gradient (natural and semi-natural vs urban and artificial areas), while *A. albus* showed significant differences both between natural and semi-natural areas and urban and artificial areas, and between agricultural and urban and artificial areas, revealing more sensitiveness to land-use change.

The land-use type influenced seed mass variability: in the small patches located in natural and semi-natural areas and in agricultural ones, we observed for both species a higher seed mass variability, being highest in the agricultural areas, while we observed a limited variability in urban and artificial areas, suggesting a homogenization in terms of seed mass within and across species in human-altered areas. Environmental drivers on the seed mass of the two species showed an opposite trend in relation to biotic, topographic and bioclimatic variables.

We observed that for two common Mediterranean species, land-use type influenced one of the most important plant functional traits (i.e., seed mass), leading to a reduction of intraspecific variability in artificial context. Understanding how and why these relations occur could improve our capacity to find adaptive strategies for environmental management.

1. Introduction

The Mediterranean basin is one of the most significantly altered hotspot on Earth (Myers et al., 2000) and therefore it has been classified as one of the most sensitive to climate change (Giorgi & Lionello, 2008). For several millennia this region has been intensively affected by human activities (Marignani et al. 2017a). Nowadays, only 4.7% of its primary vegetation remains, with a landscape strongly shaped by anthropogenic disturbance (Falcucci et al., 2007) and a constantly increasing rate of land consumption (Strollo et al., 2020). In the last 50 years, the human

pressure along the coastal zones increased worldwide, with impacts such as degradation and loss of the littoral landscape resulting from an alteration of the natural spatial pattern (Malavasi et al., 2013; Marignani et al., 2017b), while mountainous areas are abandoned and naturally reforested (Carranza et al., 2020; Falcucci et al., 2007).

In this threatened and fragmented landscape context, conservation efforts focused on the understanding and preservation of large habitat fragments, rather than the smaller ones (Cadavid-Florez et al., 2020; Fahrig, 2017). Nevertheless, small patches such as Small Woodlots Outside Forests (hereafter SWOFs; Italian National Forest Inventory;

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<http://www.infc.it>), a peculiar type of Trees Outside Forest (TOF; FAO, 2001) defined as a group of trees with an area larger than 0.05 ha and <0.5 ha (FAO, 2010, 2013), can have an important ecological value in ecosystem functioning and services (Archibald et al., 2011; Capotorti et al., 2020; Maccherini et al., 2011). These small patches, exactly likewise TOF, can indeed play an important role for climate condition, wind or soil erosion mitigation (Bellefontaine and Petit, 2001), improve water quality through phytodepuration (Endreny, 2002), promote the conservation of biodiversity, reduce the effects of habitat fragmentation (Fischer et al., 2010; Gibbons et al., 2008) and represent ecological corridors, as well as habitats for numerous animal and plant species (Bellefontaine and Petit, 2001).

The functional response of small patches like SWOFs to land-use changes, as well as their capacity to provide ecosystem services, is strongly related to changes in functional traits of coexisting species. Several ecological filters, such as abiotic and biotic drivers, are also involved in this multi-scale relationship (Keddy, 1992; Vanneste et al., 2019; Violle et al., 2007). Large-scale environmental factors could affect ecological strategies, on the other hand, local environmental variation determine niche partitioning (Vanneste et al., 2019). Finally, landscape factors such as landscape connectivity, determine species dispersion among patches and may shape the distribution of the functional traits in community assemblages (Vanneste et al., 2019). Moreover, land-use change and human activities, such as urbanization can lead to biotic homogenization (McKinney, 2006), decreasing both species and functional diversity, i.e. the species' trait compositions (McKinney, 2006; Olden & Rooney, 2006).

Surprisingly enough, we are not aware of any study focused on the ecological value and functioning of SWOFs considering, for example, SWOFs embedded within different land-use types. Although those small patches show to have a promising functional role, only a few specific studies focus on them, and in particular, on coverage estimates of TOF (Baffetta et al., 2011; Corona et al., 2011; Sallustio et al., 2018).

To exemplify the effects on species of a general pattern of land-use intensification mountains-coastland, we investigated the variation of one key plant trait - seed mass - in SWOFs located along a land-use intensification gradient for two common species (*Asparagus albus* L. and *Asparagus acutifolius* L.) in the Mediterranean areas.

Seed mass is one of the most important plant traits controlling plant population dynamics and community structure (Guo et al., 2010; Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019), playing a crucial role in interspecific interactions (Carón et al., 2014; Westoby et al., 1996). Furthermore, seed mass is important in colonization process (Vanneste et al., 2019) due to its correlation with other traits such as germination rate (Shahi et al., 2015), seedling establishment and seedling persistence (Harper et al., 1970; Fenner & Thompson, 2005; Weiher et al., 1999). Beyond its ecological importance, seed mass is also easy to measure (Chelli et al., 2019; Kattge et al., 2020). The variation in this trait can occur at all ecological levels (Guo et al., 2010; Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019): within populations, within and across species (Harper et al., 1970; Moles et al., 2005; Westoby et al., 1996), among conspecific individuals, but also within individual plants, inflorescences and fruits (Fenner & Thompson, 2005). Seed mass' variations may have important ecological implication (Cordazzo, 2002), affecting seed predation (Thompson, 1987), dispersal (Greene & Johnson, 1993) and dormancy (Harel et al., 2011) but also plant height, growth form (Garnier & Navas, 2012) and competitive plant ability (Leishman, 2001). Given the importance of this functional trait, studying and understanding the causes and consequences of the variation of the seed mass along an urbanization gradient is particularly important, in order to provide an indicator able to predict plants' responses to global changes.

For these reasons, we aimed to investigate the responses of seed mass of two congeneric species living in SWOF along a land-use intensification gradient and explore the relationship between its variation and different environmental filters. More specifically, we addressed the

following questions:

Does the land-use gradient influence seed mass and its variability at intra- and interspecific levels?

Which environmental variables mostly affect their seed mass?

2. Materials and methods

2.1. Study area and investigated species

The study was conducted in the Eastern Metropolitan City of Cagliari (Southern Sardinia, Italy), a medium-sized functional urban area characterized by three levels of fragmentation degrees (Palumbo et al., 2020). The study area covers a surface of about 18,300 ha and includes the municipalities of Maracalagonis, Quartu Sant'Elena, Quartucciu, Settimo San Pietro and Sinnai. The area is characterized by a gradient of land-use intensification that runs roughly in an east-south/west direction from mountainous areas to coastline zones (forests and semi-natural areas, agricultural areas and artificial surfaces) (Fig. 1) and an elevation gradient from 0 m a.s.l. to 700 m a.s.l.. Climate is typically Mediterranean, with a strong seasonality characterized by dry and hot summers and relatively rainy and mild winters. Canu et al. (2015) identify for this area the Mediterranean pluvioseasonal oceanic macrobioclimate, one class of continentality (strong euoceanic), four thermotypic horizons (from lower themediterranean to upper mesomediterranean) and five ombrothermic horizons (from lower dry to lower humid), resulting in a combination of 11 isobioclimates. As regards potential vegetation, the area is characterized by thermo-mesomediterranean associations of evergreen, neutrophilous or acidophilous sclerophylls. In the upper areas, the most mesophilous woods with *Quercus ilex* or *Quercus suber* and shrub elements as *Erica arborea*, *Arbutus unedo*, *Phyllirea latifolia*, *Myrtus communis* and *Juniperus oxycedrus* dominate. The high-shrub and pre-forest successions are distributed in the most thermo-xerophilous zone with wild olive shrublands (*Olea europaea* var. *sylvestris* with *Pistacia lentiscus*, *Juniperus turbinata* and *Euphorbia dendroides*) (Bacchetta et al., 2009). Due to the increasing anthropic disturbance, semi-natural areas are dominated by successional stages of thermophilous shrublands, garrigues or perennial grasslands (Fig. 1).

We studied *Asparagus acutifolius* L. and *Asparagus albus* L. (Liliaceae), two perennial species of *Asparagus* genus, with different niche breadth and present all along the gradient of land-use intensification in our study area.

A. acutifolius is a perennial, herbaceous Steno-Mediterranean species (Ferrara et al., 2011), common in shrub communities, *Quercus ilex* woods, wood glades, edges, marginal areas, from sea level to 1000–1100 m a.s.l. (Urbani et al., 2007). *A. acutifolius* is common and widely distributed in the Mediterranean basin (Ferrara et al., 2011; Sica et al., 2005), where it has been used in the traditional diet since ancient times (Benincasa et al., 2007; Ferrara et al., 2011; Mantovani et al., 2016). This species adapts to shade and to extreme temperature ranges i. e., low winter and high summer temperatures (Mantovani et al., 2019). It is a frugal species, tolerant to drought and resistant to some pathogens (Kubota et al., 2012), adapting to marginal and arid lands (Lo Porto et al., 2019). Seeds of *A. acutifolius* are described with a strong dormancy and difficult germination (Katsenios et al., 2019).

A. albus is a spiny shrub with deciduous cladodes. Flowers are hermaphrodite and the fruits, ripen by fall, are dispersed by birds (Tirado & Pugnaire, 2003); it propagates by seed and vegetative methods as well. This species is characteristic of Mediterranean maquis, linked to drylands, rocky soils and cliffs in subhumid and semiarid bioclimates, living from the sea level to 900–1000 m a.s.l. (Urbani et al., 2007; Véla, 2018). *A. albus* is distributed throughout the islands and peninsulas of South-western Europe and Northwestern Africa (Véla, 2018), with a W-Steno-Mediterranean chorotype. In Italy, it is present only in the Southern regions (Campania, Calabria, Sicily and Sardinia; Bartolucci et al., 2018).

According to Ellenberg's Indicator Values (EIV, Pignatti et al., 2005)

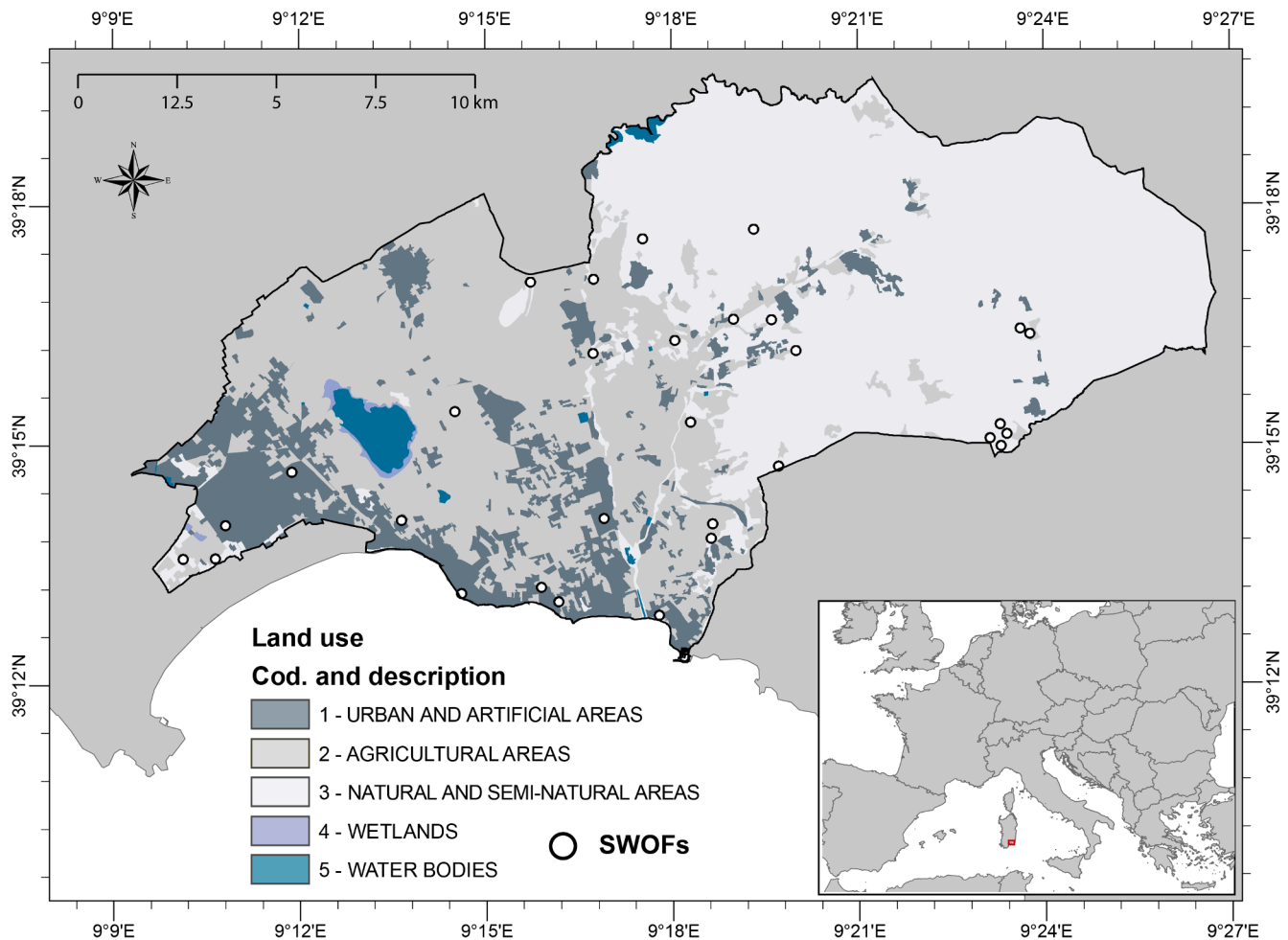


Fig. 1. Study area located in the Metropolitan City of Cagliari, Southern Sardinia, characterized by an east-south/west direction gradient of land-use intensification (natural and semi-natural, agricultural and urban and artificial areas), ranging from mountainous areas to coastline zones.

and comparing the two *Asparagus* species, *A. acutifolius* is characterized by higher values of N and R, indicating a species being more competitive in nutrient-rich soils (N) and slightly more alkaline and calcareous conditions (R) while, *A. albus* is more thermophilous and light tolerant (T, L; Table 1).

2.2. Sample design of small woodlots outside forest

Data were collected by means of a multi-phase sampling design, considering the hierarchical structure of the populations.

Using photointerpretation of digital color orthophotos (2016), we identified and mapped all SWOFs, between 0.05 and 0.5 ha. We classified the study area according to a land-use map (I hierarchical level, scale 1:25,000; RAS, 2017a): urban and artificial areas (URB), agricultural areas (AGR) and natural and semi-natural areas (NAT). Hence, according to the dominant land-use type surrounding SWOFs, each SWOF was assigned to the corresponding land-use type (URB, AGR or NAT). We excluded SWOFs with a size of <0.1 ha, as well as those

Table 1

Ellenberg indices for the two *Asparagus* species investigated. Climatic variables: light conditions (L), temperatures (T), climatic continentality (C). Edaphic conditions: moisture (U), reaction (R), nutrient availability (N), salinity (S).

Species name	L	T	C	U	R	N	S
<i>Asparagus acutifolius</i> L.	6	9	4	2	5	5	0
<i>Asparagus albus</i> L.	8	10	3	2	4	2	0

surrounded by a mixed land-use type.

From a total of 201 detected SWOFs (67 in URB, 70 in AGR, 64 in NAT) we randomly selected 30 SWOFs (8 in URB, 11 in AGR, and 11 in NAT) along the land-use gradient (Bazzato et al., 2021a).

Within the 30 SWOFs we collected seeds and information on environmental, biotic and topographic drivers.

2.3. Seed data collection

We collected mature seeds from healthy adult plants of the two *Asparagus* species during the period October-December 2019, following Pérez-Harguindeguy et al. (2013). From a total of 30 SWOFs, we found seeds of at least one species in 20 SWOFs, while in the other four sites only *A. acutifolius* individuals with no seeds were recorded. In particular, we sampled *A. acutifolius* in 18 SWOFs (5 NAT, 9 AGR, 4 URB) and *A. albus* in 14 SWOFs (3 NAT, 8 AGR, 3 URB); seeds of both species were found in 12 out of 20 SWOFs (3 NAT, 6 AGR, 3 URB). When available, we collected a minimum of 10 seeds from each individual for each species. Seeds were cleaned and air-dry stored; then, they were oven-dried at 80 °C for at least 48 h, or until equilibrium mass (Pérez-Harguindeguy et al., 2013). For each species, we weighted to 100 µg accuracy 10 seeds randomly chosen with 15 replicates from each SWOF, and then seed mass per single seed was calculated.

2.4. Environmental predictors

To explore the effect of environmental predictors on seed mass

variation, three distinct sets were considered: (i) biotic, (ii) topographic, and (iii) bioclimatic variables (Table 2). In each SWOF, we conducted a systematic sampling: we used SWOF's centroid as the middle point for a linear transect, stretching along the maximum SWOF's length. Hence, we surveyed five plots of 1 m², equally distanced one from another, along each transect (Bazzato et al., 2021a).

2.5. Biotic and structural variables

The first set of environmental predictors consisted of ten variables describing the structural and biotic characteristics of SWOFs (Table 2): trees, shrubs and herb cover, species richness, Shannon diversity index and the coefficient of variation of stem diameter of trees and shrubs at breast height (DBH).

Tree, shrub and herb coverage were visually estimated as a percentage at the plot level and then summed across the five plots in each transect per site (i.e., SWOF). For each SWOF, plant species richness and Shannon diversity index of tree, shrub and herb layer were calculated (R vegan package; Oksanen et al., 2018).

Stem diameter of trees and shrubs at breast height (1.35 m or higher) of five individuals present in, or closer to, 1 m² plot were measured for a total of 25 measures per SWOF. Based on these measurements, we calculated the coefficient of variation of the diameter at breast height (DBH) as a measure of structural diversity of SWOFs.

2.6. Topographic variables

The second set of environmental predictors consisted of variables describing topographic characteristics (Table 2) calculated for each SWOF: x and y geographical coordinates were expressed as metric units in the Monte Mario/Italy Zone 1 reference system (EPSG 3003); elevation, inclination and exposition (aspect directions in compass orientation, ranging from 10° to 332°) were derived from a Digital Terrain Model (DTM, 10 m detail) provided by Sardinia Geoportal (RAS, 2017b); coastal distance is expressed as the metric distance from the centroid of

Table 2

List of biotic, topographic and bioclimatic variables used as environmental predictors. Data refer to sites (SWOF).

Predictor set	Variable name	Variable description
Biotic	Tree	% tree cover
	Shrub	% shrub cover
	Herb	% herb cover
	spec_rich	Number of vascular plant species richness
	H	Shannon diversity index ($H = -\sum_{i=1}^S p_i \log(b)p_i$)
	CV_DBH	Coefficient of Variation of diameter at breast height (DBH)
Topographic	X	x geographical coordinate (m)
	Y	y geographical coordinate (m)
	Z	elevation (m)
	Inclination	inclination (°)
	Exposition	exposition (°)
	Coast_dist	Distance from the coastline (m)
Bioclimatic	BIO01	Annual Mean Temperature (°C)
	BIO05	Maximum Temperature of Warmest Month (°C)
	BIO06	Minimum Temperature of Coldest Month (°C)
	BIO08	Mean Temperature of Wettest Quarter (°C)
	BIO09	Mean Temperature of Driest Quarter (°C)
	BIO10	Mean Temperature of Warmest Quarter (°C)
	BIO11	Mean Temperature of Coldest Quarter (°C)
	BIO12	Annual Precipitation (mm)
	BIO13	Precipitation of Wettest Month (mm)
	BIO14	Precipitation of Driest Month (mm)
	BIO16	Precipitation of Wettest Quarter (mm)
	BIO17	Precipitation of Driest Quarter (mm)
	BIO18	Precipitation of Warmest Quarter (mm)
	BIO19	Precipitation of Coldest Quarter (mm)

each SWOF to the nearest coastline.

2.7. Bioclimatic variables

The third set of environmental predictors consisted of 14 biologically meaningful bioclimatic variables (Bazzato et al., 2021b) based on a long-term climate series derived from Canu et al. (2015). We considered bioclimatic variables related to temperature (BIO01, BIO5-BIO06, BIO10-BIO11), to precipitation (BIO12-BIO14, BIO16-BIO17), and bioclimatic variables related to both temperature and precipitation (BIO08-BIO09, BIO18-BIO19).

2.8. Statistical analyses

To investigate the difference of seed mass along grades of land-use intensification i.e. land-use type (three levels, fixed: NATural, AGRicultural, and URBan), among SWOFs (random factor, nested within land-use type, 20 levels) and species (fixed factor, two levels: *A. albus*, *A. acutifolius* crossed with land-use type and SWOF), we used a permutational univariate analysis of variance (Anderson, 2001). The advantage of this method is the possibility to accommodate random effects, hierarchical and mixed models, unbalanced and asymmetrical designs, while simultaneously maintaining robust statistical properties in a distribution-free setting (Anderson, 2017). Type III SS was used since appropriate with unbalanced design. Analyses were conducted using data of 15 replicates per SWOF for each species. We used the Euclidean distance and performed the analysis with 999 permutations of residuals under a reduced model (Anderson, 2001). Significant terms ($p < 0.05$) were investigated using a *post-hoc* permutational pairwise comparison test with 999 permutations with the PERMANOVA t statistic. We also calculated the pseudo variance component, expressed as percentage, for each source of variation. Analyses were performed using the PERMANOVA routine in the PRIMER v6 computer program (Clarke and Gorley, 2006), including the add-on package PERMANOVA+ (Anderson et al., 2008).

To identify the key factors that affect intraspecific seed mass variation of *A. albus* and *A. acutifolius*, we conducted an information-theoretic approach of a candidate set of Generalized Linear Models (GLMs) for each response variable at SWOF level (i.e., mean seed mass calculated across all 15 replicates per SWOF for each species) using the three sets of environmental drivers as predictor variables and land-use type (NAT, AGR, URB) as fixed effect.

Before performing the analyses, all predictor variables were standardized (z-scores) using “decostand” R function (Oksanen et al., 2018), in order to use the magnitude of regression coefficients to rank their relative importance. To avoid multicollinearity within each set of environmental predictors for each species, we applied a variable-selection procedure using “vifstep” function (Naimi et al., 2014) with a cut-off value of Variance inflation factor VIF = 3; only selected predictors were retained for the following steps (Table 3).

For each predictor group and each species, a subset of all candidate reduced models were automatically computed using “glmulti” R package (Calcagno, 2019). All candidate reduced models were ranked based on comparisons of AICc, a variant of Akaike's Information Criterion corrected for small sample sizes and small ratio n/K (sample size and predictors) (<40; Burnham & Anderson, 2002). All models with a difference in $\Delta AICc \leq 2$ when compared to the best model (i.e., the one with lowest AICc value) were considered to have similar plausibility and display in results with their Akaike weights (w_i , ranging from 0 to 1) and their evidence ratios (w_1/w_i) in comparison to the highest-ranked model (w_1) (Burnham & Anderson, 2002). For all subsets of candidate models where the highest Akaike weight (w_1) was below 0.90 and all other models had a small difference of evidence ratios, we used model averaging to calculate the relative importance (RI, the sum of Akaike weights w_i across all models with 95% probability where the variable appeared) of each predictor and to generate parameter coefficients for the

Table 3

Biotic, topographic and bioclimatic set of predictor variables selected by the variable-selection procedure (VIF = 3 as cut-off value).

<i>Asparagus acutifolius</i>		<i>Asparagus albus</i>	
Predictors	VIF	Predictors	VIF
Biotic			
H	1.1	H	1.1
Tree	1.5	Tree	1.7
Shrub	2.7	Shrub	2.8
Herb	1.4	Herb	1.3
CV of DBH	1.8	CV of DBH	1.8
Topographic			
X	1.8	X	1.6
Y	1.2	Y	1.2
Inclination	2.1	Inclination	1.5
Exposition	1.7	Exposition	1.1
Bioclimatic			
BIO09	1.6	BIO08	1.1
BIO10	1.5	BIO09	1.1
BIO13	1.1		

remaining predictors (Burnham & Anderson, 2002). Although a RI threshold does not exist, a high RI value of the predictor indicates that the variable is frequent among the candidate models with high Akaike weights (w_i), and it has a greater probability to be a component of the best model (Burnham & Anderson, 2002).

3. Results

A total number of 11,513 seeds of *Asparagus* were collected in 20 SWOFs: 7,143 from 160 individuals of *A. acutifolius*, and 3,597 from 149 individuals of *A. albus*.

Mean seed mass of *A. acutifolius* was 36.95 mg (SE = 0.54), in line with data available in the literature (ranging from 34.5 mg to 40.8 mg per seed; Kattge et al., 2020). It ranged from a maximum of 58.4 mg to a minimum of 15.2 mg per seed: the heavier seeds were recorded in SWOFs located in natural and semi-natural areas, while the lighter seeds were found in SWOFs enclosed in agricultural ones. Mean seed mass for *A. albus* is 28.65 (SE = 0.24), coherent with available data (28.42 with a SE = 1.52; Kattge et al., 2020). The seed mass ranged from a maximum

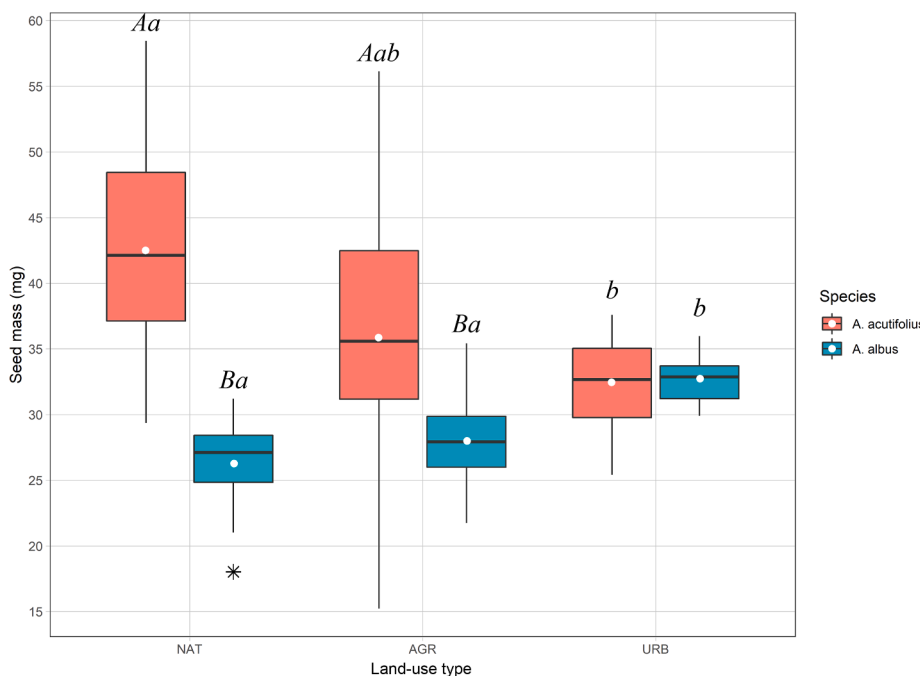


Fig. 2. Variation in seed mass (mg) for *A. acutifolius* (270 seeds) and *A. albus* (210 seeds) in SWOFs located in different land-use types: NAT areas (75 seeds of *A. acutifolius*; 45 seeds of *A. albus*), AGR areas (135 seeds of *A. acutifolius*; 120 seeds of *A. albus*), URB areas (60 seeds of *A. acutifolius*; 45 seeds of *A. albus*). Boxes span the 25th to the 75th percentile; whiskers span from 10th percentile to the 90th percentile. The bar across the box shows the median seed mass, the white point the mean seed mass and the star the outliers. Different capital letters indicate significant differences between species within each land-use type; different lower-case letters indicate significant differences between land-use types within each species.

of 36 mg to a minimum of 18 mg per seed, with heavier seeds recorded in the urban and artificial areas and the lighter ones in the natural ones. Boxplots of the seed mass variation, among different land-use types, showed an opposite trend for the two species studied (Fig. 2). Both median and mean values decreased in *A. acutifolius* along the land-use intensification gradient (from natural and semi-natural to urban and artificial areas). In contrast, these values increased in *A. albus* along the same gradient. Furthermore, for both species, the less seed mass variability was found in SWOFs located in urban and artificial areas (URB) and the highest in agricultural ones (AGR).

Permutational univariate analysis of variance revealed that almost all sources of variation significantly affected seed mass for both species (Table 4). The largest component of variation was associated with the main effect of species, followed by the main effect of SWOF, the Land-use type × Species interaction and SWOF × Species interaction (Table 4). Pairwise comparisons for the Land-use type × Species interaction revealed that within NAT and AGR areas, the contrasts between species were significant (Table 5). Moreover, within species the contrasts were all significant except for *A. acutifolius* among AGR vs. NAT and AGR vs. URB, and for *A. albus* among AGR vs. NAT (Table 5).

3.1. Effect of environmental drivers on the mean seed mass of *Asparagus acutifolius*

The model selection procedure applied to biotic predictors exploring

Table 4

Permutational univariate analysis of variance results on seed mass of *A. acutifolius* and *A. albus*. Significance codes: (*) $p < 0.05$, (***) $p < 0.001$.

Source of variation	df	MS	F	Variance component (%)
Land-use type	2	0.0225	0.31	0
Species	1	0.7033	20.73**	25.77
SWOF (Land-use type)	17	0.0821	164.19***	23.91
Land-use type × Species	2	0.2098	6.18*	22.42
SWOF (Land-use type) × Species	9	0.0339	67.89***	18.93
Residual	448	0.0005		8.96
Total	479			

Table 5

Results of PERMANOVA t statistic comparisons between species within Land-use type and among Land-use types within species. NAT – Natural and semi-natural areas, URB – Urban and artificial areas, AGR – Agricultural areas; (*) $p < 0.05$.

Contrast	t statistic
Within Land-use type - Natural and semi-natural areas (NAT) <i>A. acutifolius</i> , <i>A. albus</i>	4.7182*
Within Land-use type - Agricultural areas (AGR) <i>A. acutifolius</i> , <i>A. albus</i>	3.6557*
Within Land-use type – Urban and artificial areas (URB) <i>A. acutifolius</i> , <i>A. albus</i>	0.6509
Within species <i>A. acutifolius</i>	
AGR, NAT	1.2819
AGR, URB	0.6527
NAT, URB	2.4500*
Within species <i>A. albus</i>	
AGR, NAT	0.9102
AGR, URB	2.8562*
NAT, URB	3.8084*

mean seed mass of *A. acutifolius* identified two candidate reduced models (Table 6). The first one retained only the intercept ($w_1 = 0.268$), meanwhile, the second one also included the coefficient of variation of DBH ($w_1 = 0.100$) with a small difference in the evidence ratios between them (Table 6).

From all possible candidate models of topographic predictors, only one best model was identified with a low Akaike weight ($w_1 = 0.380$) (Table 6).

Considering bioclimatic predictor variables, two candidate reduced models were identified, but the Akaike weights of these models tended to be very small ($w_1 \ll 0.90$) (Table 6), and the values of evidence ratios confirmed there was insufficient support to the best AICc model (Table 6).

Model-averaged estimates confirmed low relative importance of all biotic predictors to explain the variation in mean seed mass of *A. acutifolius* ($RI < 0.2$), reflecting their low weight (Table 7).

Considering values of model-averaged parameter estimates and their relative importance based on the set of models within 95% confidence level, the variables most frequently found in candidates were inclination and exposition, with a high ($RI = 0.7604$) and low relative importance ($RI = 0.3582$) respectively, showing positive associations with the variation of the mean seed mass (Table 7).

Average parameter coefficients showed a positive variation in mean seed mass associated with increasing precipitation of the wettest month (BIO13) that showed the highest relative importance ($RI = 0.5305$) on the set of bioclimatic models within 95% confidence level (Table 7).

Table 6

Summary of the top regression models within 2 AICc units of the highest-ranked model predicting mean seed mass of *A. acutifolius* (ACUTI). The models are in descending order from the most to the least supported based on Akaike information criteria (AICc). For candidate subset, we reported difference in AIC value (Δi) from that of the best model; Akaike weights of the *i*th model (w_i), representing the probability that the *i*th model is the best fitting model in each candidate subset; evidence ratios ($ER = w_1/w_i$), comparing *i*th model (w_i) to the highest-ranked model (w_1).

Group of predictors	Candidate models	AICc	Δi	w_i	ER
Biotic	ACUTI ~ 1	-32.762	0.000	0.268	1.000
	ACUTI ~ 1 + CV_DBH	-30.788	1.974	0.100	2.683
	ACUTI ~ 1 + CV_DBH	-37.657	0.000	0.380	1.000
Topographic	Inclination	-33.438	0.000	0.352	1.000
	ACUTI ~ 1	-32.762	0.676	0.251	1.402

Table 7

Model-averaged estimates for predictors of mean seed mass of *A. acutifolius* response. The average parameter coefficients (β) from all candidate models with 95% probability are presented. The relative importance (RI) reflects the frequency with which a given predictor is found in the candidate models.

Group of predictors	Predictors of seed mass of <i>A. acutifolius</i>	β	Unconditional SE	RI	
Biotic	(Intercept)	0.3681	0.0222	1.0000	
	CV_DBH	0.0037	0.0084	0.1997	
	H	0.0018	0.0055	0.1630	
	Shrub	0.0024	0.0064	0.1625	
	Tree	0.0009	0.0042	0.1475	
	Herb	-0.0004	0.0038	0.1459	
	Land-use type-NAT	0.0085	0.0170	0.1265	
	Land-use type-URB	-0.0044	0.0115	0.1265	
	Topographic	(Intercept)	0.3695	0.0177	1.0000
		Inclination	0.0382	0.0273	0.7604
Exposition		0.0118	0.0186	0.3582	
X		-0.0014	0.0057	0.1639	
Y		0.0009	0.0037	0.1370	
Bioclimatic		(Intercept)	0.3687	0.0208	1.0000
	BIO13	0.0201	0.0237	0.5305	
	BIO09	0.0010	0.0042	0.1463	
	BIO10	-0.0001	0.0029	0.1333	
	Land-use type-NAT	0.0050	0.0105	0.0755	
	Land-use type-URB	-0.0026	0.0069	0.0755	

3.2. Effect of environmental drivers on mean seed mass of *Asparagus albus*

The Akaike weights of the best-ranked regression models examining the effect of biotic predictors on mean seed mass of *A. albus* showed a high probability that the first model ($w_1 = 0.457$) was the best fitting model in comparison to the second one (Table 8).

Considering topographic and bioclimatic predictor variables, five candidate reduced models were identified within 2 AICc units of the highest-ranked model (Table 8). However, Akaike weights of this subset

Table 8

Summary of the top regression models within 2 AICc units of the highest-ranked model predicting mean seed mass of *A. albus* (ALBUS). The models are in descending order from the most to least supported based on Akaike information criteria (AICc). For candidate subset, we reported difference in AIC value (Δi) from that of the best model; Akaike weights of the *i*th model (w_i), representing the probability that the *i*th model is the best fitting model in each candidate subset; evidence ratios ($ER = w_1/w_i$), comparing *i*th model (w_i) to the highest-ranked model (w_1).

Group of predictors	Candidate models	AICc	Δi	w_i	ER
Biotic	ALBUS ~ 1 + Tree + CV_DBH	-70.216	0.000	0.457	1.000
	ALBUS ~ 1 + CV_DBH	-68.593	1.622	0.203	2.250
Topographic	ALBUS ~ 1 + Land-use type + X	-54.677	0.000	0.173	1.000
	ALBUS ~ 1 + Land-use type	-54.004	0.673	0.124	1.400
	ALBUS ~ 1 + X	-53.960	0.717	0.121	1.431
	ALBUS ~ 1 + Inclination	-53.720	0.957	0.107	1.613
	ALBUS ~ 1 + Y + Inclination	-52.757	1.920	0.066	2.611
Bioclimatic	ALBUS ~ 1 + BIO19	-55.656	0.000	0.208	1.000
	ALBUS ~ 1 + Land-use type + BIO19	-54.652	1.003	0.126	1.652
	ALBUS ~ 1 + BIO06 + BIO19	-54.459	1.196	0.115	1.819
	ALBUS ~ 1 + Land-use type	-54.004	1.652	0.091	2.284
	ALBUS ~ 1 + BIO10 + BIO19	-53.658	1.998	0.077	2.716

of reduced models tended to be very small ($w_1 \ll 0.90$) and the values of evidence ratios proved to be insufficient to support the best AICc model for each subset (Table 8), highlighting the need to estimate parameters by model-averaging.

Model-averaged estimates for biotic predictors allowed us to identify two predictors with high relative importance, both retained in the highest-ranked model: coefficient of variation of DBH (RI = 1) and tree cover (RI = 0.61), which were associated with a negative and positive response of mean seed mass of *A. albus*, respectively (Table 8). Other biotic predictors – herb cover and Shannon diversity index - showed a generally low relative importance on the set of models within 95% confidence level, reflecting their low weight (Table 8).

Considering topographic predictors, the variables most frequently found in reduced models were longitude and land-use types, also retained in the first three models, with a high (RI = 0.4452) or lower (RI = 0.3580) relative importance, respectively (Table 9). Average parameter coefficients showed that mean seed mass of this species responded negatively to the increasing of longitude, and it was positively associated with the urban and artificial areas and, at the end of the gradient, negatively associated with the natural and semi-natural ones (Table 9). The remaining variables – inclination, latitude, and exposition – were less frequent than others and showed a negative relationship with the variation of mean seed mass (Table 9).

Model-averaged estimates for bioclimatic predictors showed that the precipitation of the coldest quarter (BIO19) was the variable most frequently found (RI = 0.6218) (Table 9), and it was also retained in four out of five models from the set of candidates (Table 8). Average parameter coefficients showed a positive variation in mean seed mass associated with a decline in the precipitation of the coldest quarter (BIO19) and in the mean temperature of the warmest quarter (BIO10) (Table 9). On the contrary, mean seed mass of *A. albus* responded positively to the increasing of minimum temperature of the coldest month (BIO06) and mean temperature of the driest quarter (BIO09), even if both variables had low relative importance (Table 9).

4. Discussion

Several studies highlighted the relationship between plant reproductive traits and different environmental variables; variation in seed traits, especially in seed mass, was usually related to environmental

Table 9

Model-averaged estimates for predictors of mean seed mass of *A. albus* response. The average parameter coefficients (β) from all candidate models with 95% probability are presented. The relative importance (RI) reflects the frequency with which a given predictor is found in the candidate models.

Group of predictors	Predictors of seed mass of <i>A. albus</i>	β	Unconditional SE	RI
Biotic	(Intercept)	0.2865	0.0040	1.0000
	CV_DBH	-0.0283	0.0043	1.0000
	Tree	0.0056	0.0054	0.6134
	Herb	0.0011	0.0021	0.1984
	H	-0.0005	0.0011	0.0801
Topographic	(Intercept)	0.2836	0.0088	1.0000
	X	-0.0072	0.0093	0.4452
	Land-use type -NAT	-0.0031	0.0089	0.3580
	Land-use type -URB	0.0164	0.0226	0.3580
	Inclination	-0.0045	0.0072	0.2855
	Y	-0.0030	0.0053	0.2285
	Exposition	-0.0015	0.0030	0.1511
Bioclimatic	(Intercept)	0.2843	0.0084	1.0000
	BIO19	-0.0118	0.0110	0.6218
	Land-use type -NAT	-0.0013	0.0070	0.2687
	Land-use type -URB	0.0116	0.0180	0.2687
	BIO10	-0.0036	0.0061	0.2682
	BIO06	0.0033	0.0056	0.2553
	BIO09	0.0016	0.0033	0.1525

conditions such as climate, soil nutrients and moisture (Bhatt et al., 2019; Quesada et al., 1996) but can occur under other factors, such as environmental stress caused by land-use change and habitat fragmentation (Chen and Dirmeyer, 2020). Our study area presents a well-known pattern of land-use/transformation that shows a non-random spatial pattern, but exemplifies a global pattern: we observed a gradient of anthropic use intensification of the landscape, ranging from a low intensity in the higher elevation sites, to a medium intensity agricultural use in the hilly areas and the highest intensity in the coastal and lowland areas (in Italy; see Strollo et al., 2020; Rosati et al., 2008).

Along this gradient, *A. acutifolius* seed mass decreased from natural and semi-natural to urban and artificial areas (higher to lower elevation), whereas *A. albus* seed mass increased along the same gradient, with heavier seed in SWOFs located in the urban and artificial areas than in those in natural and semi-natural ones. At intra-specific level, *A. acutifolius* seeds were significantly different at the extremes of the gradient (NAT vs URB). *A. albus* showed significant differences both between natural and semi-natural and urban and artificial areas, and between agricultural and urban and artificial areas, revealing more sensitiveness to land-use change.

Comparing the two species, at the interspecific level we observed that the land-use type influenced seed mass variability: in SWOFs located in natural and semi-natural and agricultural areas, we observed for both species a higher seed mass variability, being highest in the agricultural areas, while we observed a limited variability in urban and artificial ones, suggesting a homogenization in terms of seed mass in SWOFs located in these areas. These results highlighted that land-use change might not only shape the mean seed mass of coexisting species, but also the variability of seed mass within and across species. Urban disturbance related to human activities promote homogenization in the physical environment (McKinney, 2006): the decrease of variability and the homogenization for this trait in the two species within SWOFs located in the urban matrix can be seen as a “biotic homogenization” (McKinney, 2006), a sort of levelling in terms of functional diversity, with both heavier and lighter seed mass being disadvantaged in urban context at inter-specific level (Williams et al., 2015).

The anthropic gradient that we observed in the study area is superimposed on a natural one, therefore we investigated if the differences we detected could be attributable to environmental variables, rather than to the land-use. Hence, as a second step, we decided to explore the environmental factors that mostly influenced the seed mass variation along the land-use intensification gradient. In this context, the ecological value of small isolated patches depends not only on environmental variables per se but also on how these environmental factors are shaped and modified by different anthropic land use.

A. acutifolius seed mass is positively influenced by local factors, such as inclination and exposition, and by the precipitation of the wettest month (BIO13): in our land-use intensification gradient this corresponded to natural and semi-natural areas, usually steeper and rugged compared to the more transformed ones (i.e., agricultural and urban and artificial areas), where uneven-structured *Quercus ilex* woods dominate, characterized by a lower mesomediterranean, upper subhumid, eueceanic weak bioclimate (Canu et al., 2015).

On the contrary, *A. albus* appeared to be more sensitive considering both the highest number of predictors selected from model selection procedure and the inclusion in these models of the land-use type. Along the land-use intensification gradient, seed mass was higher in SWOFs located in urban and artificial areas and characterized by a larger tree cover and a simplified structure (i.e. reforestation and urban parks); nevertheless, even if more thermophilus and light tolerant compared to *A. acutifolius*, the mean temperature of summer could represent a limiting factor for *A. albus*, characterized by a more restricted ecological amplitude and a relatively reduced tolerance to environmental variations (Véla, 2018). Bhatt et al. (2019) hypothesized that the variability in seed mass of two species, recorded from population with similar

climatic characteristics, can be attributed to resource availability among different populations. Accordingly, the positive effect of the urban and artificial land-use type for the seed mass in *A. albus* could also be related to urban nitrogen deposition, a phenomenon described for lichen communities (Llop et al., 2017) and plant-traits (Liu et al., 2020). In the future, soil samples could help us to validate this hypothesis.

Our results demonstrated the different effect of environmental drivers on seed mass of the two species, showing an opposite trend in relation to biotic, topographic and bioclimatic variables. These opposite responses are common at intra and interspecific level. Carón et al. (2014, 2018) found species-specific responses of seed mass variation to environmental conditions in the Central Andes: along a latitudinal and elevational gradient, seed mass of tree species are strongly influenced by the elevation, with seed mass of some species increasing with elevation and lower temperatures and an opposite trend was detected for other species. In Carón et al. (2014), seed traits were studied along a latitudinal gradient in Europe; results showed that closely related *Acer* species exhibited divergent responses of seed mass to temperature variation, with *A. platanoides* more influenced by the climatic conditions than *A. pseudoplatanus*. Similarly, Soper Gordon et al. (2016) found an opposite variation pattern for seed mass of different species in relation to temperature and latitude in North America. For *Allium* species in the Tibetan plateau, Ge et al. (2020) reported a selection pressure on species with smaller seeds and less germination in higher elevation, showing that temperature, elevation and seed mass had independent effects on seed germinability.

Intraspecific variation and variability in seed mass along an environmental gradient could enhance the species' ability to cope with rapidly changing environmental conditions (Wu et al., 2018). Furthermore, these differences can also be related to the variation in other traits such as seed shape and/or plant height and have implications in seeds germination percentage and other life-history stages. Different studies affirmed the relation between seed mass and germination rate (Shahi et al., 2015) and seedling establishment and persistence (Fenner & Thompson, 2005; Harper et al., 1970; Weiher et al., 1999). Overall, the relationship between the effects of land-use type and different environmental drivers with the seed mass confirms the importance of studying this functional trait and its use as an indicator of plants responses in human-altered areas.

5. Conclusions

Environmental drivers that affect seed mass can differ between species and at the same time, the same drivers can act in a different direction and with different intensity, leading to conclusions that defy generalization patterns (Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019). We observed that for two common Mediterranean species, land-use type influenced one of the most important plant functional traits, leading to a reduction of inter- and intraspecific variability in urban and artificial areas. Monitoring seed traits, such as seed mass, can provide a promising indicator of plants' responses to human disturbance and to predict their reactions to global changes. Understanding how and why these relations occur could improve our capacity to find adaptive strategies for environmental management (Jiménez-Alfaro et al., 2016). In this framework, small woodlots outside forest should be a priority in landscape and urban planning, as well as in biodiversity management practices. Accordingly, we should enhance conservation efforts in understanding and preserving these small patches and fragments (Sallustio et al., 2018).

CRedit authorship contribution statement

Erika Bazzato: Conceptualization, Data curation, Formal analysis, Methodology, Software, Writing - original draft, Writing - review & editing. **Elisa Serra:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Simona Maccherini:**

Conceptualization, Methodology, Supervision, Writing - review & editing. **Michela Marignani:** Conceptualization, Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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