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Distribution and ecology of wild lettuces *Lactuca serriola* L. and *Lactuca virosa* L. in central Chile

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Ključne besede: alohtone vrste, višinske omejitve, ohranjanje dednine, strupena ločika, rastlinska invazija, pripotna ločika.

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Abstract

Wild lettuces (*Lactuca* L.) provide valuable genetic resources for crop breeding, but are also significant invasive weeds. We explored the distributions, habitats, and ecological characteristics of populations of wild *Lactuca* species in central Chile. We documented two species – *Lactuca serriola* L. (prickly lettuce) and *Lactuca virosa* L. (opium/bitter lettuce) in 204 localities. These observations indicate that: i) both allochthonous (Euroasian) *Lactuca* species occur and are able to regenerate in central Chile; ii) *L. serriola* forms dense populations in urbanized areas; iii) both species can expand along transport corridors to high elevations; iv) the spread of *L. virosa* and persistence of dense populations in elevations above 2,000 m a.s.l. prove the invasiveness of this species in extreme climates; v) both species may contain novel traits of interest for germplasm conservation.

Izvleček

Divje vrste ločik rodu *Lactuca* L. predstavljajo pomemben rezervoar genskih virov z uporabno vrednostjo za žlahtnitelje, lahko pa predstavljajo tudi nezaželen invazivni plevel. Preučili smo razširjenost, rastišča in ekološke značilnosti populacij divjih vrst rodu *Lactuca* v osrednjem Čilu. Na 204 lokacijah smo dokumentirali dve vrsti divje solate in sicer pripotno ločiko (*Lactuca serriola* L.) ter strupeno ločiko (*Lactuca virosa* L.). Rezultati kažejo da se obe alohtoni (evroazijski) vrsti pojavljata in uspešno obnavljata v osrednjem Čilu. *L. serriola* se pojavlja v gostih populacijah v urbanih območjih, obe vrsti se širita ob transportnih poteh do najvišjih nadmorskih višin. Širjenje in pojavljanje vrste *L. virosa* v gostih populacijah na nadmorskih višinah nad 2000 m n. v. nakazujejo invazivnost te vrste v ekstremnih klimatskih razmerah, obe vrsti pa imata nove značilnosti, ki so pomembne za ohranjanje dednine.

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Introduction

The genus *Lactuca* L. (Asteraceae) is represented by about 100 species, including one domesticated taxon – lettuce (*Lactuca sativa* L.) (Lebeda et al., 2007a; Lebeda et al., 2004). Two species – *Lactuca serriola* L. (prickly lettuce) and *Lactuca virosa* L. (opium/bitter lettuce) – both native to the Mediterranean region (Feráková, 1977), occur as non-native populations (*sensu* Pyšek et al., 2004) in corollary climates in central Chile. While the taxa are close relatives to the domesticate and have contributed as genetic resources to its improvement (Lebeda et al., 2002, 2008, 2014, 2019b), they exhibit the potential to become significant invasive species in the country (Alexander et al., 2009a, b; Alexander, 2010, 2013, 2016; Fuentes et al., 2014).

Background on target taxa and region

L. serriola L. is an annual to biennial therophyte, growing preferably on fertile, carbonate-rich soil, but its ecological amplitude is rather wide. The species is considered native to North (Mediterranean) and East Africa; West, Central, and South Asia; and to Europe, and is naturalized in Southern Africa, Australasia, North America, and South America (Lebeda et al., 2004). This is a pioneer plant of open habitats including screes, quarries, ruins, and agricultural fields. It grows in areas with disturbed soil surfaces and has become a typical weedy plant of suburbs and expanding cities (Feráková, 1977). *L. serriola* is spreading in Europe along transport corridors (railway tracks and roads), and is considered a weedy species with high invasiveness potential (Lebeda et al., 2001, 2004, 2007a, b; Alexander, 2010), including the capacity to establish at high elevations (Alexander et al., 2009a). In Europe it is frequently recorded at elevations of 200 – 600 m.a.s.l. Above this altitude it is rather rare, but has been recorded in Switzerland at 1,500 m.a.s.l., in Turkey at 1,750 m.a.s.l., in Afghanistan at 3,100 m.a.s.l., and in the northern Himalayas up to 3,600 m.a.s.l. (Lebeda et al., 2004).

L. serriola is a morphologically highly variable species, and according to the shape (division) of its leaves, two varieties have been identified: *L. serriola* L. var. *serriola* with divided cauline leaves, and var. *integrifolia* with entire cauline leaves (Feráková, 1977). Both varieties, also recognized as forms (Lebeda et al., 2001) have glabrous inflorescences. A third variety, *L. serriola* var. *coriacea* has a densely prickly upper stem and inflorescence (Feráková, 1977). Large variation in morphological traits and developmental stages, at least to some extent related to environmental conditions, has been observed (Lebeda et al., 2007a, b).

L. virosa L. is an annual to biennial thermophilous species, considered native to Europe and North Africa from lowland to submontaneous regions, mostly in the Mediterranean basin, up to 1,000 m.a.s.l. in central France, 1,560 m.a.s.l. in Switzerland, and 2,300 m.a.s.l. in Morocco (Lebeda et al., 2004). Usually it grows in ruderal (disturbed and waste) places, including roadsides, embankments, and grassy margins. As for natural habitats, sand dunes near the seashore, rocks, screes, and forest clearings are optimal (Feráková, 1977). Lebeda et al. (2004) summarized recent data on its distribution and documented that *L. virosa* is rare in central Europe, its historical synanthropic area is receding, and it is considered as an endangered species in some areas in Germany and Austria. Recent records on this species are missing from some European countries, e.g. from Czech Republic (Grulich, 2019). The species was introduced as a medicinal plant into several other countries in Europe and also into Northern America (Feráková, 1977; Lebeda et al., 2019a), and is naturalized in Australasia (Lebeda et al., 2004).

Within *L. virosa*, there is a considerable variation with regard to leaf form, spination and anthocyanin pigmentation. The following intraspecific taxa are recognized: var. *virosa* with non-lobed, entire leaves, and var. *cruenta* with divided leaves (Feráková, 1977).

Both *L. serriola* and *L. virosa* are now essentially globally distributed (Lebeda et al., 2004, 2007b). *L. serriola* is considered a weedy species in many countries (Lebeda et al., 2004, 2007b), and an invasive species in North America (Lebeda et al., 2012a, 2019a) and in Chile (Fuentes et al., 2014). *L. virosa* is considered to have similar invasiveness potential (Macaya et al., 1999).

Central Chile is one of five major regions in the world having a mediterranean-type climate, with winter-wet and summer-dry conditions, and irregular timing of rainfall events in autumn (di Castri, 1991; Guillerm, 1991). The Chilean mediterranean-climate zone can be divided physiographically into four regions: the Cordillera de los Andes in the east with numerous peaks over 5,000 m.a.s.l.; the Cordillera de la Costa to the west with peaks that seldom rise over 1,000 m.a.s.l.; the "Depresion Intermedia" of the Central Valley between these ranges; and the littoral fringe bordering the Pacific Ocean (Montenegro et al., 1991).

These eco-geographic conditions, combined with dense human population settlements and extensive agricultural practices favor the spread of non-native (Pyšek et al., 2004) and exotic (Figueroa et al., 2004) plant species introduced from the Old World Mediterranean basin, Southern Africa, and other areas with mediterranean climates (Fox, 1990; Myers, 1990; di Castri, 1991; Figueroa, et al. 2004). Entry of many non-native plants into Chile has been connected to settlement of Europeans in and after the 16th century, however exact dates are rarely known (Aschmann, 1991). Marticorena & Quezada (1985) reported 13 percent of the Chilean flora as introduced plants, while more recently, Fuentes et al. (2013) recorded 743 naturalized taxa from 361 genera, over half of which may be considered invasive. Some 113 species of introduced or naturalized herbs were recorded in the mediterranean-climate zone by Montenegro et al. (1991).

To our knowledge, no native (autochthonous) *Lactuca* species occur in Chile (Lebeda et al., 2004). Data on first records of non-native (allochthonous) *Lactuca* in the country are limited and differ by source. Cultivated lettuce (*L. sativa*) is documented from the first half of 19th century by Gay (1847), who gave a short description of the genus and examples of three cultivated types, classified as annual species *Lactuca crispa, Lactuca capitata* and *Lactuca sativa*; the author also mentioned a fourth cultivated species *Lactuca laciniata* Roth, described as a biennial with higher leaves pinnatifid and lower leaves runcinate. The name *L. laciniata* Roth. has been recognized as a synonym for *L. serriola* L. (Feráková, 1977), thus this description could be the first of *L. serriola* in Chile. Further, *L. laciniata* in Gay (1847) may represent primitive oilseed lettuce, which is characterized by a high percentage (35%) of oil in the seeds, which has been used for cooking (Boukema et al., 1990). Boukema et al. (1990) mentioned that oilseed lettuce may be either *L. serriola* or *L. sativa*, or intermediate types between these species.

The first verified record of *L. serriola* in Chile dates from 1901 (Fuentes et al., 2014). Occurrences of *Lactuca scarriola* L. (synonym for *L. serriola* L.) in Quinta Normal and other sites around Santiago de Chile was reported by Reiche (1910). In a check list of alien flora in Chile, four *Lactuca* species are mentioned – *L. serriola* (first record in 1905) and *L. virosa* (1933), as well as cultivated *L. sativa* (1955), and another non-native wild species, *Lactuca saligna* L. (1960) (Ugarte et al., 2011). *L. sativa*, *L. serriola* and *L. virosa* are the only species reported in a previous (Marticorena & Quezada, 1985) and the most recent checklist of vascular plants in Chile (Rodriguez et al., 2018).

Introduced *L. serriola* as a naturalized herb of the mediterranean-climate zone was recorded in sclerophyllous matorral and montane matorral communities in Chile (Montenegro et al., 1991). However this species was not mentioned by Montenegro et al. (1991) among the non-native species whose invasion is closely related to disturbance, and which are abundant along railway tracks, roadsides, paths, and cultivated fields.

By the end of the 20th century *L. serriola* as a weedy species was reported in central Chile from the region 4 (administrative units in Chile) – Coquimbo in the North to region 9 – Araucania in the South (Matthei, 1995). Recently the northern frontier of known distribution was expanded, reaching region 2 – Antofagasta (Novoa Quezada & Matus Ardile, 2013). *L. serriola* was mentioned as a species with high invasion potential by Fuentes et al. (2014).

L. virosa was not mentioned in previous lists of vascular plants in Chile until it was identified within herbarium specimens by Macaya et al. (1999). The original described area of distribution between the region M – Metropolitana and the province Ňuble (region 8 – Biobio) as reported by Macaya et al. (1999) was enlarged to the Northwest (region 5 – Valparaiso) and South (region 9 – Araucania) by Novoa Quezada & Matus Ardiles (2013). Macaya et al. (1999) summarized the following observations on *L. virosa*: i) this ruderal species is distributed along roads and disturbed soil, and in areas of altitudes of 700–1,500 m.a.s.l. co-exists alongside *L. serriola*. In mountains regions, it reaches higher altitudes than *L. serriola* and forms pure stand populations; and ii) this species was not likely introduced to Chile recently, given its large range. *L. virosa* is occasionally misidentified as *L. serriola*, and, because it is an non-native species, has not been given much attention by botanists.

In this study we contribute to knowledge on *L. serriola* and *L. virosa* populations in Chile. We build on assessments focused on Europe (Doležalová et al., 2001; Lebeda et al., 2001, 2007a, b, 2009), the Near East (Lebeda et al., 2012b), and North America (Lebeda et al., 2012a, 2019a, b) to record the distributions, habitats, and ecological characteristics of the species in the central region of Chile, based on field surveys conducted in 2016 and 2017. We discuss these findings in light both of their utility as genetic resources as well as the risks they represent as invasive species.

Materials and methods

Field work occurred in March 2016 and from February – March 2017, covering central Chile between 31° 54,818´S (Los Villos) and 35°59,550´S (plateau over river Maule in the Andes), and from 72°03,410´W near the Pacific coast (Lora) to 70°07´44,12´´W (Portillo) in the Andes. The total length of routes was 3,975 km. The trips included the southern part of the administrative region 4 – Coquimbo, then regions 5 – Valparaíso, M – Metropolitana, 6 – Libertador O'Higgins, and 7 – Maule. Detailed routes are displayed in Figure 1. The lowest elevation site was situated 16 m.a.s.l. (by Lora), and the highest at 2,707 m.a.s.l. (near Portillo). A wide diversity of habitats were visited, including urban areas (towns and cities), transport corridors, places with disturbed soil for house construction, abandoned areas, agricultural field margins, farmlands, and industrial areas.

Over a total of 204 sites, detailed observation and monitoring was performed at 175 locations (Figure 1), with an additional 29 road-side locations observed from the vehicle (places where it was not possible to stop). Information on the characteristics of plant populations (including number and density of plants, developmental stage, and presence of diseases and pests), habitats, and geographic locations were recorded. Determination of *Lactuca* species and infraspecific classification were performed according to Feráková (1977).

In some sites the seed samples from individual plants of *L. serriola* (180 sites) and *L. virosa* (24 sites) were collected in both years. Passport data were recorded follow-

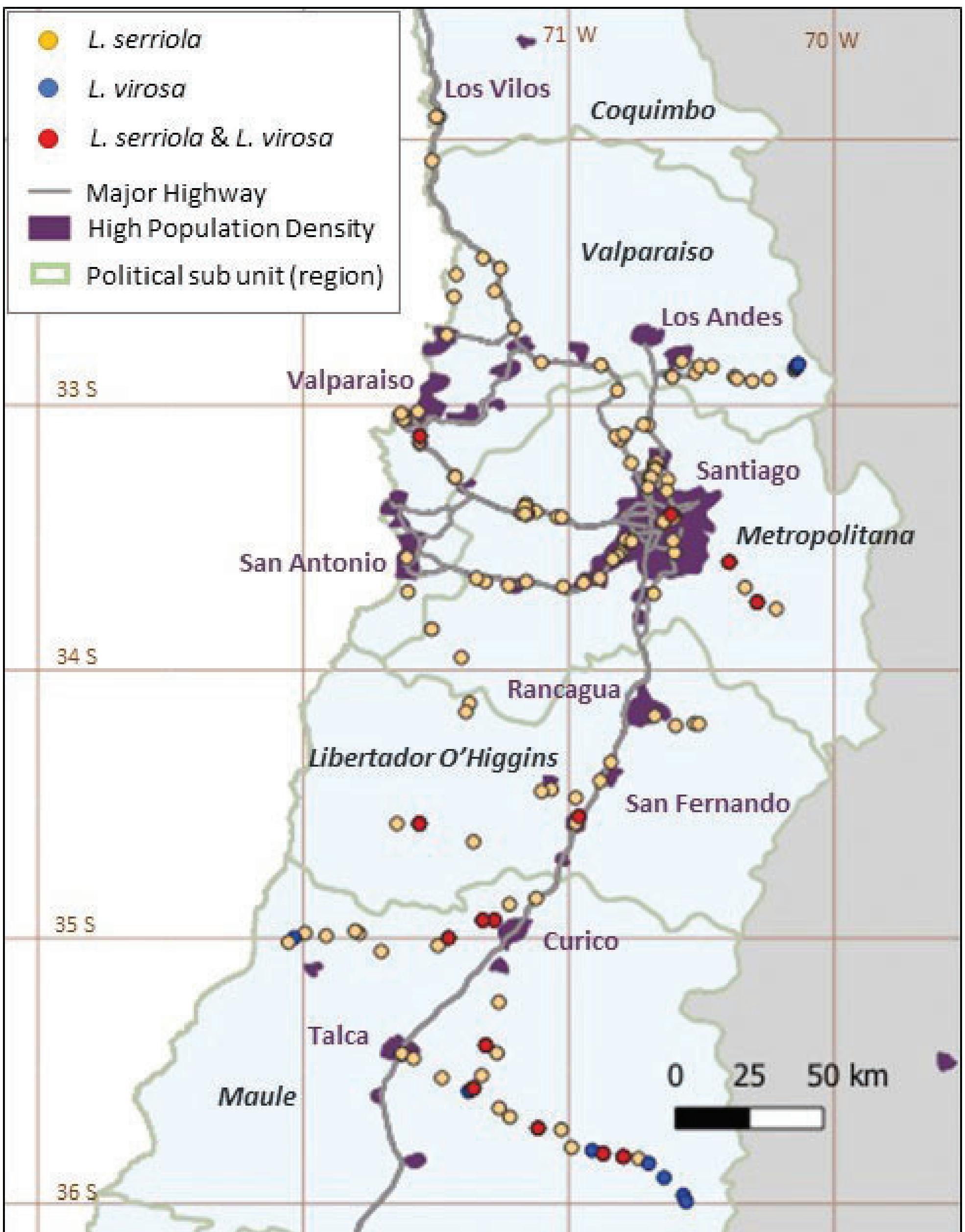

Figure 1: Routes of field observations of *L. serriola* and *L. virosa* in central Chile in 2016 and 2017.
Slika 1: Pot terenskih opazovanj vrst *L. serriola* in *L. virosa* v osrednjem Čilu v letih 2016 in 2017.

ing Lebeda et al. (2007b). The collected seed material is part of the *Lactuca* Working Collection at the Department of Botany of Palacký University in Olomouc (Czech Republic) and will be used for detailed characterization and evaluation purposes in follow-up studies.

To further characterize ecology of the sites, ecogeographic information at a resolution of 30 arc-seconds (ca. 1 km² at the equator) for 23 bioclimatic and topographic variables from WorldClim 2 (Fick & Hijmans, 2017) and a CGIAR-Consortium for Spatial Information dataset based on the NASA Shuttle Radar Topography Mission (STRM) data (Jarvis et al., 2008), were extracted for all localities (Data are by authors). These data were used to further characterize the two species with regard to their climatic and topographic niches in the field sites in central Chile, both with regard to individual eco-geographic variables as well as through multi-factorial analyses and visualizations, including principal component analysis, Mahalanobis distances, PERMANOVA, and non-metric multidimensional scaling (Oksanen et al. 2020).

Results

L. serriola alone was recorded at 166 sites, *L. virosa* alone at 21 sites, and both species at 17 sites. The positions of the 175 sites where detailed field observations were recorded and localities precisely documented by GPS are presented in Figure 1.

Individual plants of *L. serriola* L. f. *serriola* with divided cauline leaves were observed at 155 sites, *L. serriola* L. f. *integrifolia* with entire cauline leaves only at one site, and plants representing both forms at two sites. *L. virosa* L. var. *cruenta* with divided leaves was observed at four sites and *L. virosa* L. var. *virosa* with entire cauline leaves at 12 sites, while the presence of both varieties at the same site was not observed. The cauline leaf status for *L. virosa* was not adequately developed at 14 sites, hindering infraspecific classification. The divided cauline leaves of *L. serriola* f. *serriola* predominated within this species across sites, while entire leaves were more common for *L. virosa* (i.e., var. *virosa*).

Characteristics of populations and presence of diseases and pests

While the estimated number of individual plants observed varied from a few individuals to dozens and exceptionally hundreds of plants for *L. serriola*, the number of individuals of *L. virosa* per site was generally lower – from a few individual plants to a dozen. The number of plants was observed to be connected not only with climatic and topographic conditions, but also with the character of habitats and the intensity and type of human impact. For example, along roads and highways, in municipal parks, by bus stops, and around petrol stations the use of pesticides for weed control reduced the growth of the species, leaving only individuals that were missed or otherwise escaped from control. In areas with houses under construction and in ruderal (disturbed and waste) places not subject to weed control, the species‘ populations thrived.

L. serriola plants in most sites were at the stage of fruit maturity. However, in some sites, young plants were also observed. These developed from the bases of plants mowed earlier in the summer, or grew from cypselas (achenes) produced earlier the same year. We recorded two types of composed inflorescence – corymbose and pyramidal panicles of heads.

In sites where *L. virosa* plants were at a stage of fruit maturity, there were usually also leaf rosettes of young plants observed. These plants will produce seeds the following year.

Generally, there were few visible symptoms of diseases on plants recorded. Powdery mildew infection caused by *Golovinomyces bolayi* S. Takam., A. Lebeda & M. Götz (Braun et al., 2019) was recorded only on one *L. serriola* plant growing by a house in the center of Santiago de Chile, and on a number of *L. serriola* plants growing along a local road in El Sotillo. Symptoms of lettuce downy mildew (*Bremia lactucae* Regel.), as a most important disease of lettuce (*L. sativa*), were not observed. In some locations (Hualaňé, Lora, Laguna Colbún, Cajón de Maipó), aphids were seen on the inflorescence of *L. serriola* plants. *L. virosa* populations in central Chile appeared to be unaffected by pests and diseases.

Habitats

The distribution of *L. serriola* and *L. virosa* across different habitats is summarized in Table 1 and in Figure 2. *L. serriola* was more or less equally distributed in urban habitats and in the rural areas (Figures 2, 3). Inside the cities, it was recorded in ruderal or neglected areas along local roads, in places with house construction, in cracks in pavement, and near houses. Outside of cities, the distribution of *L. serriola* in ditches and in grassy areas along transport corridors predominated. *L. serriola* also occurred by bus stops, petrol stations, and in parking places near roads and highways. Its occurrence in agricultural and industrial areas was less frequently observed. It was not recorded in sandy dunes along the Pacific coast. Its distribution in urban and commercial areas between Viňa del Mar and Valparaiso by the Pacific ocean was associated with human activities (transport, houses, industry) in urban areas.

Table 1: Habitats with occurrence of *L. serriola* and *L. virosa* in central Chile observed in 2016 and 2017.
Tabela 1: Habitati, v katerih sta se pojavljali vrsti *L. serriola* in *L. virosa* v osrednjem Čilu v letih 2016 in 2017.

Category of habitat	Number of sites with *Lactuca* species		
	L. serriola	*L. serriola* and *L. virosa*	*L. virosa*
Urban (city intravilan)			
1.1 in pavement, along street, by house	16	0	0
1.2 grassy area, along water corridor	6	0	0
1.3 municipal park, grassy area	14	1	4
1.4 municipal park, along road	3	0	1
1.5 local inhabitation (suburb, condominio, village), along road	23	0	0
1.6 area with house construction	3	0	0
1.7 ruderal area in intravilan	6	0	0
Total	**71**	**1**	**5**
Countryside (outside of city, town)			
2.1 along road, by petrol station, bus stop, parking place	20	1	0
2.2 along road in grassy area, in ditch	42	7	6
2.3 along road in gravel	9	5	10
2.4 along railway track	1	0	0
2.5 ruderal area by road	4	1	0
Total	**76**	**14**	**16**
Agricultural areas (fields, farms)			
3.1 along road	9	0	0
3.2 along field	5	2	0
Total	**14**	**2**	**0**
Industrial areas			
4.1 by industrial objects	**5**	**0**	**0**
Total number of sites	**166**	**17**	**21**

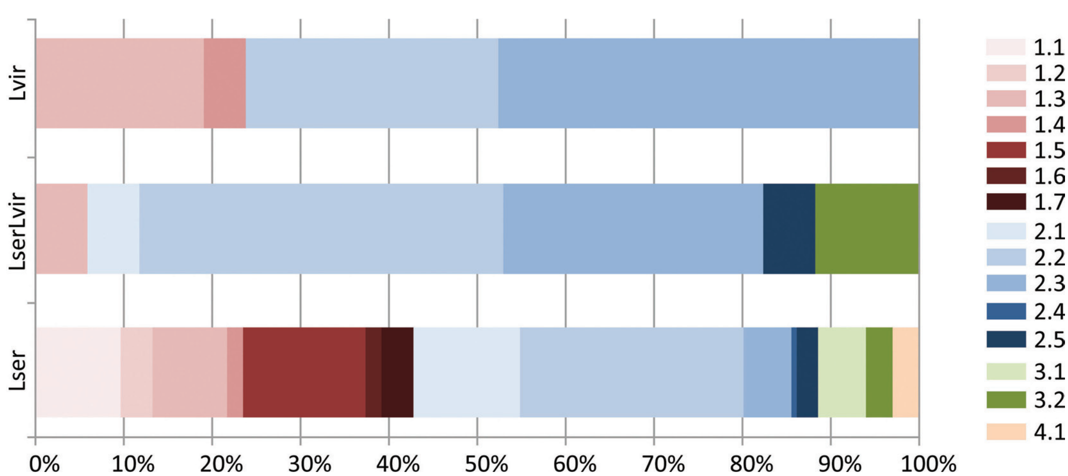

Figure 2: Frequency of occurrence of *L. serriola* and *L. virosa* in various habitat types in central Chile observed in 2016 and 2017 (Lser – presence of *L. serriola*, Lvir – presence of *L. virosa*, LserLvir – presence of *L. serriola* and *L. virosa* on monitoring site. Habitat category 1 denotes urban areas (1.1 in pavement, along street, by house; 1.2 grassy area, along water corridor; 1.3 municipal park, grassy area; 1.4 municipal park, along road; 1.5 local dwelling (suburb, condominium, village), along road; 1.6 area with house construction; 1.7 ruderal area in intravilan). Habitat category 2 denotes countryside (2.1 along road, by petrol station, bus stop, parking place; 2.2 along road in grassy area, in ditch; 2.3 along road in gravel; 2.4 along railway track; 2.5 ruderal area by road. Habitat category 3 denotes agricultural areas (fields, farms) (3.1 along road; 3.2 along field). Habitat category 4 denotes industrial areas (4.1 by industrial objects).

Slika 2: Frekvenca pojavljanj vrst *L. serriola* in *L. virosa* v različnih habitatnih tipih v osrednjem Čilu v letih 2016 in 2017 (Lser – prisotnost vrste *L. serriola*, Lvir – prisotnost vrste *L. virosa*, LserLvir – prisotnost vrst *L. serriola* in *L. virosa* na preučevanih rastiščih. Oznaka habitata 1 predstavlja urbana območja (1.1 na pločniku, ob cesti, ob hiši; 1.2 travnata območja, ob vodotoku; 1.3 mestni park, travnato območje; 1.4 mestni park, ob cesti; 1.5 stanovanjska območja (predmestje, stanovanjski bloki, vas), ob cesti; 1.6 območje stanovanjske gradnje; 1.7 ruderalna območja v urbanem prostoru). Oznaka habitata 2 predstavlja ruralna območja (2.1 ob cesti, pri bencinski črpalki, avtobusna postaja, parkirišče; 2.2 travnate površine ob cesti, v jarku; 2.3 gramoz ob cesti; 2.4 ob železniških tirih; 2.5 rudealne površine ob cesti. Oznaka habitata 3 predstavlja kmetijske površine (polja, kmetije) (3.1 ob cesti; 3.2 ob poljih). Oznaka habitata 3 predstavlja industrijske površine(4.1 ob industrijskih objektih).

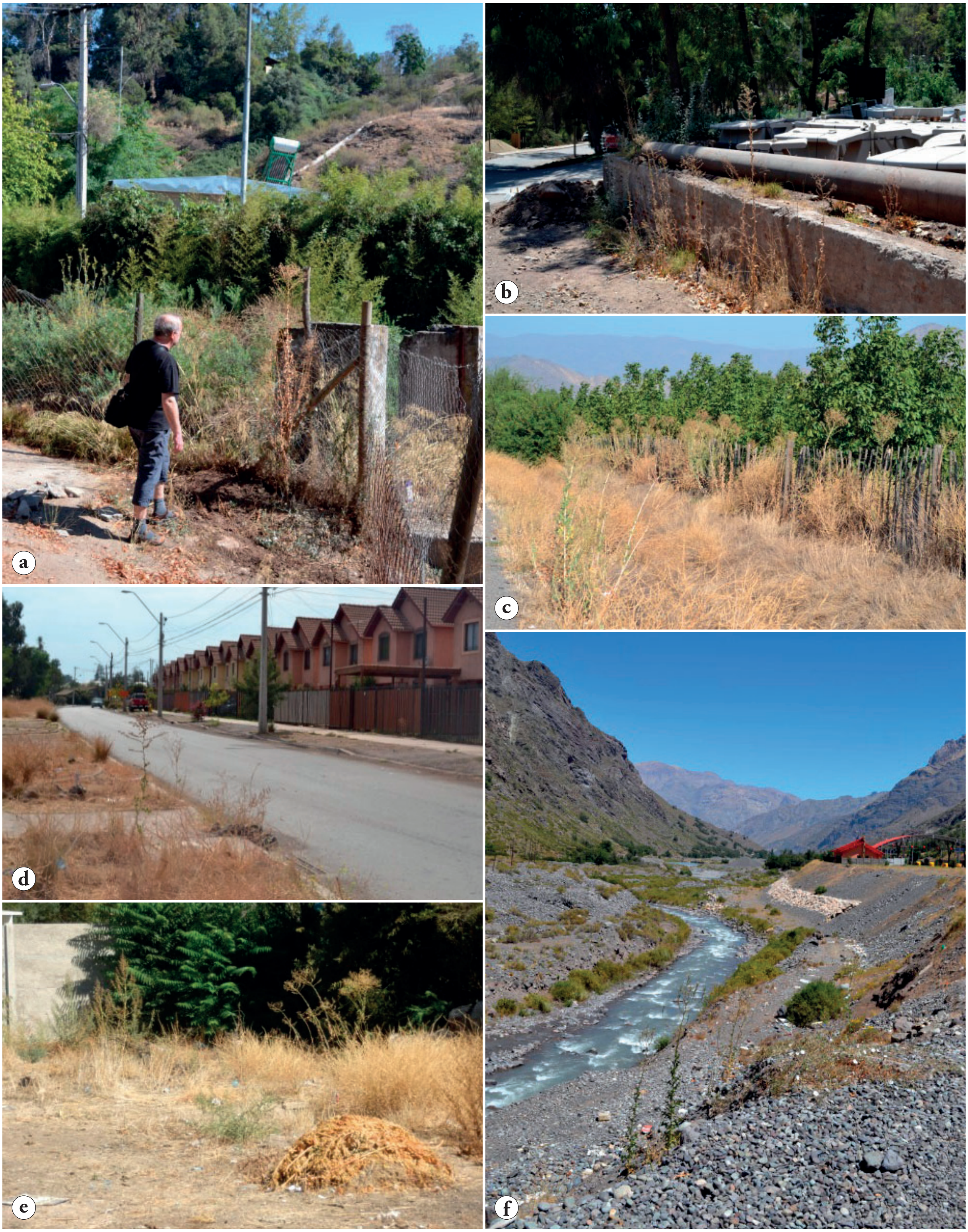

Figure 3: Habitats of *L. serriola* in Central Chile: a – Santiago, Tunel San Christobal; b – Santiago, Parque Metropolitano; c – along ruta 5 (Santiago – Las Vegas); d - Talanga; e – El Colorado; f – over Rio Blanco.
Slika 3: Habitati vrste *L. serriola* v osrednjem Čilu: a – Santiago, Tunel San Christobal; b – Santiago, Parque Metropolitano; c – ob cesti 5 (Santiago – Las Vegas); d - Talanga; e – El Colorado; f – nad reko Rio Blanco.

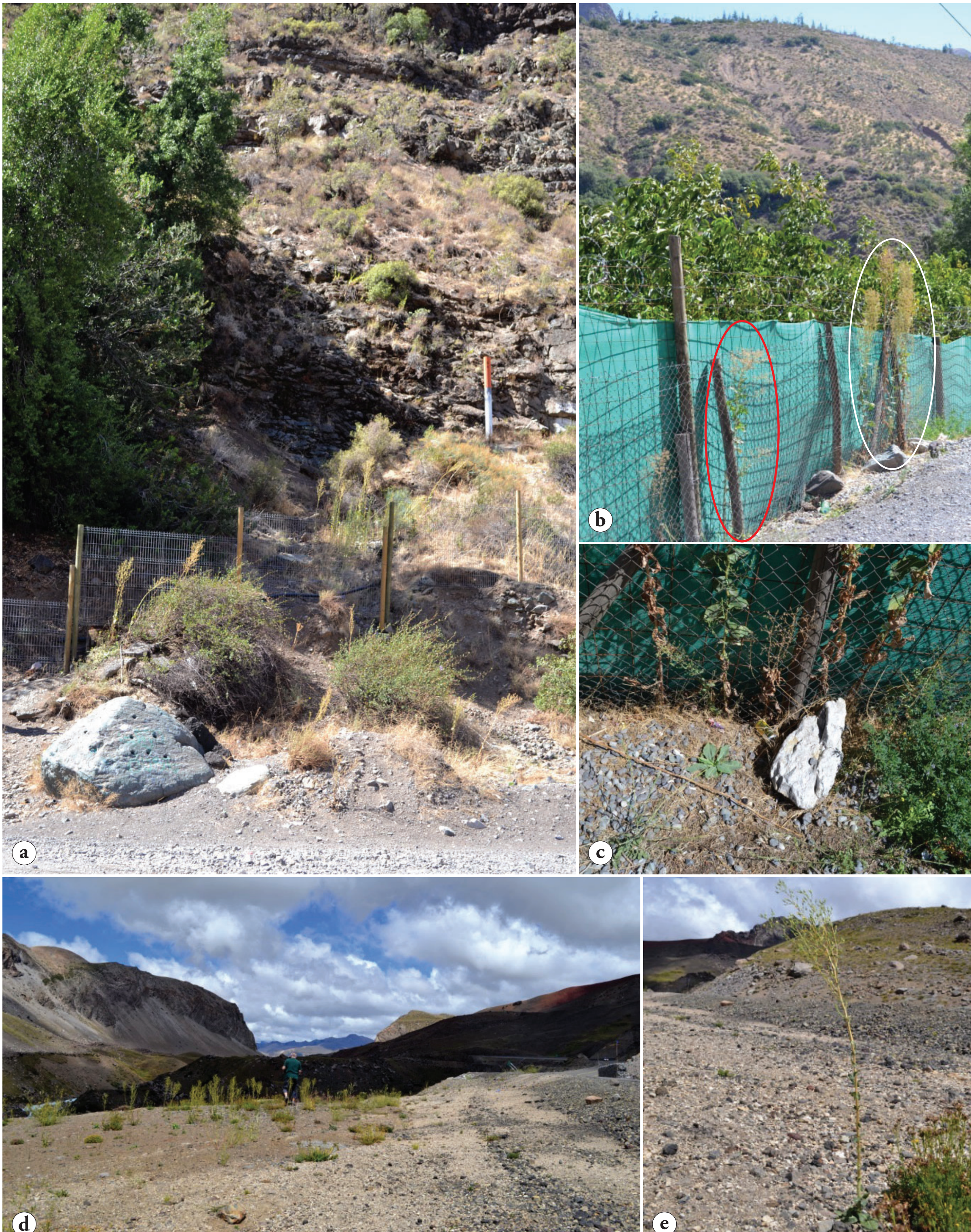

Figure 4: Habitats of *L. virosa* in Central Chile: a, b, c – road over Canjón Maipú (Figure 4b: red oval – *L. serriola*, white oval – *L. virosa*); d, e – gravel plateau over river Maule.

Slika 4: Rastišča vrste *L. virosa* v srednjem Čilu: a, b, c – cesta nad kanjonom Maipú (Slika 4b: rdeča elipsa – *L. serriola*, bela elipsa – *L. virosa*); d, e – gramozni plato nad reko Maule.

Lactuca virosa predominated along transport corridors, either alone or together with *L. serriola* (Figures 2, 4). In urban areas it was observed only in a Municipal park of the capital. It was not observed in agricultural or industrial areas.

Distributions and elevational limits

L. serriola was observed at altitudes from 18 m.a.s.l. (Licanté) to 2,235 m.a.s.l., with eleven sites located above 1,000 m.a.s.l. The lowest altitude where *L. virosa* was observed was 16 m.a.s.l. (by Lora), while nine sites were above 1,000 m.a.s.l., with the highest at 2,707 m.a.s.l. (Figure 1).

Species distributions along roads in elevational gradients were observed in detail along three routes: i) Los Andes – Portillo; ii) Pirque – Cajón Maipu; iii) Lago Colbún – plateau over Rio Maule:

i) Los Andes – Portillo

Along the R 60 from nearby Los Andes (824 m), *L. serriola* plants were observed. Dense populations were also observed in gravel over the Rio Colorado, and dispersed populations were seen at higher elevations in gravel and stones along the mountain road up to 2,235 m, and again at 2,365 m a.s.l. Above this elevation, *L. serriola* was replaced by *L. virosa* plants, which were dispersed along the road up to 2,707 m.a.s.l. (Figure 1). We did not have the opportunity to verify the presence of leaf rosettes along the mountain road and thus to confirm whether plants can reproduce in these sites.

ii) Pirque – Cajón Maipú

Near Pirque, *L. serriola* plants were observed along road G-27, then both species (*L. serriola* and *L. virosa*) were present as the road began to rise in elevation (Figure 1). Both species were recognized above 1,315 m.a.s.l. in the direction of Volcan San José, including well developed leaf rosettes of *L. virosa* (Figure 4a, b, c).

iii) Lago Colbún – plateau over Rio Maule

Along road 115 by Lago Colbún (about 300 m) *L. serriola* and *L. virosa* were observed either separately or together in sites. *L. serriola* was then recorded at 1,057 m.a.s.l., and both species documented on slopes along the road above 1,139 m.a.s.l. At 1,361 m.a.s.l. (by Baňo de Camanario), only *L. virosa* was recorded (Figure 1). The habit of plants growing along the road in altitudes around 1,500 m.a.s.l. was influenced by windy conditions. Dense populations of *L. virosa* were observed continuously in higher elevations up to 2,148 m.a.s.l. in a gravel plateau over the Rio Maule, where a relatively dense and seemingly stable population of a dozen well developed plants persisted (Figure 4d, e). We suspect that achenes are transported to higher elevations by air turbulences caused by seasonal heating and by vehicles (Cousens et al. 2008, Křístková et al. 2014, Novotná et al. 2011). Beyond this plateau, the relief changed and the soil was more rocky, so the conditions for plants were no longer favourable.

Eco-geographic niches

Some variation with regard to climatic and topographic niches was found between the two species within their occurrences in central Chile (Figure 5, Supplementary material Figure 1). In general, *L. serriola* occurrences were acclimatized to warmer temperatures, especially for exceptional environmental outlier populations, while *L. virosa* occurrences demonstrated greater acclimatization to colder temperatures, particularly at higher elevations in the Andes. While differences between the species with regard to precipitation variables were more mixed, *L. serriola* occurs overall in drier areas and *L. virosa* in wetter environments (again related to higher elevations). Also notable for both species, for certain variables, was the relatively large spread of populations across ranges, especially with regard to precipitation (Figure 5). Multi-factorial analyses of the measured variables were unable to differentiate significant climatic and topographic differences between

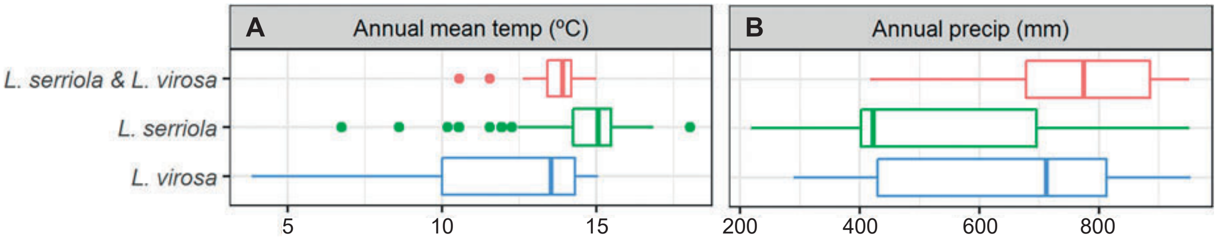

Figure 5: Climatic characterization of sites where *L. serriola*, *L. virosa*, and both species were found, for A) annual mean temperature, and B) annual precipitation. The thick vertical line represents median values across occurrences, the boxplots between 25 and 75% of variation, and circles the outliers within 90% of total variation. Please see Supplementary material Figure 1 for characterizations for all eco-geographic variables.

Slika 5: Klimatske značilnosti rastišč, kjer se posamezno pojavljata vrsti *L. serriola*, *L. virosa* ali skupaj. A) letna povprečna temperatura in B) letna količina padavin . Debela navpična črta predstavlja mediano vseh vrednosti, škatle predstavljajo variabilnost med 25 in 75%, krožci pa predstavljajo osamelce znotraj 90% celotne variabilnosti. Za značilnosti vseh eko-geografskih spremenljivk glej Sliko 1 v dodatnem materialu.

the two species populations in central Chile regarding the sites where they do not overlap, but do highlight wind speed and altitude as important contributing factors, especially for environmental outlier populations (Supplementary material Figure 2A, 2B and 2C)) suggesting that even if the species have similar environmental conditions they are not exactly equal ($p<0.01$).

Discussion

This novel information on the distributions, habitats, and ecological characteristics of *L. serriola* and *L. virosa* populations in central Chile adds considerably to the available information for the species in the region. We add 183 new occurrences for *L. serriola* and 38 for *L. virosa*; the Global Biodiversity Information Facility lists only 49 and 62 occurrences for the species in the country, respectively (GBIF 2020).

Introduced allochthonous *Lactuca* species can develop novel traits through acclimitization to newly colonized habitats, including adaptation to extreme environmental conditions and resistance to important diseases which impact the crop, as seen in *L. serriola* populations in the USA (Lebeda et al., 2014, 2019a, b). The elevational limit of 2,235 m.a.s.l. recorded for *L. serriola* during our recent observations in central Chile is significantly higher than existing records from the Mediterranean and Central Europe (Lebeda et al., 2004). The species is known from North America at elevations above 2,000 m.a.s.l. (Lebeda et al., 2012a), and from Afghanistan and the northern Himalayas at above 3,000 m.a.s.l (Lebeda et al., 2004).

The occurrence of *L. virosa* at the high elevation of 2,707 m.a.s.l. in central Chile is of interest, and supports earlier observations by Macaya et al. (1999) of acclimitization to mountainous areas. The species has not been observed in Europe or North America at this altitude (Lebeda et al., 2004, 2012a, 2019a). In 2016 we observed *L. virosa* at a high of 848 m.a.s.l. (near Pontrémolli) in Italy (Europe). In the Flora of North America, *L. virosa* is reported from Alabama, California and Washington, DC (Strother, 2006). Our surveys confirmed its continued but very rare presence in California and Washington State (Lebeda et al., 2012a).

Powdery mildew was observed on *L. serriola* in only two sites in Chile. In comparison, this disease is very common at the end of its growing season in central Europe, observed in Slovenia (Doležalová et al., 2001) and relatively frequently in Austria (Lebeda et al., 2001), Czech Republic, Germany, and the Netherlands (Lebeda et al., 2007a), in the USA and Canada (Lebeda et al., 2012a), and more recently in France, Italy, Slovakia, Poland, Hungary, and Croatia (Lebeda & Mieslerová, 2011; Mieslerová et al., 2020). We did not observe powdery mildew on *L. virosa* in Chile. In other countries *L. virosa* is infected by powdery mildew sporadically (Lebeda & Mieslerová, 2011; Mieslerová et al., 2020).

We were able to locate only one unique accession of *Lactuca* from Chile within major genebank and botanic garden databases, including the Genesys plant genetic resources portal (Global Crop Diversity Trust 2019), the United Nations Food and Agriculture Organization World Information and Early Warning System on Plant Genetic Resources for Food and Agriculture (WIEWS) (2019), the Global Biodiversity Information Facility (2019), and the USDA National Plant Germplasm System (2019). The accession (CGN 18677) is of *L. virosa*, donated to the Centre for Genetic Resources (Netherlands) in 1996 by a Dutch seed company, with no further provenance information other than that it comes from the Andes region in Chile (Global Crop Diversity Trust 2019).

Given that the surveyed *Lactuca* species in central Chile occur at higher elevations and present noticeably less impacts from disease than in other regions, among other traits of interest, and that populations from the area are poorly represented in *ex situ* repositories, further collecting of these species for germplasm conservation may be warranted. Further, our review of the overlap of the study sites with conservation areas listed in the World Database of Protected Areas (IUCN 2019) indicated that none of the occurrences we visited are in a conservation area. While these non-native species would certainly not be applicable for targeted conservation in protected areas, further surveying of protected areas for the species, and collection of found populations for germplasm conservation prior to eradication, may be considered.

The occurrence of *L. serriola* in urban areas corresponds with the results of Figueroa et al. (2020) who recorded this species in soil seed banks in urban vacant lots of Santiago de Chile (Pauchard et al., 2004, 2006). Gärtner et al. (2015) focused their study on characterising the diversity, composition and distribution of native and non-native ruderal species present in different suburbs of Santiago de Chile; *L. serriola* was recorded on 2 sites and *L. virosa* on 5 sites out of 41 surveyed.

The presence of non-native ruderal plant species was monitored by Hauck et al. (2016) in La Campana National Park, central Chile, however they do not mention the presence of *L. serriola*. Teillier et al. (2010) monitored the presence of alien species in the western slope of the Coastal Range (Valparaiso province), and *L. serriola* was observed on 15 sites from 33 sites investigated. As stressed by Figueroa et al. (2004), future experimental research should be aimed at study of mechanisms underlying the spread of non-native species on converted soils, and factors directly associated with changes in soil and land use.

Our recent observations support the conclusions of Lembrechts et al. (2016, 2017) that roads may play a more important role as drivers of species range changes than previously assumed. From data on the *Lactuca* species presented in this paper it is evident that Chilean roadsides serve as corridors for species movements and as such trigger range change dynamics of species (whether native or non-native) into new climatic zones (Paiaro et al., 2011), such as with *L. virosa* in high altitudes in the Andes. Our observations also support the assertion by Lembrechts et al. (2016) and McDougall et al. (2018) that roadsides can serve as important early detection tools, where shifts in species ranges will become visible first. Roadside monitoring systems might however be sensitive to short-term population fluctuations (Lembrechts et al., 2016).

In the Chilean mountains, there has been minimal management of non-native species (Pauchard & Alaback, 2004), probably because their direct economic impacts are not yet significant, or at least not well enough documented. In general the focus of management of non-native species is limited to agricultural systems, where control of borders, early detection, and rapid response are key strategies (McDougall et al., 2011). Awareness of threats from non-native species in natural systems is growing, as evidenced by new laws proposed for safeguarding the Chilean Protected Area Systems (Pauchard et al., 2012) and the creation of the Laboratory of Biological Invasions (Fuentes et al., 2014, 2015).

The climate in central Chile appears to facilitate the distribution of weedy *Lactuca* species from the Old World Mediterranean region. Alongside *L. serriola* and *L. virosa*, such species in the genus also include *Lactuca saligna* L. and *Lactuca viminea* (L.) J. et C. Presl. *L. saligna* grows from lowlands to low montane elevations in Europe, mostly in open sunny exposures, on waste places, borders of woodlands, arable fields, river banks, and also along railways and roads as a weed (Feráková, 1977). It is currently reported from only a few locations in the USA (Lebeda et al., 2012a), namely from Salinas, California which also has a mediterranean climate (di Castri, 1991). We see no reason why this species could not find suitable conditions for its entry and settlement in the equivalent mediterranean-climate zone in Chile. *L. viminea* is an apophyte growing in vineyards, around ruins, on walls, screes, and in quarries (Feráková, 1977). It was observed in France and Italy (Lebeda et al., 2001), and is very frequent in the coastal rocky parts of Croatia and in the Croatian islands in the Adriatic sea (namely Brač and Mljet) (E. Křístková, pers. communication), however it has not yet been observed in the New World.

Conclusions

Novel information on the distributions, habitats, and ecological characteristics of populations of non-native *Lactuca* species in central Chile were generated. These observations indicate that: i) both allochthonous (Euroasian) *Lactuca* species occur and are able to regenerate in central Chile; ii) *L. serriola* forms dense populations in urbanized areas; iii) both species can expand along transport corridors to high elevations; iv) the spread of *L. virosa* and persistence of dense populations in elevations above 2,000 m a.s.l. prove the invasiveness of this species in extreme climates; v) both species may contain novel traits of interest for germplasm conservation; and vi) both species should be monitored (and treated) in urbanized and agricultural areas, as well as in mountainous areas.

Supplementary material on-line

Figure S1 – Climatic and topographic characterization of sites where *L. serriola*, *L. virosa*, and both species were found.

Figure S2 – A. Non-metric multidimensional scaling, B. principal component analysis, and C. Biplot of principal component analysis.

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