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Implications of a phylogeographic approach for the selection of *Ceutorhynchus assimilis* as a potential biological control agent for *Lepidium draba*

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ABSTRACT

The root-galling weevil, *Ceutorhynchus assimilis* Paykull (Coleoptera, Curculionidae), has been selected as one of the candidates to control *Lepidium draba* L. (Brassicaceae), a highly invasive weed in western North America. Originally been described as oligophagous, also attacking crop species, previous studies indicated that a specific host race to *L. draba* exists in *C. assimilis*. We therefore explored the evolutionary history and phylogeographic structure of this weevil by sampling individuals from 67 populations, spanning 12 countries and five different host plant species including *L. draba*. To explore the genetic diversity of *C. assimilis*, we analyzed the *COI* gene sequences of 458 individuals. Analysis revealed three distinct evolutionary lineages, one of which, the so-called *Lepidium* host race, was only found on *L. draba* and appears to occur in a restricted geographic area, ranging between northern Spain and northern Italy. These results allow us to targeting sites for collection of the *Lepidium* host race and justify the prioritization of *C. assimilis Lepidium* host race as a candidate for the *L. draba* biological control.

1. Introduction

Heart-podded hoary cress, *Lepidium draba* L. ssp. *draba* [= *Cardaria draba* (L.) Desv.] (Brassicacae), is a perennial rhizomatous weed, introduced to the US as a contaminant of seed shipments from Eurasia in the late 19th century (Gaskin et al., 2005; Hinz et al., 2012). The species has since spread throughout North America and is especially problematic in the West, where it is a declared noxious weed in 15 US states, three Canadian provinces, and also in Mexico (Rice, 2014; USDA-NRCS, 2016). *Lepidium draba* competes with native plants, decreasing local biodiversity (Francis and Warwick, 2008; Puliafico et al., 2011). Besides its ecological impact, it causes economic losses by invading several crops (McInnis et al., 2003; Mulligan and Findlay, 1974) where it also poses a dual problem: as well as being a weed, it provides an alternative food source for major crop pests, such as the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Dosdall and Moisey, 2004; Fox and Dosdall, 2003). Furthermore, the weed, which is well adapted to sub-irrigated pastures and rangelands, is toxic to cattle due to alkaloid compounds, thus becoming a serious problem for livestock and forage production (Francis and Warwick, 2008; McInnis et al., 2003).

The invasive success of *L. draba* is related to its vegetative reproduction by an extensive rhizome system as well as its high seed production (Francis and Warwick, 2008; McInnis et al., 2003; Mulligan and Findlay, 1974). The use of herbicides is costly, not always feasible and mechanical control is not effective due to the extensive underground rhizome system of the weed (Miller et al., 1994). These limitations have motivated the exploration of alternative methods, and a classical biological control project was started in 2001 (Anonymous, 2004).

Among the known natural enemies of *L. draba* in its native range in Eurasia, *Ceutorhynchus assimilis* Paykull, 1792 [syn. *Ceutorhynchus pleurostigma* (Marsham, 1802)] (Coleoptera, Curculionidae) (Colonnelli, 1993) has been prioritized as a of candidates for biological control (Fumanal et al., 2004a,b; Hinz et al., 2013, 2016; Virag et al., 2016). Adults lay most of their eggs in young and soft roots of the plant, causing the development of galls in which the three larval instars of the weevil develop before larvae leave the galls and pupate in the soil

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(Hoffman, 1954). Across its Eurasian distribution, the weevil has been assumed to display a broad host range and is listed as a pest of more than 13 plant species including crops (Dennis, 1987; Hoffman, 1954; Jourdheuil, 1963). However, Fumanal et al. (2004b) proposed that *C. assimilis* is probably a complex of morphocryptic entities that differ in their host-plant spectrum within the family Brassicaceae and one of

Table 1
Sampling details and summary statistics of genetic diversity of the sampled *Ceutorhynchus assimilis* populations used in this study.

Pop id	Country	Latitude	Longitude	Host	*n*	H	Hd	± SD	π	± SD	*r*
A54	France	48.56	−4.14	*Brassica oleracea*	6	4	0.800	0.172	0.002	0.001	1.450
A50	France	46.25	0.46	*Brassica oleracea*	15	3	0.362	0.145	0.001	0.001	0.569
A51	France	46.39	0.68	*Brassica oleracea*	7	4	0.809	0.130	0.002	0.001	1.457
II	France	46.36	0.56	*Brassica napus*	5	2	0.600	0.175	0.001	0.001	0.900
III	France	46.36	0.46	*Brassica oleracea*	4	2	0.500	0.265	0.003	0.002	0.750
Y	France	46.19	0.44	*Sinapis arvensis*	1	/	/	/	/	/	/
A23	France	47.13	4.96	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A67A22	France	45.97	4.72	*Lepidium draba*	7	2	0.476	0.171	0.001	0.001	0.714
A83*	France	45.78	3.18	*Lepidium draba*	20	3	0.510	0.091	0.009	0.005	0.800
A68	France	45.47	4.50	*Lepidium draba*	8	1	0.000	0.000	0.000	0.000	0.000
A66	France	45.50	4.85	*Lepidium draba*	27	6	0.624	0.093	0.003	0.002	1.067
A69*	France	45.26	4.84	*Lepidium draba*	14	2	0.264	0.136	0.006	0.004	0.396
A81	France	45.25	6.42	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A82	France	45.19	5.67	*Lepidium draba*	10	2	0.200	0.154	0.001	0.001	0.300
A65*	France	44.98	4.88	*Lepidium draba*	17	5	0.772	0.070	0.013	0.007	1.375
A64*	France	44.48	4.76	*Lepidium draba*	3	2	0.667	0.314	0.015	0.011	1.000
A70*	France	44.29	4.73	*Lepidium draba*	27	3	0.544	0.081	0.001	0.001	0.877
A20*	France	43.88	5.01	*Lepidium draba*	3	3	1.000	0.272	0.017	0.013	2.000
A71*	France	43.72	4.19	*Lepidium draba*	1	/	/	/	/	/	/
A0*	France	43.64	3.84	*Lepidium draba*	6	1	0.000	0.000	0.000	0.000	0.000
B	France	43.69	3.90	*Sinapis arvensis*	6	3	0.600	0.215	0.001	0.001	1.000
L	France	43.69	3.90	*Diplotaxis erucoides*	3	2	0.667	0.314	0.007	0.005	1.000
A49*	France	43.69	3.90	*Lepidium draba*	9	2	0.222	0.166	0.006	0.004	0.333
NS*	France	43.55	3.95	*Lepidium draba*	4	2	0.500	0.265	0.001	0.001	0.750
VV*	France	43.69	3.87	*Lepidium draba*	7	2	0.571	0.119	0.004	0.002	1.125
VVS	France	43.69	3.87	*Sinapis arvensis*	1	/	/	/	/	/	/
Q	France	43.69	3.87	*Diplotaxis erucoides*	3	1	0.000	0.000	0.000	0.000	0.000
A21*	France	43.38	3.47	*Lepidium draba*	3	3	1.000	0.272	0.002	0.002	2.000
A55*	France	42.82	3.02	*Lepidium draba*	16	3	0.242	0.135	0.003	0.002	0.375
A6*	France	43.20	2.35	*Lepidium draba*	6	2	0.600	0.129	0.001	0.001	2.000
A3*	France	43.55	5.32	*Lepidium draba*	3	3	1.000	0.272	0.019	0.015	2.000
A1*	France	43.42	6.45	*Lepidium draba*	4	2	0.500	0.265	0.004	0.003	0.750
A2*	France	43.75	7.39	*Lepidium draba*	4	2	0.500	0.265	0.012	0.008	0.750
A72*	Italy	43.85	7.84	*Lepidium draba*	16	1	0.000	0.000	0.000	0.000	0.000
A80*	Italy	44.90	8.06	*Lepidium draba*	7	2	0.286	0.196	0.006	0.004	0.429
A19*	Italy	45.07	9.97	*Lepidium draba*	3	2	0.667	0.314	0.021	0.016	1.000
A73	Italy	44.19	9.63	*Lepidium draba*	4	1	0.000	0.000	0.000	0.000	0.000
A74	Italy	43.69	10.36	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A75	Italy	42.73	11.14	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A12A13	Italy	41.87	12.50	*Brassica oleracea*	10	2	0.200	0.154	0.001	0.001	0.300
A45	Italy	42.14	12.60	*Diplotaxis erucoides*	9	4	0.694	0.147	0.002	0.001	1.202
A53	Italy	42.51	12.32	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A76	Italy	42.35	13.35	*Lepidium draba*	4	2	0.500	0.265	0.001	0.001	0.750
A77	Italy	42.72	13.93	*Lepidium draba*	3	2	0.667	0.314	0.001	0.001	1.000
A78	Italy	43.68	13.27	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A79	Italy	44.41	11.59	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
VIV	Italy	45.42	11.00	*Brassica oleracea*	5	4	0.900	0.161	0.013	0.008	1.700
A84*	Spain	41.98	−4.43	*Lepidium draba*	28	3	0.140	0.087	0.001	0.001	0.214
A59*	Spain	41.29	1.29	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A60*	Spain	41.77	2.72	*Lepidium draba*	5	2	0.400	0.237	0.001	0.001	0.600
A58	Spain	40.36	0.31	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000
A24	Netherlands	51.79	4.93	*Sinapis arvensis*	5	5	0.900	0.161	0.002	0.001	1.700
A26	Germany	50.05	8.36	*Lepidium draba*	5	2	0.400	0.237	0.001	0.001	0.600
A27	Germany	48.89	9.14	*Lepidium draba*	5	2	0.400	0.237	0.002	0.001	0.600
A14	Austria	47.69	16.40	*Brassica napus*	2	2	1.000	0.500	0.009	0.009	/
A16	Austria	47.85	16.53	*Lepidium draba*	3	2	0.667	0.314	0.001	0.001	1.000
SL	Slovakia	48.24	18.31	*Lepidium draba*	5	4	0.900	0.161	0.004	0.003	1.700
SL2	Slovakia	48.29	20.15	*Lepidium draba*	3	3	1.000	0.272	0.005	0.004	2.000
A43	Hungary	46.18	19.03	*Lepidium draba*	5	2	0.400	0.237	0.001	0.001	0.600
V	Greece	38.80	22.51	*Sinapis arvensis*	5	2	0.600	0.175	0.002	0.001	0.900
VI	Greece	38.80	22.51	*Brassica oleracea*	5	3	0.700	0.218	0.002	0.001	1.200
VII	Greece	38.80	22.51	*Lepidium draba*	5	2	0.400	0.237	0.001	0.001	0.600
A28	Turkey	37.88	30.71	*Lepidium draba*	6	2	0.333	0.215	0.001	0.001	0.500
CA11	Turkey	38.71	34.91	*Lepidium draba*	4	1	0.000	0.000	0.000	0.000	0.000
A31A36	Armenia	40.74	44.82	*Lepidium draba*	5	3	0.700	0.218	0.001	0.001	1.200
LRD	Georgia	42.31	43.35	*Lepidium draba*	1	/	/	/	/	/	/
A61	Russia	45.18	37.66	*Lepidium draba*	5	1	0.000	0.000	0.000	0.000	0.000

* Indicates the presence of the *Lepidium* host race; *n*: Number of individuals analyzed; H: Number of haplotypes; Hd: Gene diversity and its standard deviation; π: Nucleotide diversity and its standard deviation; *r*: Allelic richness after rarefaction.