GENETIC ANALYSIS OF INVASIVE POPULATIONS OF VENTENATA DUBIA (POACEAE): AN ASSESSMENT OF PROPAGULE PRESSURE AND PATTERN OF RANGE EXPANSION IN THE WESTERN UNITED STATES

by

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The following individuals read and discussed the thesis submitted by student Inna Pervukhina-Smith, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

This thesis is dedicated to my family: Gordon L Smith for his love and support throughout the project, Gordie Smith for inspiration to continue, and Teddy Lovekins the Chow for his dedication in accompanying me on field trips.

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ABSTRACT

Molecular markers prove to be an invaluable tool in assessing the introduction dynamics, pattern of range expansion, and population genetics of an invasive species. *Ventenata dubia* (Leers) Coss. (Aveneae; ventenata) is a diploid, primarily self-pollinating, annual grass native to Eurasia and Northern Africa. The grass has a detailed herbarium collection history in the western United States since its discovery in eastern Washington in 1952. Genetic analysis of 51 invasive populations (1636 individuals) of *V. dubia*, coupled with historical records, suggests moderate propagule pressure from multiple introductions, followed by local or regional range expansion. Enzyme electrophoresis detected nine multilocus genotypes (MLGs) across eight western US states. A single MLG, referred to as the most common genotype (MCG), was detected in 37 of 51 (72.5%) invasive populations across all states. The other eight MLGs were generally found in fewer populations, with limited geographic distributions. Despite multiple introductions, invasive populations exhibit low levels of genetic admixture, low levels of genetic diversity within populations (A = 1.03, %P = 2.94, Hexp = 0.007) and high genetic differentiation among populations (G_{ST} = 0.864). The apparent reduced evolutionary potential of most *V. dubia* populations did not preclude the initial establishment and rapid spread of this species across its new range in the western US.

Keywords: admixture, enzyme electrophoresis, founder effects, genetic diversity and structure, herbarium specimens, most common genotype, multilocus genotypes, multiple introductions, propagule pressure, range expansion

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INTRODUCTION

Biological invasions occur when individuals are introduced into a new region, in which their descendants persist, proliferate, and spread beyond their original points of introduction (Mack et al. 2000; Lockwood et al. 2013). Invasive organisms can be introduced through either deliberate or accidental means (Mack and Erneberg 2002; Hulme et al. 2008; Lehan et al. 2013). Regardless of how they were introduced, the presence of many invasive species has resulted in severe negative ecological consequences (Simberloff et al. 2013), high economic costs (Pimentel et al. 2005), and is a leading threat to biodiversity worldwide (Sala et al. 2000). In extreme cases, invasive species can result in the extinction of native species (Novak 2007; Boyer 2008; Bellard et al., 2016). Invasive species also can degrade ecosystems by altering community structure (Hejda et al. 2009), ecosystem processes (Gandhi and Herms 2010), nutrient fluxes (Liao et al. 2007; Clark et al. 2010), and disturbance regimes (e.g., the fire regime) (D'Antonio and Vitousek 1992; Balch et al. 2013, Gaertner et al. 2014).

Due to the negative ecological consequences and high economic costs of invasive species, the need for predicting which non-native species will become invasive and which native communities will be invaded is of critical importance (Mack et al. 2000; Heger and Trepl 2003; van Kleunen et al. 2015). Recently, attention has been focused on the "invasion process", a series of stages by which biological invasions occur. Every stage in the invasion process is critical for an invasion to occur because all stages may be associated with small population sizes (Kolar and Lodge 2001; Lockwood et al. 2005) that

are inherently at high risk of extirpation (Shaffer 1981; Lande 1993). Thus, an emerging concept to best predict establishment success is propagule pressure (introduction effort) (Kolar and Lodge 2001; Lockwood et al. 2005; Colautti et al. 2006; Simberloff 2009; Novak 2011; Ricciardi et al. 2011; Blackburn et al. 2015). Propagule pressure is described as the number of individuals in any specific release event (propagule size), the number of discrete events per unit time (propagule number), as well the overall genetic variability of the founding populations (propagule richness) (Lockwood et al. 2005; Simberloff 2009; Ricciardi et al. 2011). High propagule pressure translates to large population sizes, high immigration rate, and high genetic diversity which can overcome stochastic processes, resulting in the establishment of non-native species (Simberloff 2009).

Because an invasion can arise from a single, or multiple, source populations and potentially over a long period of time, an interdisciplinary approach can be useful in its reconstruction (Wilson et al. 2009; Estoup and Guillemaud 2010; Estoup et al. 2010; Pawlak et al. 2015). Collection history, as well as current distribution data, can provide insights about early introduction sites and the patterns of range expansion. In addition, the use of molecular markers can provide a detailed picture of the genetic signatures of propagule pressure, the amount and distribution of genetic diversity within and among populations, and the occurrence and consequences of post-introduction events (Kolbe et al. 2004; Novak 2011; Estoup and Guillemaud 2010; Gaskin et al. 2013). Evidence of high propagule pressure can be detected by the presence of 1) a large number of genotypes/haplotypes among invasive populations, 2) similar genetic diversity between native and invasive populations, with little evidence of founder effects, and 3) presence of admixtures in which invasive populations contain genotypes from different native

populations (Novak and Mack 2005; Huttanus et al. 2011).

Ventenata dubia (Leers) Coss. (Poaceae, common names ventenata, wiregrass, North Africa grass) is a diploid ($2n = 14$), primarily self-pollinating (hereafter referred to as selfing), winter annual grass in the Aveneae (oat tribe). The species is native to central, southern, and eastern Europe, northern Africa, western Asia, and the Caucasus region (Prather 2018). In many parts of its range, *V. dubia* occurrences are scarce, and the plant is considered rare in Italy, Portugal, Ukraine, and Switzerland; near threatened in Slovakia, endangered in Germany and the Czech Republic, locally protected in France, and extinct in Serbia (R.F.H. Sforza and S.J. Novak, unpublished data). In its native range, *V. dubia* inhabits anthropogenically disturbed sites, basalt quarries, agricultural fields, pastures, and dry, open habitats (Contu 2013; Fryer 2017).

There are eight described species in *Ventenata* (The Plant List 2013), however *V. dubia* is the only species known to be introduced into the United States (US) (Fryer 2017). Although the first occurrence record of *V. dubia* was only in 1952 in Spokane County, Washington (Flora of North America Editorial Committee 1993), the grass has spread rapidly across the western US (Wallace et al. 2015). *Ventenata dubia* now occurs throughout much of the Pacific Northwest (Idaho, Oregon, and Washington) as well as California, Utah, Montana, Wyoming and most recently Nevada. In addition, the plant is found in Canada, (British Columbia, Alberta, Ontario, Quebec, New Brunswick, and Saskatchewan) and several records exist near the Great Lakes and the Northeast (Ohio, Wisconsin, New York, and Maine), however limited records over time suggest that the persistence of the plant in these areas is incidental (Fryer 2017).

In its invasive range, *V. dubia* grows in habitats ranging from sea level to mid-

elevations (0-1800m) (Pavek et al. 2011), which receive 350-1,120 mm of annual precipitation (Prather 2009). *Ventenata dubia* is most commonly found in dry, open, disturbed areas such as fields, pastures, roadsides and rangelands; however, it can also be found in moist swales, and vernal pools and roadside ditches that become dry in the summer (Fryer 2017). In the Pacific Northwest, *V. dubia* replaces native vegetation and endangers native communities such as grasslands, sagebrush steppe, woodland, riparian shrub and Palouse prairie vegetation (Butler 2011; Wallace et al. 2015; Fryer 2017).

Ventenata dubia can form dense stands, and has the potential to increase fuel load, alter fire regimes and promote further invasion, much like *Bromus tectorum* (cheatgrass) (Brooks et al. 2004). Economic losses associated with *V. dubia* include 20% decrease in crop yields, especially in Kentucky Bluegrass and Timothy hay production. Moreover, because contaminated hay bales are rejected for export, prices of $200-$215/ton are reduced to $70-$100/ton (Fountain 2011). In eastern Washington and northern Idaho, regional losses are estimated to be at least $6.7 million (Prather 2018).

No previous studies have assessed the genetic diversity, introduction dynamics, and pattern of spread of *V. dubia* in its invasive range, and the species provides an excellent opportunity to obtain insights into the mechanisms of biological invasion and an initial assessment of the population genetic consequences associated with invasion. In this study we will 1) assess the introduction dynamics (single vs multiple introductions) and estimate propagule pressure for the invasion of *V. dubia* in the western US, 2) assess the pattern of range expansion of the species in its new range, 3) determine the level of genetic diversity within invasive populations of *V. dubia*, and 4) determine the genetic structure of these invasive populations. Results of this study will allow us to better

understand the invasion of *V. dubia* into the western US. These data will also allow for a comparison of introduction dynamics and population genetics of *V. dubia* with other primarily selfing, invasive, annual grass species in the western US such as *B. tectorum* and *Taeniatherum caput - medusae* (medusahead).

MATERIALS AND METHODS

Herbarium Specimens

Historic records of *V. dubia* were accessed through online herbarium databases such as the Consortium of Pacific Northwest Herbaria (http://www.pnwherbaria.org), Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/), Intermountain Regional Herbarium Network (http://intermountainbiota.org) and Global Biodiversity Information Center (http://www.gbif.org/). Vouchered specimen records from all years were targeted for population sampling, specifically the first record of occurrence in each county. When possible, verification of specimens was done visually via digitized vouchers, or by the species descriptions available on file.

Plant Collections and Sampling

In the invasive range, mature panicles (or entire plants) were collected from 51 populations spanning eight western states during the months of June – August, prior to seed dispersal. Samples from Oregon were collected in 2014-2016; Idaho, Montana, and Washington during 2015 – 2016, and California, Nevada, Utah and Wyoming during 2016. Collection localities were typically located in areas disturbed by human activities, especially roadsides where mowing operations take place. In each population, 27 – 40 plants were collected haphazardly, based on the size of the population. To prevent the collection of full siblings, individuals were collected 1-3 m apart. For small populations, all individuals were collected. Plant material was placed individually in numbered

envelopes and stored at room temperature until analysis.

All populations were collected by the procedure described above, apart from the population from Utah. Due to the time of collection, and the condition of the plants, *V. dubia* litter and debris was collected and placed in individual packets, with each litter sample collected approximately 20 meters apart. From the litter and debris, a single *V. dubia* seed was sampled from each packet and germinated for genetic analysis.

The 51 invasive populations analyzed in this study were chosen based on their historical significance (early collection sites, see Fig.1, Appendix A & B), geographic distribution, as well as having enough viable seeds, and these populations were assigned to four sub-regions: 1) Coastal Range: populations generally located west of Cascade/Sierra Nevada Mountains; 2) Columbia Basin: populations from the Columbia Basin in eastern Washington and the Blue Mountains region of eastern Oregon; 3) Great Basin: populations from the Snake River Plains and the Great Basin; and 4) Rocky Mountains: populations from and east of the Northern Rocky Mountains and north-central Wyoming (Fig. 2). Populations were assigned to these four sub-regions based on geographic features which may prevent gene flow among populations from different sub-regions.

Voucher specimens were collected for each population to be digitized and processed at the Snake River Plains Herbarium at Boise State University, Boise, Idaho.

Enzyme Electrophoresis

Ventenata dubia caryopses (hereafter referred to as seeds) were stored in the laboratory for at least three months to allow for after- ripening. After this time, seeds were

extracted from the lemma and three seeds per individual were germinated in Petri dishes lined with moistened filter paper. Seeds germinated 36-48 hours after watering, and seedlings were harvested for analysis after 10-14 days of growth. Due to the small amount of tissue of *V. dubia* seedlings, it was necessary to use two to three seedlings from each maternal plant (family). It was not possible to grow seedlings for longer periods of time because of enzyme degradation within the plant tissue. In addition, the highly selfing mating system of *V. dubia* (see Results section) means that, in almost all cases, all progeny from the same maternal plant are genetically identical.

Genetic analysis was performed using enzyme electrophoresis (allozymes), following the procedures of Soltis et al. (1983), with modifications described by Novak et al. (1991). Root and leaf tissue were macerated in Tris-HCl grinding buffer- PVP solution (pH 7.5). Several buffer systems and various enzymes were tested to determine the optimal band visualization conditions for *V. dubia*. After optimization, plants were assessed for their allozyme diversity at 15 enzymes, and these enzymes were visualized using four buffer systems: buffer system 1, isocitrate dehydrogenase (IDH), glyceraldehyde-3-phosphate dehydrogenase (G3PDH) and glucose-6-phosphate dehydrogenase (G6PDH); buffer system 7, alcohol dehydrogenase (ADH), glutamate oxalacetate transaminase (GOT), and phosphoglucoisomerase (PGI); buffer system 8, aldolase (ALD), colorimetric esterase (CE), glutamate dehydrogenase (GDH), leucine aminopeptidase (LAP) and triosephosphate isomerase (TPI); buffer system 9, malate dehydrogenase (MDH), phosphoglucomutase (PGM), shikimate dehydrogenase (SKDH, and 6-phosphogluconate dehydrogenase (6PGD).

Multilocus Genotype Assignment

Each *V. dubia* individual was assigned a multilocus genotype (MLG) based on the different alleles present at four polymorphic loci. One genotype is referred to as the "Most Common Genotype" (MCG) and occurs most frequently throughout the introduced range of *V. dubia* because it has the most common combination of alleles at all polymorphic loci. Individuals which varied by one allele from the MCG, were considered a different MLG.

Data Analysis

Genetic (Allozyme) Diversity

Allozyme diversity of the 51 invasive populations of *V. dubia* located in the western US was analyzed using the programs POPGENE 1.32 (Yeh and Boyle 1997) and R package "PopGen Report" v 3.0 (Gruber and Adamack 2015). For every individual, allozyme information was entered as their multilocus genotype. Range-wide genetic diversity parameters for *V. dubia* populations in the invasive range include total number of alleles, number of alleles per locus, number of polymorphic loci, percentage of polymorphic loci and percentage of polymorphic populations.

The Index of Association (I_A) was used to test whether loci exhibit linkage disequilibrium (non-random association of alleles between loci) (Brown et al. 1980). The less biased version, rbarD, accounts for the number of loci sampled (Agapow and Burt 2001) where a value of 0.0 indicates no linkage disequilibrium, and a value of 1.0 indicates complete disequilibrium. Both indexes are calculated with the program "poppr" (Kamvar et al. 2015), using 999 permutations. An additional test was run to "clone correct" the data., A pairwise I_A over all loci was performed to ensure that linkage is not

the result of a single pair of loci.

Within-population genetic diversity was quantified using the following parameters: the mean number of alleles per locus (A), the number of polymorphic loci within each population (#P), the percent polymorphic loci per population (%P), the expected mean heterozygosity (Hexp) which was calculated using the unbiased estimate method of Nei (1978), the mean observed heterozygosity (Hobs), and the number of multilocus genotypes detected with each population (#MLG). The means of these parameters are used to describe the level of genetic diversity (on average) within populations of *V. dubia* in its invasive range in the western US.

To test for deviation from Hardy-Weinberg expectations, Wright's (1965) fixation index (F = 1 - Hobs/Hexp) was calculated for each polymorphic locus in a population using POPGENE 1.32 (Yeh and Boyle 1997). The significance of any deviation was determined using a χ^2 test.

Genetic Differentiation Among Populations

The R package "mmod" (Winter 2012) was used to calculate Nei and Chesser (1983) estimators of gene diversity and genetic differentiation. Using mmod, the total gene (allelic) diversity (H_T) was partitioned into the within-population component (H_S) and the among-population component (D_{ST}), with these parameters related by the following equation $H_T = H_S + D_{ST}$. The parameter G_{ST} describes the proportion of the total gene diversity that is partitioned among populations, and was calculated as $G_{ST} = 1 - H_S / H_T$. G_{ST} is a measure of the level of genetic differentiation among populations.

Analysis of molecular variance (AMOVA) was used to estimate the amount of

genetic variation partitioned within and among populations. In addition, a hierarchical analysis was performed to determine the amount of genetic variation partitioned within and among populations in the four geographic regions described above. AMOVA was calculated using R package "poppr" (Kamvar et al. 2015).

In order to graphically represent genetic differentiation among populations, an UPGMA phenogram was generated using the program POPGENE 1.32 (Yeh and Boyle 1997) based on Nei's (1978) unbiased genetic distance. This method was used as an alternative to Neighbor joining tree, as the UPGMA procedure assumes the same evolutionary rate for all lineages.

Bayesian Assignment Analysis

The Bayesian assignment software STRUCTURE (Pritchard et al. 2000) was used to determine the number of genetic clusters (K) for the 51 invasive populations of *V. dubia* using the method of Evanno et al. (2005). A modified hierarchical approach was used to determine the most likely number of genetic clusters as described in Vähä et al. (2007) and Olafsson et al. (2014). An initial partitioning STRUCTURE analysis was run with 10 repetitions, with K set to 1–10 with 10,000 iterations and 100,000 Markov Chain Monte Carlo (MCMC) simulations; this approach captures the major structure of invasive populations. In the second and third round of analysis, populations which were assigned to different subgroups were analyzed separately. For invasive populations, individuals with an assignment of 0.8 *q* or greater were included in the second and third round of analysis, while individuals with <0.8 *q* assignment were not used in subsequent runs. Hierarchical sub-structuring was completed when K was determined to be unequivocal (*q* assignment was equal among groups).

STRUCTURE results were run with the program "Pophelper 2.0", an R package program specifically designed to analyze and visualize population structure as well as the online web app (http://pophelper.com/) (Francis 2016). Additional graphical representation was obtained using STRUCTURE HARVESTER (Earl 2012) by web service at http://taylor0.biology.ucla.edu/structureHarvester/#.

Genotypic Diversity, Richness, and Evenness

The R package "poppr" (Kamvar et al. 2015) was used to calculate the mean values as measures of genetic diversity, richness, and evenness: Shannon-Wiener Index of MLG diversity (H) (Pielou 1966; Grünwald et al. 2003), Simpson's Index lambda (λ) (Simpson 1949) and E5 (Hill's modified ratio) (Alatalo, 1981; Ludwig and Reynolds 1988), where Simpson's Index lambda (λ) is calculated as one minus the sum of squared genotype frequencies and range between 0 (no genotypes are different) to 1 (all genotypes are different). Additionally, the measure of genotypic richness was calculated by direct observation of the number of unique genotypes contained in populations (#MLGs).

RESULTS

Herbarium Specimens

In Appendix A we list the first-collected herbarium specimens of *V. dubia* within counties across eight western US states, and this information reveals several patterns about its introduction and range expansion across the region (Fig 1). The grass was first reported in Spokane County, Washington [No accession] in 1952, with the next specimens collected in Kootenai County, Idaho [WTU273715] in 1957 and in Benewah County, Idaho [WTU273743] in 1960. Another pre-1970 report of the grass occurred in south-central Washington (Klickitat County [WS247993] in 1962). In the decades of the 1970s and 1980s, several records exist in areas near these five pre-1970 reports of the grass, as well as a few isolated records in California and southern Idaho (Placer County, California [UCD94425] 1983, Elmore County, Idaho [ID037447] 1986). In the 1990s, there was an increase in the number of *V. dubia* herbarium specimens across seven states in the western US: California, Idaho, Montana, Oregon, Utah, Washington, and Wyoming. Four specimens were collected in western Oregon (Willamette Valley) and three specimens were collected in northern California, with additional specimens collected in Washington and northeast Oregon. Simultaneously, several new state records also occurred in Montana, Utah and Wyoming (Ravalli County, Montana [MONT79339] 1995, Cache County, Utah [UTC00216696] 1995, Sheridan County, Wyoming [RM655052] 1997). More recent records (2000s, and forward in time) appear to expand from neighboring counties in most states, while most records were collected in southern

Idaho and northwestern and southern Montana. The most recent state records occurred in three counties in Nevada in the year 2016 (Washoe County, [V84851], Douglas County, [SRP58611], Elko County, [SRP61395] (Appendix A).

Allozyme Diversity Patterns

Of the 51 invasive populations (1636 total individuals; 32.1 individuals per population) of *V. dubia* from the western US analyzed at 26 allozyme loci, 15 populations (29.4 %) were polymorphic at one or more loci. Among all 1636 individuals, 30 alleles were identified (1.15 alleles/locus) and four loci were polymorphic (15.4%): *Ce-2, Ce-5, Pgi-2, Tpi-2*. Each polymorphic locus had two alleles. Six of 15 polymorphic populations exhibited diversity at four loci (Appendix C).

An analysis of the modified index of association (rbarD) revealed varying degrees of linkage disequilibrium among polymorphic loci (Fig. 3a), and the range-wide total for invasive populations yielded a value of rbarD = 0.5217638, with a p = 0.001, showing significant support for the hypothesis that overall, alleles across different loci are linked (Fig. 3a). Clone corrected data confirmed these results (rbarD = 0.4207867, p = 0.001) (Fig. 3b), further supporting the evidence of significant linkage disequilibrium among loci. A graphical representation of the degree of linkage among loci reveals that most alleles observed at different loci (four of six loci pairs) are associating somewhat randomly in invasive populations of *V. dubia* (rbarD = ~ 0.5) and range from 0.4386– 0.5185. The loci which show the highest association of linkage are CE5: PGI2 (rbarD = 0.5185) (Fig. 3c). Loci which show the least degree of linkage are CE2:PGI2 (rbarD = 0.2518) (See Appendix D for rbarD values). While linkage disequilibrium between loci does occur among invasive populations, we did not detect complete disequilibrium (1.0), thus all loci

will be retained in all analyses according to the recommendations of Flint-Garcia et al. (2003).

Multilocus Genotypes

Across 51 invasive populations of *V. dubia*, nine MLGs were detected (Fig. 4a), with 36 of 51 populations (70.6%) contained a single MLG (Table 1). Twenty-seven of 51 (52.9%) populations were composed of only the MCG (depicted by dark blue) (Fig. 4b), while 70.5% (36 of 51) of populations contained at least one individual with the MCG. Of all 1636 individuals analyzed, 1030 (63%) were found to have the MCG. Populations containing the MCG are widespread and found in every state: California (five of eight populations), Idaho (all eight populations), Montana (all four populations), Oregon (eight of 16 populations), Washington (seven of 10 populations), and the only MLG detected in Utah, Nevada and Wyoming (Fig. 4b).

The second most frequent MLG (depicted by yellow) was found in 11 of 51 (21.6%) populations, with 10 of these populations located in Washington and Oregon (Fig. 4b). The yellow MLG makes up 14.2% of all individuals analyzed (232 of 1636). The other seven MLGs were more locally distributed and occurred at lower frequencies: red (5.6%), orange (4.4%), black (4.1%), dark grey (2.8%), green (2.2%), teal (1.8%) and light grey (1.8%). These low-frequency genotypes occur primarily in the western portion of the invasive range in western portions of California, Oregon, and Washington. For instance, populations which contain the red and black MLGs were primarily found in northern California and western Oregon, with only a few individuals in a population in eastern Oregon also having this MLG. Two MLGs (teal and green) were each found in

only one population, in California and Oregon, respectively. The locations and distributions of the remaining three MLGs (orange, dark grey and light grey) are shown in Fig. 4b.

Genetic Diversity Within Populations

Among the 51 invasive populations analyzed, the mean number of alleles (A) was 1.03, the number of polymorphic loci (#P) and percent polymorphic loci (%P) are 0.76 and 2.94, respectively, expected mean heterozygosity (Hexp) was (0.0072) and mean observed heterozygosity (Hobs) was 0.00009 (Table 2). Only two of the 1636 *V. dubia* individuals analyzed in this study were heterozygous (*Pgi - 2ab*), and both individuals were in the population from Mosquito Creek, Oregon (*Hobs* = 0.0044). The *H*obs value for all other populations is 0.0000 (Table 2). The populations with the highest amount of genetic diversity were Joe Rausch's Shaketable, Oregon (A = 1.15, %P = 15.38, *H*obs 0.0764), Mosquito Creek, Oregon (A = 1.15, %P = 15.38, *H*obs = 0.0608) and Starkey, Oregon (A = 1.15, %P = 15.38, *H*obs = 0.0311); all three of these populations contained four polymorphic loci. Other populations with four polymorphic loci included Little Squab Creek, Idaho, Pullman, Washington, and Kalama, Washington. Thirty-eight populations lacked any allozyme diversity (Table 2). All populations which contained at least one polymorphic locus showed a significant ($p < 0.001$) deviation from Hardy-Weinberg equilibrium. Significant deviations from Hardy–Weinberg equilibrium were observed in 39 polymorphic loci. Wright's fixation index (F) values for *Pgi*-2 and *Tpi*-2 in the population from Mosquito Creek, Oregon (0.850), is due to the presence of two heterozygous individuals at both loci (Table 3).

On average, populations from the Columbia Basin sub-region had the highest

level of genetic diversity (A = 1.05, %P = 4.61, *H*obs = 0.0140), followed by populations from the Coastal Range sub-region (A = 1.03, %P = 3.53, *H*obs = 0.0075) and the Great Basin sub-region (A = 1.02,%P = 2.66, *H*obs = 0.0043). Populations from the Rocky Mountains sub-region had the lowest genetic diversity (A = 1.00, % P = 0.35, *H*obs = 0.0012) (Table 2).

Genetic Differentiation Among Populations

Averaged across the four polymorphic loci, Nei's (1987) total gene (allelic) diversity (H_T) is 0.349, the within-population component of gene diversity (H_S) is 0.048, and the among–population component of gene diversity (D_{ST}) is 0.301. The proportion of total gene diversity partitioned among populations (G_{ST}) is 0.864 (Table 4), indicating that 86.4% of the total allelic diversity is partitioned among populations. All four polymorphic loci had relatively high values for total gene diversity (H_T = 0.248 – 0.395), and values for the proportion of total gene diversity partitioned among populations (G_{ST}) ranged from 0.849 – 0.881, indicating high genetic structure at all four loci (Table 4).

Analysis of molecular variance (AMOVA) was used to partition genetic diversity within and among populations (Table 5a) and showed that 14.59% of the genetic diversity was partitioned within populations, while 85.23% of the genetic diversity was partitioned among populations. A second AMOVA analysis was conducted to determine how much genetic diversity was hierarchically partitioned (Table 5b). This analysis showed that 14.14% of the genetic diversity was partitioned within populations, 72.66% of the diversity was partitioned among populations within regions, and 13.03% of the diversity

was partitioned among regions.

A UPGMA dendrogram, based on Nei's (1978) genetic distance values, showed the genetic relationships among the 51 invasive populations of *V. dubia* analyzed in this study (Fig. 5). Most populations occurred in four distinct clusters. The largest cluster contains populations representing predominantly the Columbia Basin, Great Basin, and the Rocky Mountains sub-regions. The second and third cluster contains populations which are distributed in the Coastal Range sub-region exclusively. Cluster 4 contains populations predominantly assigned to the Columbia Basin and Coastal Range sub-regions. Populations from Hamilton, Montana, Joe Rausch's Shaketable, Oregon, Lake Pillsbury, California, and JB Charbonneau GS, Oregon, were excluded from clustering assignment as the populations were the only populations on their respective branches.

Bayesian Assignment Analysis

STRUCTURE analyses were run for invasive populations using the method of Evanno et al. (2005) to determine the number of genetic clusters (K). The first analysis included two simulations, one run with K 1-10 with 10,000 iterations and 100,000 Markov Chain Monte Carlo (MCMC) repetitions, and the second set at K 1-8 with 100,000 iterations and 1,000,000 Markov Chain Monte Carlo (MCMC) repetitions. Both simulations resulted in similar support for K=2 (Appendix E). The second simulation produced two clusters (red and green) (Fig. 6a). Approximately 63% of individuals (1033 of 1636) were assigned to the red cluster with 0.8 or greater *q* assignment. The hierarchical sub-structure analysis of red cluster alone resulted in unequivocal assignment (approximately 50/50 probability) and could not be subdivided further. Approximately

37% (603) of the individuals were assigned to the green cluster and only one individual was discarded from the next round of analysis.

The second round of independent STRUCTURE analyses of the green cluster included 603 individuals, and resulted in a SubK=2, (Appendix E) Although the ΔK figure generated by STRUCTURE HARVESTER showed the greatest change between K=3 and K=4, (Appendix E), the greatest value of ΔK obtained using the method of Evanno et al. (2005) (not shown) determined a K = 2. Approximately 62% individuals (372 of 602) were assigned to the light blue cluster, and approximately 38% (230 of 602) were assigned to the orange cluster with > 0.8 *q* probability (Fig. 6b). Further sub-structuring of the orange cluster yielded unequivocal assignment and could not be subdivided further. No individuals were discarded for the third round of analysis.

The analysis of the light blue cluster (n = 372) showed a SubK=2 (Appendix E) which assigned 159 individuals to the dark blue cluster (43%), and 146 individuals (39%) to the lilac cluster with > 0.8 *q* probability (Fig. 6c). Approximately 18% (67) of individuals were discarded in the final analysis; however, both clusters (dark blue and lilac) could not be subdivided further and showed unequivocal results (approximately 50/50 probability) and were not rerun. The total number of clusters by hierarchical sub-structuring analysis of populations in the invasive range resulted in four genetic clusters (indicated in red, orange, dark blue, and lilac in Fig. 6).

These four genetic clusters do not correspond to the four population sub-regions, rather membership in these clusters appears to be based on the MLGs present in invasive populations of *V. dubia*. For instance, the red genetic cluster consisted of populations and individuals with the MCG (Fig. 6a); whereas, the green

cluster contained populations and individuals composed of the remaining eight MLGs. Sub-structuring analysis of the green genetic cluster assigned populations and individuals with the yellow MLG (see Fig. 4a) to the orange cluster, and populations that contained individuals with the seven low-frequency MLGs were the assigned to the light blue cluster (Fig. 6b). Sub-structuring analysis of the light blue genetic cluster assigned individuals in the 13 remaining populations to the dark blue and lilac clusters (Fig. 6c), with many of these 13 populations exhibiting varying amounts of admixture.

Genotypic Richness, Diversity, and Evenness

Shannon-Wiener index of MLG diversity ranged from 0.14 to 0.74 in polymorphic populations, and was highest in Mosquito Creek, Oregon (H = 0.74), followed by Joe Rausch's Shaketable, Oregon, and Lower Lake, California (H = 0.69). Simpson's Index (λ) ranged from 0.06 to 0.50 in genetically variable populations and was highest in Joe Rausch's Shaketable, Oregon and Lower Lake, California ($\lambda = 0.50$), followed by Wilderness Village, Washington ($\lambda = 0.47$). Hill's modified ratio for evenness (E5) ranged from 0.44 to 1.0, among polymorphic populations, with an overall mean value of 0.69 (Table 6). The 36 populations which had no allozyme variability had a value of zero for both indices, while evenness cannot be computed for populations lacking genetic diversity. Populations which had multilocus genotypes in near equal abundance were detected at Lake Pillsbury, California (E5 = 1.0), followed by Joe Rausch's Shaketable, Oregon (E5 = 0.99), and Wilderness Village, Washington (E5 = 0.95).

Compared to the overall mean of all populations (H = 0.14), populations from the

Coastal Range had the highest diversity values (H = 0.21), followed by populations from the Columbia Basin (H = 0.17), while populations from the Rocky Mountains had the lowest diversity (H = 0.05). Populations from the Rocky Mountains showed the highest values for evenness (E5 = 0.80), followed by populations from the Columbia Basin (E5 = 0.72); populations from the Great Basin had the lowest evenness value (E5 = 0.60) (Table 6).

DISCUSSION

Multiple Introduction and Spread

The western US has an extensive history of biological invasions. Eurasian annual grasses such as *B. tectorum* and *T. caput-medusae* have invaded millions of hectares throughout the western US and become dominant across the landscape (Novak and Mack 2001; Mack 2011; Germino et al. 2016). The relatively recent introduction and rapid range expansion of *V. dubia* suggests that this grass joins the ranks of these other invasive annual grasses that have caused severe ecological damage and high economic costs across much of the western US. Therefore, this and other research projects involving *V. dubia* are timely for gaining a better understanding of this invasion; especially if this information is implemented in the management of the species to reduce its ecological and economic harm.

The use of herbarium specimens to reconstruct the introduction and spread of an invasive plant can sometimes be challenging (e.g., records can be fragmentary) (Delisle et al. 2003), however herbarium specimens also provide unequivocal information concerning the occurrence of a plant at a certain place and time. *Ventenata dubia* has a detailed collection history in the western US (Fig. 1), and this history is consistent with the pattern often associated with multiple introductions and local or regional range expansion (Lambrinos 2001; Chauvel et al. 2006). Based on herbarium records and population collections made during this study, *V. dubia* now appears to occur in at least

22 Oregon, 18 Idaho, 15 Washington, 10 California, nine Montana, three Nevada, one Wyoming, and one Utah counties.

Any inferences drawn from the collection history of an invasive species can be further assessed using molecular data. The detection of nine homozygous multilocus genotypes among the 51 invasive populations of *V. dubia* analyzed in this study (Table 1, Fig. 4) suggests that multiple and separate introduction events into the western US have occurred. The most common genotype (MCG, blue color) was found to be widespread across the western US (Fig. 4b), it was detected in *V. dubia* populations in every state. Moreover, this genotype occurs in the localities where the grass was first reported (Spokane County, Washington and Kootenai County, Idaho) and now predominates in populations in the Rocky Mountains, Great Basin and Columbia Basin sub-regions. The occurrence of the MCG across this large area may reflect the following sequence of events: the introduction of this multilocus genotype into Spokane County, and its subsequent spread as range expansion of *V. dubia* proceeded eastward and southward through several major highways (e.g., Interstate 90 and the Highway 95/55 corridors, respectively).

An alternative scenario for the widespread distribution of the MCG in the eastern portion of the study area involves independent (multiple) introductions of this multilocus genotype into various locations in the region. Such a scenario may explain the occurrence of the MCG in the isolated and localized populations of the grass in Wyoming and Utah. This alternative scenario involves the independent uptake of individuals with the MCG from a native population (or populations), their transport from the native range in Eurasia to the western US, and their release and establishment into several locations in the new

range. Although our allozyme data does not allow us to differentiate between these two scenarios, this latter scenario appears less parsimonious.

The second most common genotype (yellow) shows a different geographic pattern of distribution (Fig. 4b). This multilocus genotype has been detected in 11 of 51 invasive populations of *V. dubia*, with 10 of these populations located in Oregon and Washington. Several scenarios may explain the distribution of this genotype. In the first scenario, this genotype was introduced into Klickitat County, Washington, in 1962, and spread from this original point of introduction as range expansion of the grass proceeded in several directions. In an alternative scenario, this genotype may have been independently introduced into several localities where it now occurs. For instance, the yellow genotype was found in two populations in western Washington (Kalama and Toledo), and both populations are separated from Klickitat County by the Cascade Mountain Range. In addition, this genotype was also detected in a population near Klamath Lake, OR, which is located far south of Klickitat County.

Additional evidence for multiple introductions exists in the distribution of low-frequency genotypes which are found throughout the four sub regions. For instance, the light grey genotype is found in only two populations, Hamilton, Montana (Rocky Mountains sub-region) and Eugene, Oregon (Coastal Range sub-region) (Table 1, Fig. 4b). Multiple introductions also appear to have occurred into populations in the Coastal Range sub-region: eight of the nine multilocus genotypes detected among all 51 invasive populations from the western US were detected among the 12 populations analyzed from this sub-region. Three of these eight genotypes (dark grey, black and teal) were only detected within populations from this sub-region. All 12 populations assigned to the

Coastal Range sub-region are located west of the Cascade and Sierra Nevada mountain ranges and are therefore geographically isolated from the other populations analyzed in this study. In general, the genotypes detected among Coastal Range sub-region populations have limited geographical distributions. For instance, in Oregon, the red genotype was detected in Monmouth (where the grass was first collected in 1984) and Sherwood, and the black genotype was detected in Eugene and Roseburg. In the Coastal Range sub-region, the red and black genotypes were also detected in the population sampled near Lower Lake, California. These results suggest that these genotypes may have been introduced independently into Oregon and California.

Propagule Pressure

The number of multilocus genotypes or haplotypes found among invasive populations can provide an estimate of propagule pressure (Novak and Mack 2005; Huttanus et al. 2011). The detection of nine multilocus genotypes among the 51 invasive populations of *V. dubia* analyzed here (Table 1, Fig. 4) suggest moderate propagule pressure associated with the introduction of this species into the western US. And if each multilocus genotype is the product of an independent introduction event, the detection of nine genotypes translates into a minimum of nine separate introduction events. Our estimate of propagule pressure would increase if the same genotype was introduced into different portion of the species' invasive range. For instance, the broad distribution of the MCG across much of the eastern portion of the study area may result from independent introductions into several localities in this area. Our estimate of propagule pressure can be considered reliable due to the detection of different genotypes in localities associated

with the earliest herbarium specimens of the grass in the western US.

Similar with collection history information, the distribution of these nine multilocus genotypes among invasive populations (Fig. 4b) suggests that range expansion of *V. dubia* in its invasive range has occurred at a regional or local geographical scale. If the MCG was introduced just once in the eastern portion of the study area, its distribution would most likely have occurred through regional range expansion. If, as stated above, the widespread distribution of the MCG in this region is the result of multiple introductions, range expansion of the grass in this area would have occurred at a more local scale. The distribution of other multilocus genotypes among invasive populations of *V. dubia*, especially genotypes in the Coastal Range sub-region, appears to be the result of mostly local range expansion. Evidence for regional and/or local range expansion is provided by the lack of genetic admixture among invasive populations; only 15 of 51 (29.4%) invasive population have two or more multilocus genotypes. Among all 51 invasive populations analyzed in this study, the populations from Eugene and Roseburg, OR, are the only populations which possess three multilocus genotypes.

Genetic Diversity and Genetic Structure

The genetic diversity and genetic structure of invasive populations is influenced by multiple factors: the level and structure of genetic diversity within and among native populations, propagule pressure, and the pattern of range expansion of a species in its new range (Novak and Mack 2005; Taylor and Keller 2007; Keller and Taylor 2008; Pawlak et al. 2015; Novak and Mack 2016). With small founder population size, a single or a few introduction events (low propagule pressure) and local range expansion, invasive

populations often exhibit reduced genetic diversity and increased genetic differentiation, in comparison to native populations (Brown and Marshall 1981; Novak and Mack 2005; Wares et al. 2005; Dlugosch and Parker 2008; Barrett 2015). In addition, the level and structure of both native and invasive populations is strongly influenced by the mode of reproduction and mating system of a species (Stebbins 1957; Barrett et al. 2008; Pannell 2015). For instance, plant species with higher rates of selfing have lower levels of genetic diversity within populations and higher genetic differentiation among populations, compared to predominantly outcrossing species (Brown and Burdon 1987; Slatkin and Barton 1989; Hamrick and Godt 1996; Sork et al. 1999).

The allozyme data reported here provides an initial assessment of the genetic consequences of the introduction and range expansion of *V. dubia* in the western US. Despite evidence for multiple introductions into its invasive range (i.e., moderate propagule pressure), the level of genetic diversity, on average, within the 51 invasive populations of *V.* dubia reported here (Table 2: A = 1.03, #P = 0.76, %P = 2.94, Hexp = 0.007 and Hobs = 0.00009) is low in comparison with the level of diversity reported for other plant species. For a comparison of the genetic diversity of the study species with other plant species, that possess various life-history traits, see Hamrick and Godt (1996). These results for *V. dubia* are consistent with theoretical predictions (Nei et al. 1978; Watterson 1984; Novak and Mack 2005) and suggest that even moderate propagule pressure was not enough to overcome founder effects, the reduction and/or alteration of genetic diversity expected with introduction events. In addition, the low level of genetic diversity detected within these invasive populations likely stems from the local and/or regional pattern of range expansion described above. With local and/or regional range

expansion, the multilocus genotype(s) introduced into a geographic area would not intermix with the genotype(s) introduced into another area (genetic admixture would be reduced). The low level of genetic diversity detected within these invasive populations is also associated with the highly selfing mating system of *V. dubia*. Evidence for the selfing mating system of this species is provided by the detection of only two heterozygous individuals in a single population (Mosquito Creek, Oregon) among all 51 invasive populations (and 1636 individuals) from the western US. All F values for the polymorphic loci detected in these populations were significantly different from 0.0 (indicating a significant deviation from Hardy-Weinberg equilibrium) (Table 3) and the mean value of Hobs for all 51 invasive populations is 0.00009.

The values for the genetic diversity parameters reported here for *V. dubia* are similar with the values reported for invasive populations of *B. tectorum* and *T. caput-medusae*, two highly selfing, annual grasses invasive in the western US, using the same molecular marker (allozymes). As summarized by Novak and Mack (2016), the range in genetic diversity parameters for invasive populations of *B. tectorum* from different sub-regions across the US and Canada (A = 1.01 – 1.05, %P = 1.05 – 5.14, Hexp 0.002 – 0.014, Hobs = 0.0000 – 0.0002) are comparable to the values reported here for *V. dubia*. The values of genetic diversity parameters for 46 invasive populations of *T. caput-medusae* in the western US (A = 1.02, %P = 1.90, Hexp = 0.005, Hobs = 0.0001) are similar to those of *V. dubia* (S.J. Novak, unpublished data).

The genetic structure of invasive populations is determined by propagule pressure, pattern of range expansion and the mating (reproductive) system of the species (Brown and Marshall 1981; Hamrick and Godt 1996; Novak and Mack 2005). In this

study we have documented multiple introductions (moderate propagule pressure), local and/or regional range expansion from these putative points of introduction, and the highly selfing mating system of *V. dubia*. In combination, these factors have resulted in the regional distribution of certain genotypes as revealed in the UPGMA cluster diagram (Fig. 5) and the results of our STRUCTURE analysis (Fig. 6).

These factors have also produced the relatively high genetic structure reported here for invasive populations of *V. dubia*. For instance, the results of AMOVA indicate that 85% of the total genetic diversity is partitioned among populations and only 15% of the total diversity is partitioned within populations (Table 5). Similar results are reported for gene diversity statistics (Nei and Chesser 1983) (Table 4), which indicates that 86.4% of the total diversity is partitioned among populations (G_{ST} = 0.864). This level of genetic differentiation among populations of *V. dubia* is greater than that reported for invasive populations of other selfing grass species such as *B. tectorum* (Novak and Mack 2016) and *Brachypodium stacei* (Shiposha et al. 2016), but very similar to the level reported for *T. caput-medusae* (G_{ST} = 0.907) (S.J. Novak, unpublished data).

Conclusion

Much like other invasive annual grasses (e.g., *B. tectorum* and *T. caput-medusae)*, results of this genetic analysis indicate that *V. dubia* was introduced multiple times into the western US. Despite multiple introductions, invasive populations exhibit low levels of genetic admixture, low levels of genetic diversity within populations and high genetic differentiation among populations; most likely due to a local and/or regional pattern of range expansion. However, this putative reduced evolutionary potential did not preclude

the initial establishment of *V. dubia* and has not limited its rapid spread across its new range.

Gaining insights into other aspects of this invasion will require the genetic analysis of native populations, using the same genetic marker (Bossdorf et al. 2005; Novak and Mack 2005; Novak 2011). Identifying the same multilocus genotypes within and among native populations will provide evidence confirming the multiple introduction hypothesis and will aid in identifying the geographic origins (source populations) of this invasion (Novak 2011). Population genetic data from native populations will also allow a more precise estimate of the degree to which founder effects have influence the genetic diversity and structure of invasive populations (Novak and Mack 2005; Dlugosch and Parker 2008), and will allow an assessment of the role of post-introduction evolution versus prior adaptation in this invasion (Hufbauer et al. 2011; Rey et al. 2012). Finally, the genetic analysis of native and invasive populations within the same experimental framework can inform programs aimed at managing the invasion of *V. dubia* in the western US, especially efforts to search for effective and specific biological control agents (Gaskin et al. 2011).

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TABLES AND FIGURES

Table 1 Identity and frequency of multilocus genotypes (MLG) detected within 51 invasive populations *Ventenata dubia* from the western US. N is the number of individuals in each population, a description of the color of each MLG is provided in Fig. 4, MLG count refers to the number of individuals in a population with each genotype, and MLG frequency refers to the proportion of individuals in a population with each MLG.

Region	Population	N	MLG	MLG Count	MLG frequency
Coastal Range	1.Wilderness Village, WA	34	Blue	21	0.62
			Dark Grey	13	0.38
	2. Toledo, WA	28	Yellow	28	1.00
	3. Kalama, WA	25	Blue	1	0.04
			Yellow	24	0.96
	4. Sherwood, OR	30	Red	30	1.00
	5. Monmouth, OR	33	Red	33	1.00
	6. Eugene, OR	42	Light Grey	1	0.03
			Orange	3	0.07
			Black	38	0.9
	7. Roseburg, OR	39	Dark Grey	1	0.03
			Black	9	0.23
			Orange	29	0.74
	8. Bigelow, OR	32	Orange	32	1.00
	9. Tennant Rd, CA	30	Blue	30	1.00
	10. Hidden Valley Rd, CA	30	Teal	30	1.00
	11. Lake Pillsbury, CA	32	Dark Grey	32	1.00
	12. Lower Lake, CA	38	Red	18	0.47
			Black	20	0.53
Columbia Basin	13. Husum, WA	29	Yellow	29	1.00
	14. Lyle, WA	35	Yellow	35	1.00

	15. Sims Corner, WA	35	Blue	28	0.8
			Orange	7	0.02
	16. Spangle, WA	35	Blue	35	1.00
	17. Rosalia, WA	29	Blue	29	1.00
	18. Pullman, WA	35	Blue	33	0.94
			Yellow	2	0.06
	19. Anatone, WA	30	Blue	30	1.00
	20. Flora, OR	30	Blue	30	1.00
	21. Mill Creek, OR	33	Blue	33	1.00
	22. Starkey, OR	35	Blue	31	0.89
			Yellow	4	0.11
	23. Mosquito Creek, OR	35	Blue	8	0.23
			Yellow	25	0.71
			Het: Blue, Yellow	2	0.06
	24. Keeny Meadows, OR	19	Blue	19	1.00
	25. Joe Rausch’s Shaketable, OR	35	Blue	19	0.54
			Yellow	16	0.46
	26. North Finger Rd, OR	35	Yellow	35	1.00
Great Basin	27. Ochoco Mountains, OR	30	Blue	30	1.00
	28. Silver Lake, OR	34	Blue	34	1.00
	29. Klamath Lake, OR	31	Orange	1	0.03
			Yellow	30	0.97
	30. Pine Creek, CA	30	Blue	30	1.00
	31. Ahjumawi Lava SP, CA	30	Blue	30	1.00
	32. Susanville, CA	27	Blue	19	0.70
			Red	8	0.30
	33. Emigrant Gap, CA	30	Blue	30	1.00
	34. Stateline, NA	31	Blue	31	1.00

	35. Elko, NV	36	Blue	36	1.00
	36. Mountain City, NV	30	Blue	30	1.00
	37. JB Charbonneau GS, OR	39	Red	3	0.08
			Green	36	0.92
	38. Little Squab Creek, ID	35	Blue	32	0.91
			Yellow	3	0.09
	39. Lucky Peak, ID	36	Blue	36	1.00
	40. Hill City, ID	30	Blue	30	1.00
Rocky Mountains	41. Old Sardine Canyon Rd, UT	30	Blue	30	1.00
	42. Kirkham Campground, ID	30	Blue	30	1.00
	43. Sugarloaf Peninsula, ID	31	Blue	31	1.00
	44. Tensed, ID	35	Blue	35	1.00
	45. Beauty Bay, ID	30	Blue	30	1.00
	46. Bison Range, MT	33	Blue	33	1.00
	47. Hamilton, MT	36	Blue	8	0.22
			Light Grey	28	0.78
	48. Gibbonsville, ID	30	Blue	30	1.00
	49. Bozeman, MT	30	Blue	30	1.00
	50. Triple Tree, MT	27	Blue	27	1.00
	51. Soldier Creek, WY	27	Blue	27	1.00

Table 2 Within-population genetic diversity parameters for 51 invasive populations of *Ventenata dubia* from the western US analyzed in this study. Parameters are the sample size of each population (N), mean number of alleles per locus (A), number of polymorphic loci per population (#P), percent polymorphic loci per population (%P), mean observed heterozygosity (Hobs), and expected mean heterozygosity (Hexp) (unbiased estimate method of Nei (1978). Populations are organized based on the four geographic regions, and the regional mean values and total mean of all parameters are provided.

Region	Population	N	A	#P	%P	Hobs	Hexp
Coastal Range	1.Wilderness Village, WA	34	1.04	1	3.85	0.0000	0.0182
	2. Toledo, WA	28	1.00	0	0.00	0.0000	0.0000
	3. Kalama, WA	25	1.15	4	15.38	0.0000	0.0118
	4. Sherwood, OR	30	1.00	0	0.00	0.0000	0.0000
	5. Monmouth, OR	33	1.00	0	0.00	0.0000	0.0000
	6. Eugene, OR	42	1.08	2	7.69	0.0000	0.0117
	7. Roseburg, OR	39	1.12	3	11.54	0.0000	0.0292
	8. Bigelow, OR	32	1.00	0	0.00	0.0000	0.0000
	9. Tenant Rd, CA	30	1.00	0	0.00	0.0000	0.0000
	10. Hidden Valley Rd, CA	30	1.00	0	0.00	0.0000	0.0000
	11. Lake Pillsbury, CA	32	1.00	0	0.00	0.0000	0.0000
	12. Lower Lake, CA	38	1.04	1	3.85	0.0000	0.0192
Coastal Range Mean		*33*	*1.04*	*0.9*	*3.53*	*0.0000*	*0.0075*

Columbia Basin	13. Husum, WA	30	1.00	0	0.00	0.0000	0.0000
	14. Lyle, WA	35	1.00	0	0.00	0.0000	0.0000
	15. Sims Corner, WA	35	1.08	2	7.69	0.0000	0.0246
	16. Spangle, WA	35	1.00	0	0.00	0.0000	0.0000
	17. Rosalia, WA	30	1.00	0	0.00	0.0000	0.0000
	18. Pullman, WA	35	1.15	4	15.38	0.0000	0.0166
	19. Anatone, WA	30	1.00	0	0.00	0.0000	0.0000
	20. Flora, OR	30	1.00	0	0.00	0.0000	0.0000
	21. Mill Creek, OR	33	1.00	0	0.00	0.0000	0.0000
	22. Starkey, OR	35	1.15	4	15.38	0.0000	0.0311
	23. Mosquito Creek, OR	35	1.15	4	15.38	0.0044	0.0608
	24. Keeny Meadows, OR	19	1.00	0	0.00	0.0000	0.0000
	25. Joe Rausch’s Shaketable, OR	35	1.15	4	15.38	0.0000	0.0764
	26. North Finger Rd, OR	35	1.00	0	0.00	0.0000	0.0000
	27. Ochoco Mountains, OR	30	1.00	0	0.00	0.0000	0.0000
Columbia Basin Mean		*32*	*1.05*	*1.2*	*4.61*	*0.0003*	*0.0140*
Great Basin	28. Silver Lake, OR	34	1.00	0	0.00	0.0000	0.0000
	29. Klamath Lake, OR	31	1.08	2	7.69	0.0000	0.0048

	30. Pine Creek, CA	30	1.00	0	0.00	0.0000	0.0000
	31. Ahjumawi Lava SP, CA	30	1.00	0	0.00	0.0000	0.0000
	32. Susanville, CA	27	1.04	1	3.85	0.0000	0.0160
	33. Emigrant Gap, CA	30	1.00	0	0.00	0.0000	0.0000
	34. Stateline, NA	31	1.00	0	0.00	0.0000	0.0000
	35. Elko, NV	36	1.00	0	0.00	0.0000	0.0000
	36. Mountain City, NV	30	1.00	0	0.00	0.0000	0.0000
	37. JB Charbonneau GS, OR	39	1.08	2	7.69	0.0000	0.0109
	38. Little Squab Creek, ID	35	1.15	4	15.38	0.0000	0.0241
	39. Lucky Peak, ID	36	1.00	0	0.00	0.0000	0.0000
	40. Hill City, ID	30	1.00	0	0.00	0.0000	0.0000
Great Basin Mean		*32*	*1.02*	*0.7*	*2.66*	*0.0000*	*0.0043*
Rocky Mountains	41. Old Sardine Canyon Rd, UT	30	1.00	0	0.00	0.0000	0.0000
	42. Kirkham Campground, ID	30	1.00	0	0.00	0.0000	0.0000
	43. Sugarloaf Peninsula, ID	31	1.00	0	0.00	0.0000	0.0000
	44. Tensed, ID	35	1.00	0	0.00	0.0000	0.0000
	45. Beauty Bay, ID	30	1.00	0	0.00	0.0000	0.0000
	46. Bison Range, MT	33	1.00	0	0.00	0.0000	0.0000

	47. Hamilton, MT	36	1.04	1	3.85	0.0000	0.0133
	48. Gibbonsville, ID	30	1.00	0	0.00	0.0000	0.0000
	49. Bozeman, MT	30	1.00	0	0.00	0.0000	0.0000
	50. Triple Tree, MT	30	1.00	0	0.00	0.0000	0.0000
	51. Soldier Creek, WY	27	1.00	0	0.00	0.0000	0.0000
Rocky Mountains Mean		*31*	*1.00*	*0.1*	*0.35*	*0.0000*	*0.0012*
Overall Mean		**32**	**1.03**	**0.76**	**2.94**	**0.00009**	**0.00723**

Table 3 Fixation indices (F) for each polymorphic locus in 51 invasive populations of Ventenata dubia from the western US. Values of 1.00 indicate complete deviation from Hardy-Weinberg equilibrium. All values are significant at P < 0.001.

Population	Locus	F*
Wilderness Village, WA	*Pgi-2*	1.0
Kalama, WA	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	1.0
	Tpi-2	1.0
Eugene, OR	*Ce-2*	1.0
	Pgi-2	1.0
Roseburg, OR	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	1.0
Lower Lake, CA	*Ce-5*	1.0
Sims Corner, WA	*Ce-5*	1.0
	Pgi-2	1.0
Pullman, WA	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	1.0
	Tpi-2	1.0
Starkey, OR	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	1.0
	Tpi-2	1.0
Mosquito Creek, OR	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	0.8504
	Tpi-2	0.8504
Joe Rausch's Shaketable, OR	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	1.0
	Tpi-2	1.0
Klamath Lake, OR	*Ce-2*	1.0
	Tpi-2	1.0
Susanville, CA	*Ce-2*	1.0
JB Charbonneau, OR	*Ce-5*	1.0
	Pgi-2	1.0
Little Squab, OR	*Ce-2*	1.0
	Ce-5	1.0
	Pgi-2	1.0
	Tpi-2	1.0
Hamilton, MT	*Ce-5*	1.0

Table 4 Nei's (1987) gene diversity statistics of 51 invasive populations of Ventenata dubia from the western US. See text for a description of the Nei's gene diversity statistics parameters.

Locus	H_T	H_S	D_{ST}	G_{ST}
Ce-2	0.395	0.049	0.346	0.876
Ce-5	0.376	0.056	0.320	0.851
Pgi-2	0.375	0.057	0.318	0.849
Tpi-2	0.248	0.030	0.218	0.881
Mean	0.349	0.048	0.301	0.864

Table 5 Analysis of Molecular Variance (AMOVA) using 'poppr' (Kamvar et al. 2015) of 51 invasive populations of Ventenata dubia from the western US. Part a) shows the amount of genetic variation partitioned within and among populations; and b) is a hierarchical analysis for the amount of genetic variation partitioned within populations, among populations within regions, and the four geographic regions.

		d.f	Sum of Squares	Variation Component	Percentage Variation
(a)	Among populations	50	1980.995	0.61442	85.23
	Within populations	1586	335.415	0.10519	14.59
	Within individuals	1636	2.000	0.00122	00.16
	Total	3271	2318.411	0.72084	--
(b)	Among regions	3	342.7165	0.09697	13.03
	Among populations within regions	47	1638.2789	0.54059	72.66
	Among samples within populations	1585	335.4153	0.10520	14.14
	Within samples	1636	2.0000	0.00122	00.16
	Total	3271	2318.4108	0.74399	--

Table 6 Multilocus genotype and genotypic diversity parameters for 51 invasive populations of *Ventenata dubia* from the western US. Parameters include the number of multilocus genotypes (#MLG); diversity parameters include Shannon-Wiener Index of MLG diversity (H), Simpson's Index (λ), and measure of Evenness (E5). Evenness is not reported for populations containing one MLG (-). Populations are organized based on regions, and the regional mean values and total mean of all parameters are provided

Region	Population	#MLG	H	λ	E.5
Coastal Range	1.Wilderness Village, WA	2	0.67	0.47	0.95
	2. Toledo, WA	1	0.00	0.00	-
	3. Kalama, WA	2	0.17	0.08	0.46
	4. Sherwood, OR	1	0.00	0.00	-
	5. Monmouth, OR	1	0.00	0.00	-
	6. Eugene, OR	3	0.37	0.18	0.48
	7. Roseburg, OR	3	0.65	0.39	0.70
	8. Bigelow, OR	1	0.00	0.00	-
	9. Tennant Rd, CA	1	0.00	0.00	-
	10. Hidden Valley Rd, CA	1	0.00	0.00	-
	11. Lake Pillsbury, CA	1	0.00	0.00	-

	12. Lower Lake, CA	2	0.69	0.50	1.00
Coastal Range Mean		*1.6*	*0.21*	*0.14*	*0.72*
Columbia Basin	13. Husum, WA	1	0.00	0.00	-
	14. Lyle, WA	1	0.00	0.00	-
	15. Sims Corner, WA	2	0.50	0.32	0.73
	16. Spangle, WA	1	0.00	0.00	-
	17. Rosalia, WA	1	0.00	0.00	-
	18. Pullman, WA	2	0.22	0.11	0.49
	19. Anatone, WA	1	0.00	0.00	-
	20. Flora, OR	1	0.00	0.00	-
	21. Mill Creek, OR	1	0.00	0.00	-
	22. Starkey, OR	2	0.36	0.20	0.60
	23. Mosquito Creek, OR	3	0.74	0.43	0.70
	24. Keeny Meadows, OR	1	0.00	0.00	-
	25. Joe Rausch’s Shaketable, OR	2	0.69	0.50	0.99

	26. North Finger Rd, OR	1	0.00	0.00	-
	27. Ochoco Mountains, OR	1	0.00	0.00	-
Columbia Basin Mean		*1.4*	*0.17*	*0.10*	*0.70*
Great Basin	28. Silver Lake, OR	1	0.00	0.00	-
	29. Klamath Lake, OR	2	0.14	0.06	0.44
	30. Pine Creek, CA	1	0.00	0.00	-
	31. Ahjumawi Lava SP, CA	1	0.00	0.00	-
	32. Susanville, CA	2	0.61	0.42	0.86
	33. Emigrant Gap, CA	1	0.00	0.00	-
	34. Stateline, NA	1	0.00	0.00	-
	35. Elko, NV	1	0.00	0.00	-
	36. Mountain City, NV	1	0.00	0.00	-
	37. JB Charbonneau GS, OR	2	0.27	0.14	0.53
	38. Little Squab Creek, ID	2	0.29	0.16	0.55
	39. Lucky Peak, ID	1	0.00	0.00	-
	40. Hill City, ID	1	0.00	0.00	-

Great Basin Mean		*1.3*	*0.10*	*0.06*	*0.60*
Rocky Mountains	41. Old Sardine Canyon Rd, UT	1	0.00	0.00	-
	42. Kirkham Campground, ID	1	0.00	0.00	-
	43. Sugarloaf Peninsula, ID	1	0.00	0.00	-
	44. Tensed, ID	1	0.00	0.00	-
	45. Beauty Bay, ID	1	0.00	0.00	-
	46. Bison Range, MT	1	0.00	0.00	-
	47. Hamilton, MT	2	0.56	0.38	0.80
	48. Gibbonsville, ID	1	0.00	0.00	-
	49. Bozeman, MT	1	0.00	0.00	-
	50. Triple Tree, MT	1	0.00	0.00	-
	51. Soldier Creek, WY	1	0.00	0.00	-
Rocky Mountain Mean		*1.1*	*0.05*	*0.03*	*0.80*
Overall Mean		**1.35**	**0.14**	**0.09**	**0.69**

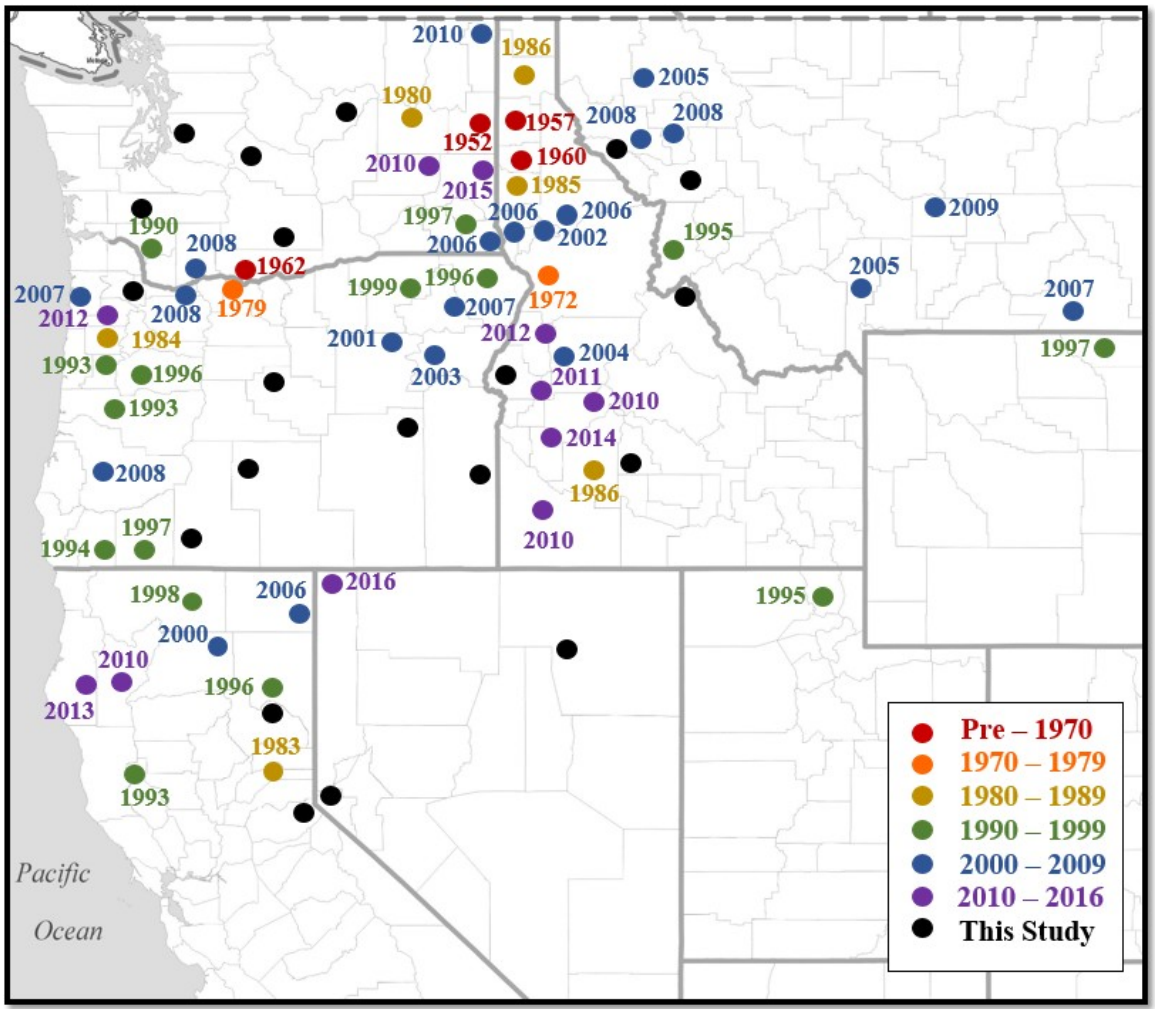

Figure 1 Date and location of first detection of Ventenata dubia in each county in California, Idaho, Montana, Nevada, Oregon, Utah, Washington and Wyoming, based on herbarium specimens. Collection dates are color coded by decade. Black dots with no dates represent new county record specimens acquired over the course of this study (2015 – 2016).

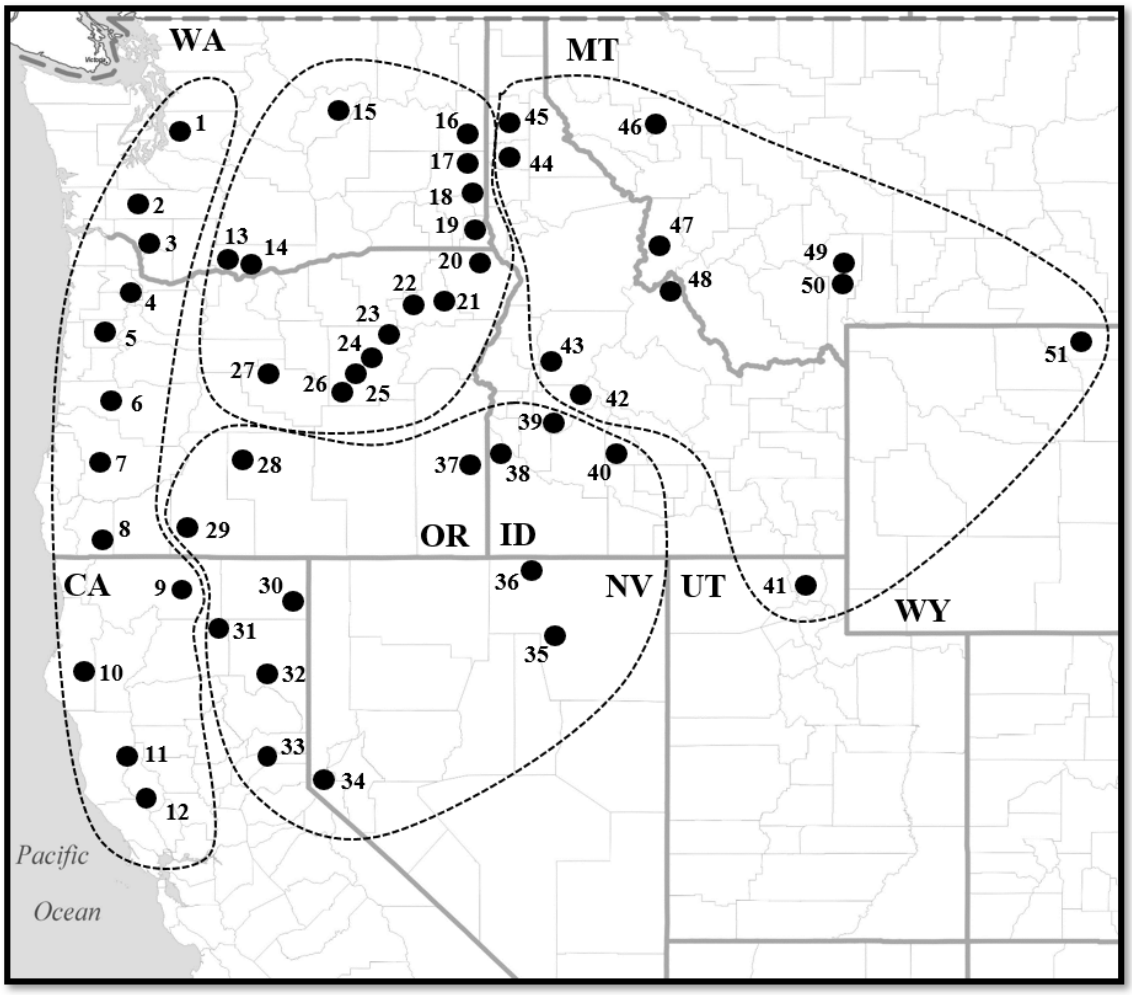

Figure 2 Collection locations for the 51 invasive populations of Ventenata dubia from the western US analyzed in this study. Population numbers correspond to the locality data provided in Supplemental Information Table 2. Dashed lines represent regional population groups: Coastal Range, Columbia Basin, Great Basin, and Rocky Mountains.

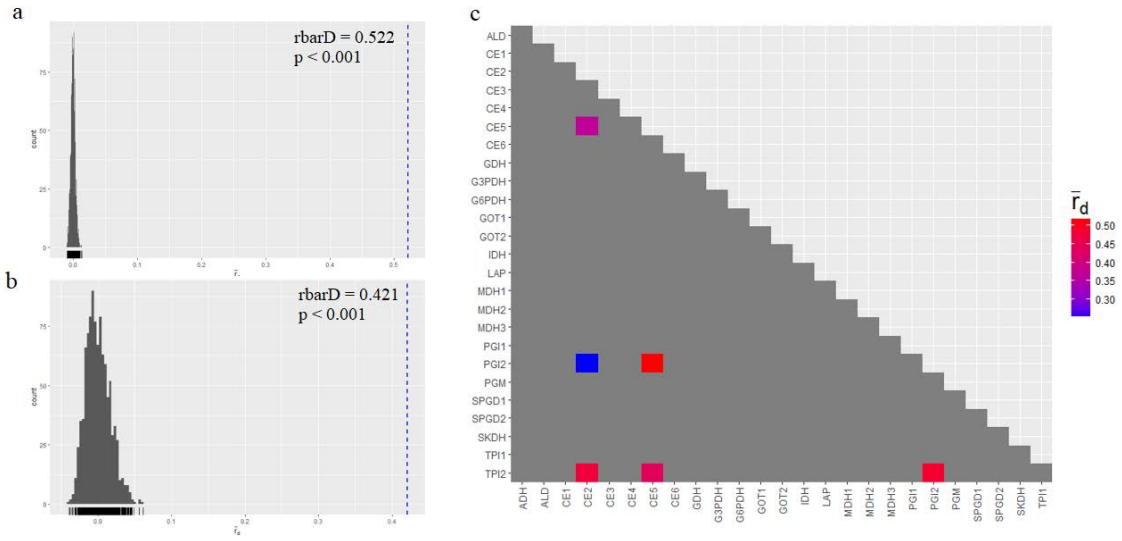

Figure 3 RbarD values for 51 invasive populations of Ventenata dubia from the western US. a.) RbarD distribution scale; b.) RbarD values for clone corrected data; and c.) Heatmap depicting the extent of linkage disequilibrium among polymorphic loci only, pairwise rbarD over all loci. Values shown in color range between rbarD 0.2518 – 0.5185, see appendix for complete values. Colors in grey represent monomorphic pairs of loci.

a.)

Color	Multilocus Genotype
	1. ACBBBAABA
	2. AAABBBABB
	3. AABBBAABA
	4. ACABBBABA
	5. AABBBBABA
	6. ACABBAABA
	7. ACBBBBABA
	8. AAABBAABA
	9. AAABBBABA

b.)

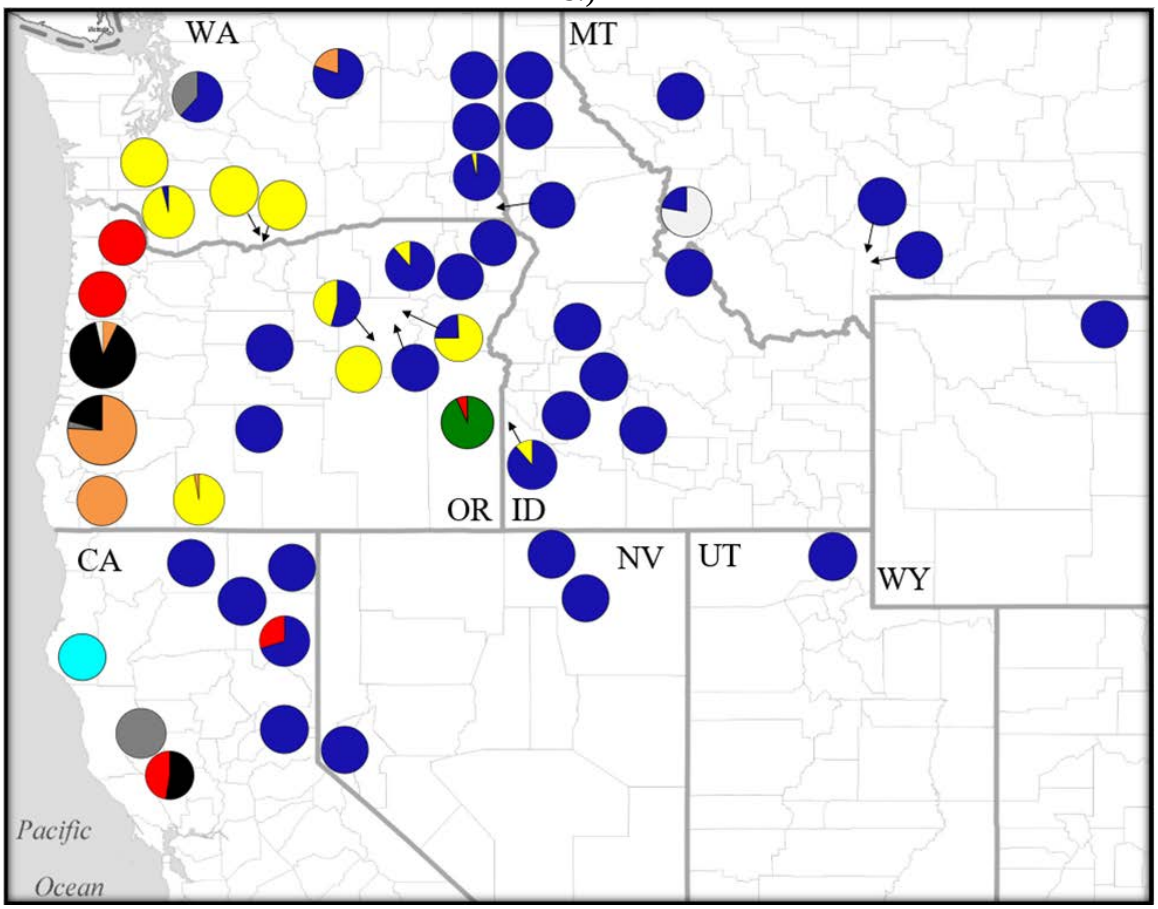

Figure 4 a.) Multilocus genotypes detected in all invasive populations of *Ventenata dubia* from the western US analyzed in this study. Letters represent different alleles at each of nine homozygous polymorphic loci: Ce-1, Ce-2, Ce-5, Gdh, G3pdh, Pgi-2, 6Pgd-1, Tpi-1, Tpi-2. Genotype number and color are assigned by order of discovery. b.) Map showing the distribution of multilocus genotypes (MLG) detected in 51 invasive populations of *Ventenata dubia*. Color of each multilocus genotype follows Fig. 4a. The most common genotype (MCG) is shown in blue. Sizes of the pie diagrams vary only to enhance legibility.

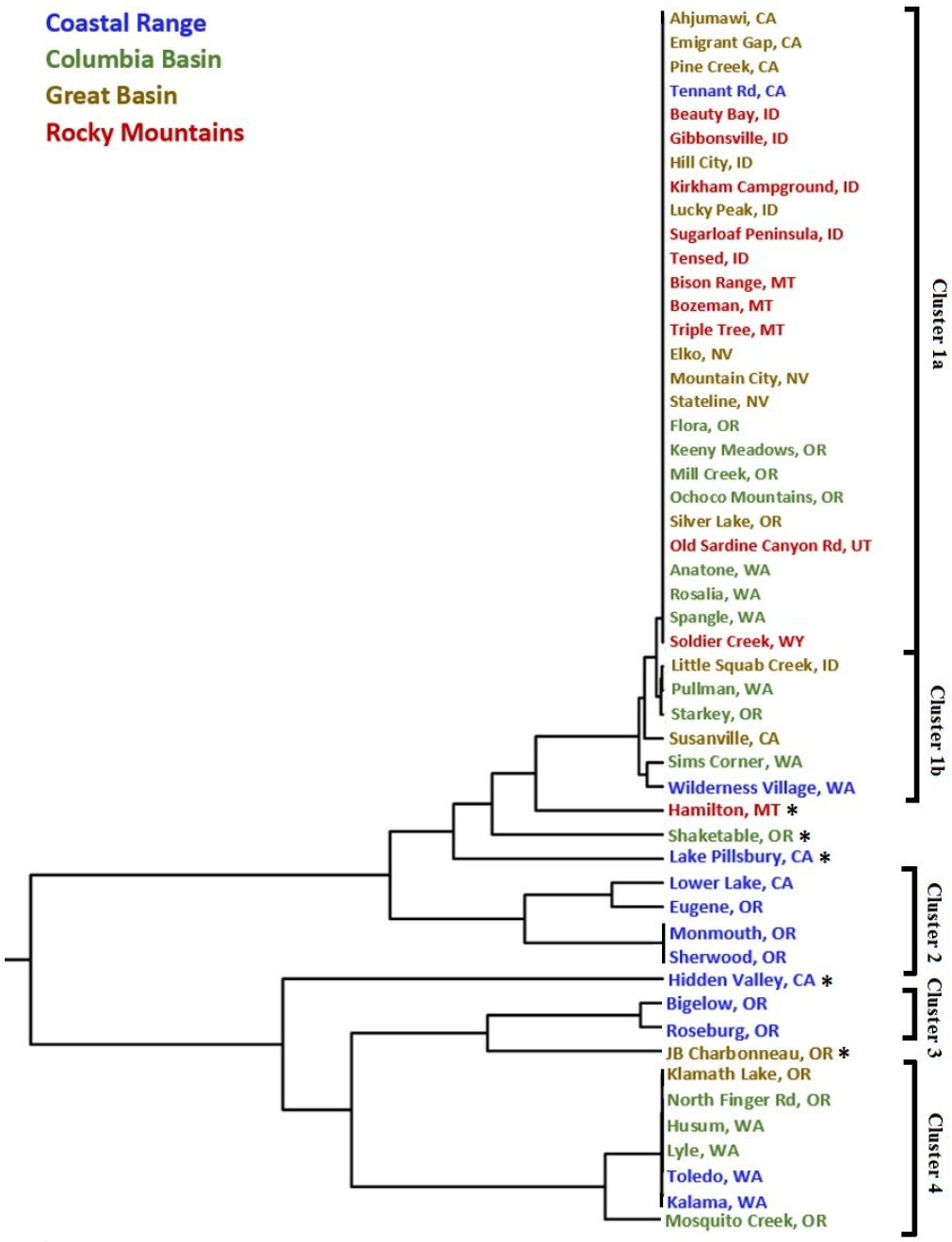

Figure 5 Unweighted pair-group method with arithmetic averaging (UPGMA) phenogram for the 51 invasive populations of Ventenata dubia analyzed in this study. Populations indicated by (*) are the only populations on their respective branches and are therefore not assigned to a cluster.

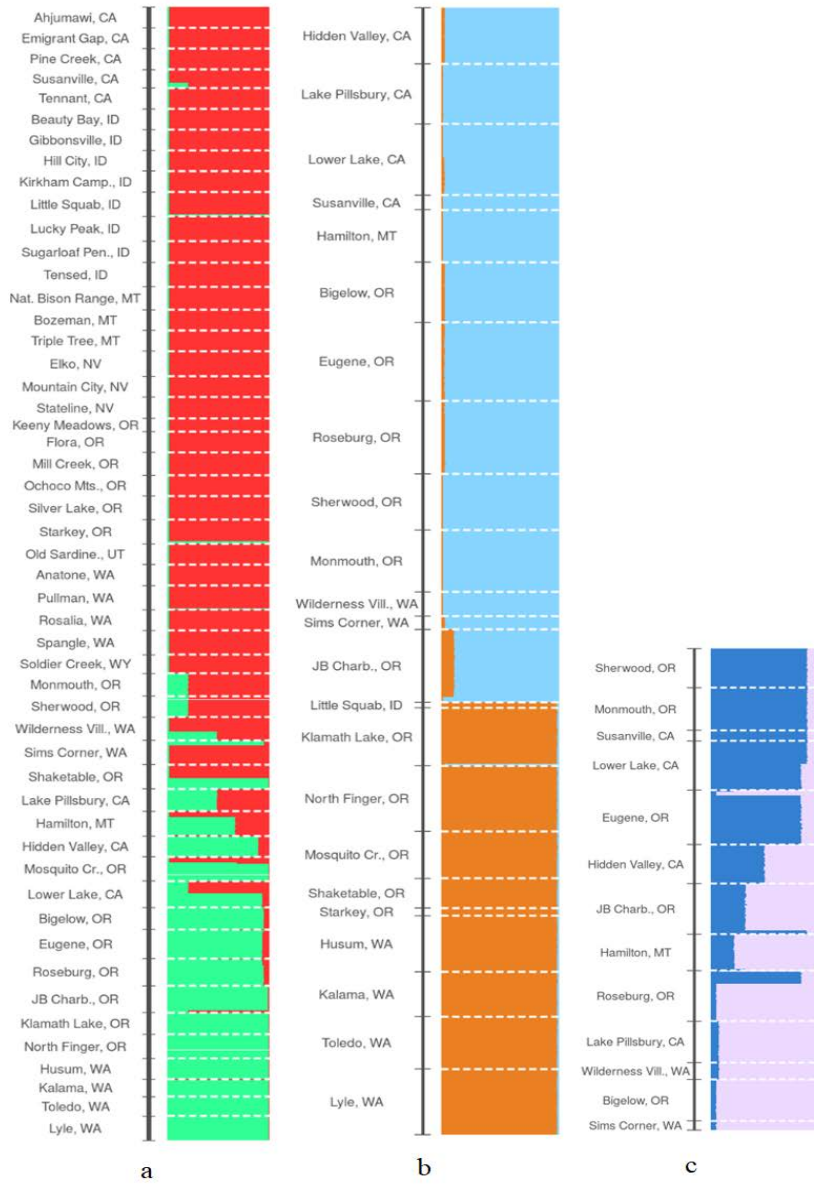

Figure 6 STRUCTURE (Pritchard et al. 2000) bar plots of the genetic clusters identified for invasive populations of *Ventenata dubia*. a) the initial partitioning analysis of 51 invasive populations (K=2), b) results for invasive populations based on the hierarchical sub-structuring analysis of the green cluster (subK=2), and c) results for invasive populations based on the hierarchical sub-structuring analysis of light blue cluster (subK=2).

APPENDIX A

Table A Collection records of *Ventenata dubia* from years 1952–2016. Earliest detection record vouchers for each county are provided in Fig. 1.

Date	Location	Herbarium Accession Number
California		
1983	Emigrant Gap, Placer Co.	UCD94425
1993	Lake Pillsbury, Lake Co.	CHSC105744
1996	Susanville, Lassen Co.	CHSC66423
1998	Tennant, Trinity Co.	CHSC71517
2000	Burney, Shasta Co.	CDA18976
2006	Alturas, Modoc Co.	CDA20820
2010	Weaverville, Trinity Co.	HSC100214
2013	Disnmore, Humboldt Co.	HSC102701
2015	South Lake Tahoe, El Dorado Co.	SRP56807
2016	Crescent Mills, Plumas Co.	SRP58604
Idaho		
1957	Beauty Bay, Kootenai Co.	WTU273715
1960	Tensed, Benewah Co.	WTU273743
1972	White Bird, Idaho Co.	ID037448
1985	Moscow, Latah Co.	ID037451
1986	Sandpoint, Bonner Co.	ID037460
1986	Mountain Home, Elmore Co.	ID037447
2002	Kamiah, Lewis Co.	BLMMD1249
2004	Lake Cascade, Valley Co.	CIC38244
2006	Weippe, Clearwater Co.	ID037446
2006	Craig Mountain, Nez Perce Co.	ID037445
2010	Lowman, Boise, Co.	CIC40660
2010	Bald Mountain, Owyhee Co.	BBLM-OWY4595
2011	Ola, Gem Co.	SRP43453
2012	Meadows Hill, Adams Co.	CIC44591
2014	Hidden Springs, Ada Co.	SRP50879
2015	Midvale, Washington Co.	SRP57957
2015	Hill City, Camas Co.	SRP 61731
2016	Gibbonsville, Lemhi Co.	SRP 61378
Montana		
1995	Black Bear Point, Rivalli Co.	MONT79339
2005	Grubb Mountain, Flathead Co.	MONTU131024
2005	Bozeman, Gattalin Co.	MONT84964
2007	Fort Smith, Big Horn Co.	RM804695
2008	Plains, Sanders Co.	MONT82301
2008	Wildhorse Island, Lake Co.	MONT82299
2009	Judith Gap, Wheatland Co.	MONT82328
2016	DeBorgia, Mineral Co.	SRP 61379
2016	Missoula, Missoula Co.	SRP 61380
Nevada		
2016	Nat. Antelope Refuge, Washoe Co.	V84851
2016	Stateline, Douglas Co.	SRP58611
2016	Mountain City, Elko Co.	SRP61395

Oregon		
1979	Rowena, Wasco Co.	OSC186835
1984	Monmouth, Polk Co.	OSC166735
1993	Eugene, Lane Co.	OSC188567
1994	Dryden, Josephine Co.	CIC27691
1996	Sweet Home, Linn Co.	SRP22816
1996	Corvallis, Benton Co.	OSC186302
1996	Flora, Wallowa Co.	ID037444
1997	Jackson Co.	SOC17438
1999	Meacham, Umatilla Co.	RM640513
2001	Dale, Grant Co.	RM1922673
2003	Baker City, Baker Co.	OSC202084
2007	Tillamook, Tillamook Co.	OSC226440
2007	Cove, Union Co.	GBIF614972113
2008	Roseburg, Douglas Co.	SRP043284
2008	Beacon Rock, Multnomah Co.	OSC228315
2012	Willamina, Yamhill Co.	WTU393886
2015	Silver Lake, Lake Co.	SRP057987
2015	Arock, Malheur Co.	SRP057975
2015	Stinkwater Summit, Harney Co.	SRP057959
2015	Ochoco Mountains, Crook Co.	SRP057961
2015	Sherwood, Washington Co.	SRP 61626
Utah		
1995	Paradise, Cache Co.	UTC00216696
Washington		
1952	Spokane Co.	No specimen
1962	Lyle, Klickitat Co.	WS247993
1980	Creston, Lincoln Co.	WS283941
1990	Kalama, Cowlitz Co.	WTU331454
1993	Pullman, Whitman Co.	WTU345391
1997	Umatilla National Forest, Garfield Co.	WTU348093
2008	Stevenson, Skamania Co.	WTU383805
2010	Ritzville, Adams Co.	WTU382093
2010	Metaline Falls, Pend Oreille Co.	WTU382128
2015	Anatone, Asotin Co.	SRP057724
2016	Yakima Co.	SRP 61382
2016	Toledo, Lewis Co.	SRP 61381
2016	Wilderness Village, King Co.	SRP 61386
2016	Easton, Kittitas Co.	SRP 61387
2016	Sims Corner, Douglas Co.	SRP61384
Wyoming		
1997	Sheridan Co.	RM655052

APPENDIX B

Table B Locality data for 51 invasive populations of *Ventenata dubia* from the western US. Populations were assigned to the four geographic regions based on their location. For each population, county, population name (including state), population number (which corresponds to the numbers in Fig. 2), latitude, longitude, and elevation (in meters) are provided.

Region	County	Population	Latitude	Longitude	Elevation
Coastal Range	King	1.Wilderness Village, WA	47°24'44.68"N	122°01'28.00"W	137
	Lewis	2. Toledo, WA	46°28'29.18"N	122°52'58.64"W	101
	Cowlitz	3. Kalama, WA	45°58'51.01"N	122°49'24.71"W	15
	Washington	4. Sherwood, OR	45°21'28.00"N	122°51'39.00"W	71
	Polk	5. Monmouth, OR	44°52'23.00"N	123°13'43.89"W	56
	Lane	6. Eugene, OR	44° 3'26.00"N	123°10'51.00"W	120
	Douglas	7. Roseburg, OR	43°10'21.70"N	123°21'40.00"W	198
	Josephine	8. Bigelow, OR	42°05'10.48"N	123°16'45.80"W	1065
	Siskiyou	9. Tennant Rd, CA	41°37'21.12"N	121°59'28.64"W	1420
	Humboldt	10. Hidden Valley Rd, CA	40°26'24.76"N	123°40'18.22"W	726
	Lake	11. Lake Pillsbury, CA	39°24'25.53"N	122°59'02.91"W	531
	Lake	12. Lower Lake, CA	38°54'59.74"N	122°42'00.59"W	569
Columbia Basin	Klickitat	13. Husum, WA	45°47'25.00"N	121°29'40.00"W	152
	Klickitat	14. Lyle, WA	45°42'34.00"N	121°20'24.00"W	33
	Douglas	15. Sims Corner, WA	47°42'49.21"N	119°21'46.66"W	719

	Spokane	16. Spangle, WA	47°27'28.44"N	117°23'19.68"W	740
	Whitman	17. Rosalia, WA	47°13'24.60"N	117°21'12.24"W	708
	Whitman	18. Pullman, WA	46°43'24.95"N	117°08'38.06"W	744
	Asotin	19. Anatone, WA	46°09'36.00"N	117°06'18.72"W	1016
	Wallowa	20. Flora, OR	45°52'00.48"N	117°15'57.60"W	1329
	Union	21. Mill Creek, OR	45°17'21.50"N	117°45'00.05"W	1263
	Union	22. Starkey, OR	45°16'37.50"N	118°20'28.86"W	978
	Grant	23. Mosquito Creek, OR	44°45'25.00"N	118°48'27.00"W	1316
	Grant	24. Keeny Meadows, OR	44°36'29.51"N	118°58'01.37"W	1673
	Grant	25. Joe Rausch’s Shaketable, OR	44°15'55.00"N	119°22'32.00"W	1347
	Grant	26. North Finger Rd, OR	44°41'34.87"N	119°15'36.60"W	1352
	Crook	27. Ochoco Mountains, OR	44°25'54.11"N	120°28'44.12"W	1249
Great Basin	Lake	28. Silver Lake, OR	43°10'25.79"N	121°06'45.09"W	1330
	Klamath	29. Klamath Lake, OR	42°24'12.00"N	122°02'46.60"W	1263
	Modoc	30. Pine Creek, CA	41°25'18.71"N	120°25'27.96"W	1512
	Shasta	31. Ahjumawi Lava SP, CA	41°05'41.12"N	121°24'34.66"W	1009
	Lassen	32. Susanville, CA	40°23'31.78"N	120°47'18.09"W	1431
	Placer	33. Emigrant Gap, CA	39°18'31.17"N	120°41'02.88"W	1394

	Douglas	34. Stateline, NA	38°58'15.14"N	119°56'08.99"W	1906
	Elko	35. Elko, NV	40°57'18.17"N	115°52'28.55"W	1942
	Elko	36. Mountain City, NV	41°49'20.72"N	115°54'27.93"W	1807
	Malheur	37. JB Charbonneau GS, OR	44°36'14.46"N	123°14'24.61"W	66
	Owyhee	38. Little Squab Creek, ID	43°21'48.82"N	116°55'17.76"W	1266
	Boise	39. Lucky Peak, ID	43°36'07.39"N	115°59'17.22"W	958
	Camas	40. Hill City, ID	43°18'34.96"N	115°01'41.45"W	1554
Rocky Mountains	Cache	41. Old Sardine Canyon Rd, UT	41°34'40.12"N	111°54'36.33"W	1599
	Boise	42. Kirkham Campground, ID	44°04'04.39"N	115°31'25.40"W	1242
	Valley	43. Sugarloaf Peninsula, ID	44°35'47.40"N	116°03'55.44"W	1473
	Benewah	44. Tensed, ID	47°07'31.80"N	116°47'15.07"W	787
	Kootenai	45. Beauty Bay, ID	47°36'46.44"N	116°40'40.44"W	655
	Lake	46. Bison Range, MT	47°21'34.99"N	114°13'36.23"W	850
	Ravalli	47. Hamilton, MT	46°11'29.42"N	114°10'26.85"W	1121
	Lemhi	48. Gibbonsville, ID	45°34'42.51"N	113°57'55.80"W	1472
	Gattalin	49. Bozeman, MT	45°40'14.95"N	111°01'40.15"W	1511
	Gattalin	50. Triple Tree, MT	45°36'47.05"N	111° 00'05.18"W	1644

Sheridan	51. Soldier Creek, WY	44°49'57.70"N	107°05'55.23"W	1325

APPENDIX C

Table C Allele frequencies for all polymorphic loci across the 51 invasive populations of *Ventenata dubia*. Numbers in parenthesis are the sample sizes for each population. Populations in each state are arranged regionally, and by assigned population number.

Coastal Range

Locus	Allele	1. Wilderness Village WA (34)	2. Toledo WA (28)	3. Kalama WA (25)	4. Sherwood OR (30)	5. Monmouth OR (33)	6. Eugene OR (42)	7. Roseburg OR (39)	8. Bigelow OR (32)
Ce-2	*a*	-	1.000	0.960	1.000	1.000	0.905	0.231	-
	c	1.000	-	0.040	-	-	0.095	0.769	1.000
Ce-5	*a*	-	1.000	0.960	1.000	-	1.000	0.974	1.000
	b	1.000	-	0.040	-	1.000	-	0.026	-
Pgi-2	*a*	0.617	-	0.040	1.0000	1.000	0.929	0.231	-
	b	0.383	1.000	0.960	-	-	0.071	0.77	1.000
Tpi-2	*a*	1.000	-	0.040	1.000	1.000	1.000	1.000	1.000
	b	-	1.000	0.960	-	-	-	-	-

Columbia Basin

Locus	Allele	9. Tennant Rd CA (30)	10. Hidden Valley CA (30)	11. Lake Pillsbury CA (32)	12. Lower Lake CA (38)	13. Husum WA (30)	14. Lyle WA(35)	15. Sims Corner WA (35)	16. Spangle WA (35)
Ce-2	*a*	-	1.000	-	1.000	1.000	1.000	-	-
	c	1.000	-	1.000	-	-	-	1.000	1.000
Ce-5	*a*	-	-		0.526	1.000	1.000	0.200	-
	b	1.000	1.000	1.000	0.474	-	-	0.800	1.000
Pgi-2	*a*	1.000	-	-	1.000	-	-	0.800	1.000
	b	-	1.000	1.000	-	1.000	1.000	0.200	-
Tpi-2	*a*	1.000	1.000	1.000	1.000	-	-	1.000	1.000
	b	-	-	-	-	1.000	1.000	-	-

Locus	Allele	17. Rosalia WA (30)	18. Pullman WA (35)	19. Anatone WA (30)	20. Flora OR (30)	21. Mill Creek OR (33)	22. Starkey OR (35)	23. Mosquito Cr OR (35)	24. Keeny Meadows OR (19)
Ce-2	*a*	-	0.057	-	-	-	0.114	0.714	-
	c	1.000	0.943	1.000	1.000	1.000	0.886	0.286	1.000
Ce-5	*a*	-	0.057	-	-	-	0.114	0.714	-
	b	1.000	0.943	1.000	1.000	1.000	0.886	0.286	1.000
Pgi-2	*a*	1.000	0.943	1.000	1.000	1.000	0.886	0.257	1.000
	b	-	0.057	-	-	-	0.114	0.743	-
Tpi-2	*a*	1.000	0.943	1.000	1.000	1.000	0.886	0.257	1.000
	b	-	0.057	-	-	-	0.114	0.743	-

Great Basin

Locus	Allele	25. Joe Rausch's Shaketable OR (35)	26. North Finger OR (35)	27. Ochoco Mtns OR (30)	28. Silver Lake OR (34)	29. Klamath Lk. OR (31)	30. Pine Creek CA (30)	31. Ahjumawi CA (30)	32. Susanville CA (27)
Ce-2	*a*	0.457	1.000	-	-	0.968	-	-	0.296
	c	0.543	-	1.000	1.000	0.032	1.000	1.000	0.704
Ce-5	*a*	0.457	1.000	-	-	-	-	-	-
	b	0.543	-	1.000	1.000	1.000	1.000	1.000	1.000
Pgi-2	*a*	0.543	-	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.457	1.000	-	-	-	-	-	-
Tpi-2	*a*	0.543	-	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.457	1.000	-	-	-	-	-	-

Locus	Allele	33. Emigrant Gap CA (30)	34. Stateline NV (31)	35. Elko NV (36)	36. Mountain City NV (30)	37. JB Charbonneau OR (39)	38. Little Squab ID (35)	39. Lucky Peak ID (36)	40. Hill City ID (30)
Ce-2	*a*	-	-	-	-	1.000	0.086	-	-
	c	1.000	1.000	1.000	1.000	-	0.914	1.000	1.000
Ce-5	*a*	-	-	-	-	0.923	0.086	-	-
	b	1.000	1.000	1.000	1.000	0.077	0.914	1.000	1.000
Pgi-2	*a*	1.000	1.000	1.000	1.000	0.077	0.914	1.000	1.000
	b	-	-	-	-	0.923	0.086	-	-
Tpi-2	*a*	1.000	1.000	1.000	1.000	1.000	0.914	1.000	1.000
	b	-	-	-	-	-	0.086	-	-

Rocky Mountains

Locus	Allele	41. Old Sardine UT (30)	42. Kirkham ID (30)	43. Sugarloaf Pen. ID (31)	44. Tensed ID (35)	45. Beauty Bay ID (30)	46. Bison Range. MT (33)	47. Hamilton MT (36)	48. Gibbonsville ID (30)
Ce-2	*a*	-	-	-	-	-	-	-	-
	c	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Ce-5	*a*	-	-	-	-	-	-	0.778	-
	b	1.000	1.000	1.000	1.000	1.000	1.000	0.222	1.000
Pgi-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	-	-	-	-	-	-	-	-
Tpi-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	-	-	-	-	-	-	-	-

Locus	Allele	49. Bozeman MT (30)	50. Triple Tree MT (30)	51. Soldier Creek WY (27)
Ce-2	*a*	-	-	-
	c	1.000	1.000	1.000
Ce-5	*a*	-	-	-
	b	1.000	1.000	1.000
Pgi-2	*a*	1.000	1.000	1.000
	b	-	-	-
Tpi-2	*a*	1.000	1.000	1.000
	b	-	-	-

APPENDIX D

Table D Summary of pairwise I_A and rbarD values for all loci. Values correspond to the heatmap shown in Fig. 3c.

Loci	I_A	rbarD
CE2:CE5	0.3689408	0.3689424
CE2:PGI2	0.2517471	0.2517699
CE2:TPI2	0.4715804	0.4746439
CE5:PGI2	0.5184812	0.5185506
CE5:TPI2	0.4356351	0.4386123
PGI2:TPI2	0.4842231	0.4866699

APPENDIX E

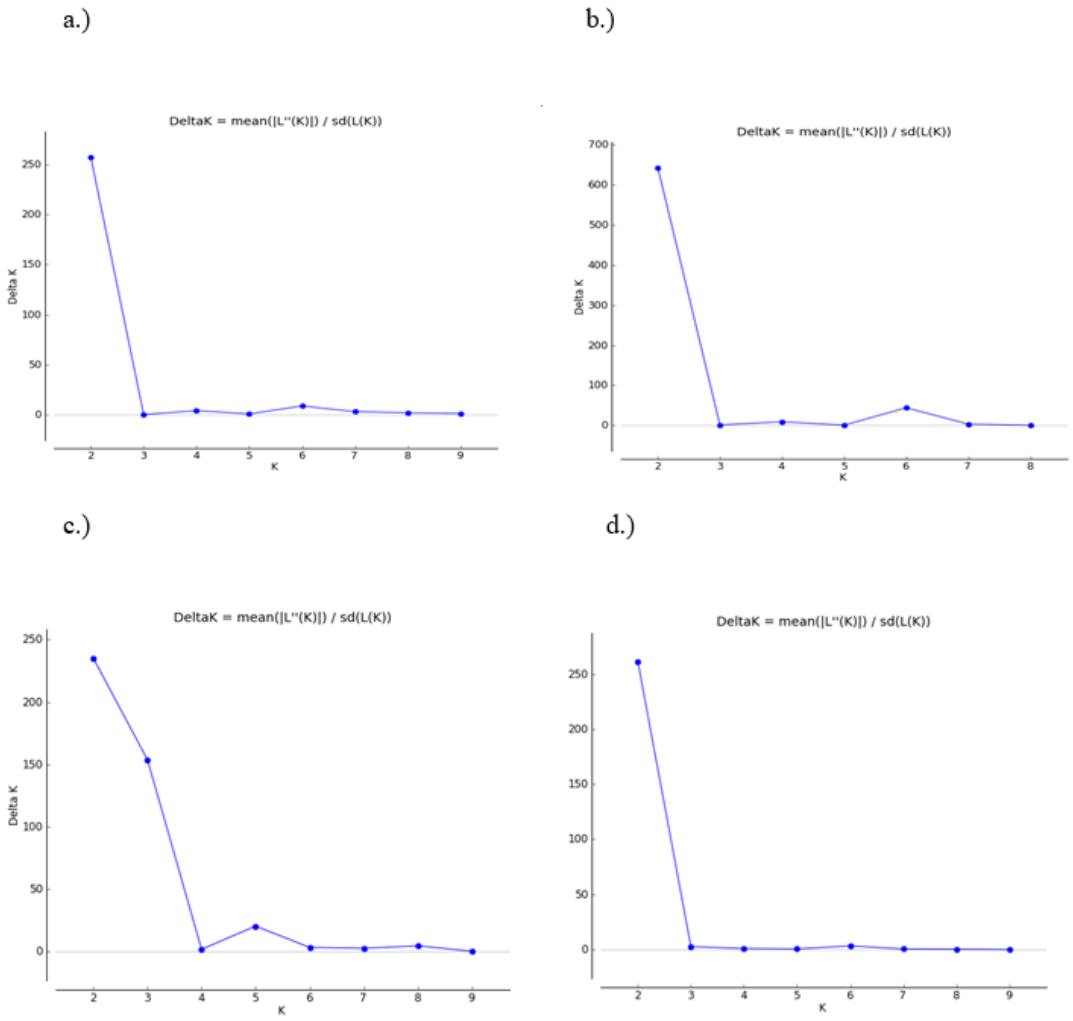

Figure E STRUCTURE results to determine the most likely number of genetic clusters (K), using the ΔK method of Evanno et al. (2005), for the 51 invasive populations of *Ventenata dubia.* a) cluster analysis (K=2) first simulation (10,000 iterations, 100,000 MCMC), b.) cluster analysis (K=2) for simulation 100000 iterations, 1,000,000 MCMC c.) substructure of the green genetic cluster (SubK=2) from Fig. 6a.d.) substructure of the light blue genetic cluster (SubK=2) from Fig. 6b.