

The effect of reproductive system on invasiveness: lessons from South American weevils

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Abstract

Successful invasion of a species into novel, marginal areas often requires the ability to face different ecological characteristics than those prevailing in its native environment. In insects, one of the factors that affect invasiveness is the reproductive system. Unisexuality provides advantages because a single specimen can initiate a new population. Unisexual reproduction precludes breakup of genetic combinations that promote ecological specialization, although it may limit evolutionary potential for colonization. In order to assess the importance of the reproductive mode in the colonization ability of the weevils that are native to South America, we compared 1 bisexual and 2 parthenogenetic species that expanded their ranges in the last 2 centuries. First, for parthenogenetic species we tested clonality of the sample. Second, we proposed central and marginal areas through phylogeographic and habitat modeling analyses, and identified the pathways of dispersal for each species. Bisexual *Naupactus xanthographus* (Germar) (Coleoptera: Curculionidae) expanded its range westward to areas with similar environmental constraints than in its native ecosystem. Conversely, parthenogenetic *Naupactus leucoma* Boheman and *Naupactus cervinus* Boheman (both Coleoptera: Curculionidae) invaded other continents where they had low to null predicted habitat suitability. While a single clone of *N. cervinus* successfully established around the world in areas with apparently adverse conditions, clones of *N. leucoma* expanded their range to areas only moderately suitable. We conclude that parthenogenesis is a driver in these particular species for colonization of marginal habitats. However, *N. cervinus* also would have pre-existing adaptations that allowed it to establish in areas with apparently low potential to survive.

Key Words: adaptation; colonization; Naupactini; parthenogenesis; phylogeography; habitat modeling analysis

Resumen

La colonización de áreas marginales a menudo requiere que la especie invasora sea capaz de enfrentar características ecológicas diferentes a aquellas que predominan en su área nativa. En los insectos, uno de los factores que afectan la capacidad invasiva figura el sistema reproductivo. La unisexualidad proporciona varias ventajas, entre ellas la capacidad de fundar una nueva población a partir de un único espécimen y evitar la ruptura de las combinaciones genéticas que promueven la especialización ecológica, esta última puede limitar el potencial evolutivo para la colonización. A fin de evaluar la importancia del modo reproductivo en la capacidad colonizadora de un grupo de gorgojos nativos de Sudamérica, comparamos dos especies con reproducción partenogenética y una especie bisexual que expandieron su rango geográfico a lo largo de los últimos 200 años. Por un lado, para las especies partenogenéticas pusimos a prueba la hipótesis de reproducción clonal. Además, propusimos áreas centrales y marginales a través de análisis filogeográficos y de modelado ecológico del hábitat e identificamos las rutas de dispersión de cada especie. La especie bisexual *Naupactus xanthographus* (Germar) (Coleoptera: Curculionidae) expandió su rango hacia el oeste, estableciéndose en áreas con restricciones ambientales similares a las de su área nativa. Por el contrario, las especies partenogenéticas *Naupactus leucoma* Boheman y *Naupactus cervinus* Boheman (ambos Coleoptera: Curculionidae) invadieron otros continentes, donde las predicciones de ocurrencia en base a las condiciones del hábitat son bajas a nulas. Un único clon de *N. cervinus* consiguió establecerse en áreas con condiciones aparentemente adversas y los clones de *N. leucoma* solo expandieron su rango a áreas moderadamente adecuadas. Concluimos que la partenogénesis es un factor fundamental en la colonización exitosa de hábitats marginales de estos gorgojos. Sin embargo, *N. cervinus* tendría adaptaciones pre-existentes que le habrían permitido el establecimiento en áreas con un potencial aparentemente bajo para la supervivencia.

Palabras Claves: adaptación; colonización; Naupactini; partenogénesis; filogeografía; análisis de modelado del hábitat

Biological invasions are one of the largest threats to native biodiversity, next only to habitat destruction and climate change (D'Antonio & Kark 2002). Invasions affect ecosystem functioning, animal and plant health, and human economies worldwide (Narščius et al. 2012). Globalization has become one of the principal drivers of species dispersal, increasing the negative impact of bioinvasions (Perrings et al. 2010).

However, not all exotic species (i.e., species intentionally or unintentionally transferred by humans outside their natural range) become successful in a new environment. Native environments and areas of introduction often differ in their ecological characteristics. Novel habitats and environmental conditions may sometimes be overcome through genetic adaptations that would allow the alien species to succeed.

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Studies on adaptation to marginal habitats and evolution of species ranges constitute the heart of invasion biology, and yield fruitful testing grounds for theoretical predictions about the successful introduction of species into novel areas (e.g., Kawecki 2008). These studies have shown that adaptation to new habitats depends on complex interactions between dispersal, habitat quality, and type and strength of selection, among other factors. One of the factors affecting the ability of a species to invade new, marginal environments is the reproductive system (e.g., Brown & Burdon 1987), and its impact on the dynamics of adaptation during invasion remains only partially understood (Bazin et al. 2014). The study of invasive species with different reproductive modes within a taxon may bring some light into this interesting and relatively unexplored topic.

The South American tribe Naupactini comprises numerous parthenogenetic species of economic importance as pests that invaded other continents (Lanteri & Normark 1995), among which are the “Fuller’s rose weevil” *Naupactus cervinus* Boheman (Coleoptera: Curculionidae), and the white-fringed weevil, *Naupactus leucoloma* Boheman (Coleoptera: Curculionidae) (Guzmán et al. 2012; Lanteri et al. 2013; Rodrigoero et al. 2016). These species have unisexual lineages, as rearing experiments and population sex ratios suggested (Buchanan 1939; Lanteri & Normark 1995). Currently, their populations are exclusively composed of females throughout their distribution, although some males (presumably extinct) were reported for both species in their native ranges during the last century (Lanteri 1986, 1993; Lanteri & Marvaldi 1995). Conversely, *Naupactus xanthographus* (Germar) (Coleoptera: Curculionidae) only reproduces sexually (Guzmán et al. 2012).

All 3 species are native to Argentina, Brazil, Paraguay, and Uruguay. Bisexual *N. xanthographus* successfully colonized only the neighbor country of Chile, while parthenogenetic *N. cervinus* and *N. leucoloma* spread to far areas like Australia, New Zealand, North America (Mexico, USA), Polynesia, Perú, South and Central Europe, Israel, and northern and southern Africa (Chadwick 1965; Guzmán et al. 2012; Germann 2016; Rodrigoero et al. 2016). The 3 weevils are highly polyphagous and cause damage to more than 100 hosts plants (fruit trees, ornamental trees, vegetables, pastures, and other hosts) (Lanteri et al. 2002). Adults feed on the aerial parts of the host plants, mainly leaves, while larvae feed on the roots, causing the most severe damage.

Unisexuality provides advantages for invading new areas because a single unmated female can initiate a new colony. Thus the impact of inbreeding depression, the cost of mate searching, and male production are avoided. As a result, parthenogenetic species may colonize areas where sexual individuals have difficulties in establishing a population. It also allows genotypes that happen to be adaptive to be transmitted unaltered (co-adapted gene complexes) (Crow & Kimura 1965), thus facilitating ecological specialization (Sunnucks et al. 1997). Nevertheless, unisexual reproduction could limit the evolutionary potential for colonizing new habitats, since unisexual lineages are prone to accumulate deleterious mutations. One may question: does unisexuality per se guarantee the success of invasion? Is any attribute already present in parthenogenetic lineages (i.e., pre-existing adaptation), a sine qua non condition to determine a successful outcome like the occurrence of genotypes with habitat tolerance? Might local adaptation be a consequence of evolution of a genetically diverse population due to multiple introductions?

To gain knowledge on the role of the reproductive system and adaptations in invasive success, we will compare the performance of bisexual and parthenogenetic weevils (indeed, clones of species with a mixed mode of reproduction) that are closely related and partially co-distributed (Guzmán et al. 2012; Rodrigoero et al. 2016). In previous papers we employed both phylogeographic and

habitat modeling analyses to identify the original area of distribution and principal pathways of dispersal. In this contribution, we will focus on the impact of the reproductive system in the areas of introduction. In addition to previous research (Guzmán et al. 2012; Rodrigoero et al. 2016), the comparison carried out in the present work will allow us to test hypotheses on invasion of novel areas not addressed before, and may reveal emerging patterns not visible in previous contributions.

Hypotheses to be tested

Premise 1: Parthenogenesis doubles the reproductive rate (Kearney 2005).

Hypothesis 1: If parthenogenesis per se is enough to guarantee the success of invasion, no invader genotypes will be recovered for unisexual species, i.e., every parthenogenetic clone will be capable of colonizing a marginal area with similar environmental requirements. For bisexual species, the range of invaded areas will be smaller.

Premise 2: Successful invaders would be species that, in their native ranges, have evolved traits that predispose them to successfully survive the selection regimes encountered during transport, introduction, establishment, and spread (Suárez & Tsutsui 2008).

Hypothesis 2: If pre-existing adaptations are the key to thriving in novel environments, then a successful invader genotype will be identified among the clones of the parthenogenetic species, both for suitable and unsuitable environments.

Premise 3: One key to invasion success may be the occurrence of multiple introductions, which transform among-population variation in native ranges to within-population variation in introduced areas (Kolbe et al. 2004; Dlugosch & Parker 2008).

Hypothesis 3: If local adaptation as a consequence of multiple introductions is the cause of a successful establishment and spread in a new territory, then many different and highly divergent clones and higher estimates of genetic variation than those from the native area should be recovered.

In order to test all these hypotheses, we compared extent of genetic diversity and distribution of *N. cervinus*, *N. leucoloma*, and *N. xanthographus* in both their native and invaded ranges. The reproductive mode of the putative unisexual species (i.e., *N. cervinus* and *N. leucoloma*) from their native areas of distribution was assessed by the analysis of co-segregation of mitochondrial (uniparental) vs. nuclear (biparental) markers, and the identification of clones (i.e., linkage disequilibrium among nuclear markers as a consequence of lack of recombination). We also identified central and marginal geographic areas for these species based on habitat suitability by habitat modelling analysis, and on the distribution of genetic variability and genealogical criteria using a phylogeographic approach. Finally, pathways of dispersal and single/multiple introductions were inferred through phylogeographic approaches.

Materials and Methods

We analyzed 601 individuals collected across Argentina, Brazil, Uruguay, Chile, Australia, New Zealand, Spain, and Pacific Islands. All 601 specimens were sequenced for the COI mitochondrial gene. Two types of nuclear markers were studied: The Internal Transcribed Spacer 1 in *N. cervinus* and about 250 Amplified Fragment Length Polymorphisms from the remaining 2 species. The high level of variation found in *N. cervinus* enabled us to apply a Bayesian phylogeographic approach, assuming a continuous diffusion model of dispersion through the landscape that infers the possible routes of colonization that occurred in the past and in current times (Bloomquist et al. 2010). For the other 2 species, we applied a landscape interpolation

of molecular variability (Miller 2005). To estimate the most suitable environmental conditions and the potential distribution of the species under study, we modeled the probability distribution for its occurrence on the basis of several environmental constraints (Phillips et al. 2006). To test for non-random associations among amplified fragment length polymorphisms markers we measured multi-locus linkage disequilibrium by the Index of Association (Smith et al. 1993) and its modification r_d and also the R index (Dorken & Eckert 2001). For a detailed description of the methods and software used, see Guzmán et al. (2012) and Rodríguez et al. (2016).

Results

ESTIMATES OF GENETIC DIVERSITY

Naupactus cervinus showed the highest level of genetic diversity. Twenty-four mitochondrial haplotypes (A–X) and 18 nuclear alleles (I–XVIII) were found, in addition to some traces of hybridization ($N = 417$) (Rodríguez et al. 2010, 2016, 2018). Two highly divergent lineages were identified, 1 occurring in forest areas and another in open vegetation areas. Overall estimates for COI variation were: $\pi = 0.009$ and $Hd = 0.854$. Almost all areas of introduction showed no variation for this marker (Table 1).

Conversely, *N. leucoloma* showed the lowest estimates of genetic diversity, because only 4 mitochondrial haplotypes (L1–L4) in the whole sample were reported ($N = 72$). One of these is present in almost all the individuals (86% of the sample bearing “L1”), and the remaining 3 are differentiated by only 1 substitution compared to the former one (Guzmán et al. 2012). Overall estimates for COI variation were: $\pi = 0.001$ and $Hd = 0.319$ (Guzmán et al. 2012). Mitochondrial variation in areas of introduction was extremely low (Table 1).

Naupactus xanthographus showed an intermediate level of genetic variation between the 2 former weevils, with 7 mitochondrial haplotypes (X1–X7) ($N = 107$) (Guzmán et al. 2012). Overall estimates for COI variation were: $\pi = 0.007$ and $Hd = 0.724$ (Guzmán et al. 2012).

GENETIC EVIDENCE OF UNISEXUAL REPRODUCTION IN *NAUPACTUS LEUCOLOMA* AND *NAUPACTUS CERVINUS*

These 2 species have a mixed mode of reproduction, with both bisexual populations (only in native areas) and parthenogenetic lineages. In order to investigate the reproductive mode in the sample of *N. cervinus*, we assessed the occurrence of clonality through the analysis of multi-locus genotypes (mitochondrial + nuclear markers). Co-segregation of mitochondrial haplotypes and nuclear genotypes (i.e., almost

every mitochondrial haplotype and its derivatives exclusively associated with a single nuclear genotype) was taken as a hint of an ancient clonality. In other words, the mitochondrial phylogenetic tree shows coevolution with the nuclear tree, suggesting that co-segregation has been occurring for a long time. Analysis of linkage disequilibrium between both genomes also was a clue to this type of reproduction (Rodríguez et al. 2010). Analysis of multi-locus genotypes yielded 40 clones in the whole sample.

For *N. leucoloma* we demonstrated the occurrence of linkage disequilibrium and significant levels of nonrandom association among amplified fragment length polymorphisms markers (Guzmán et al. 2012). Moreover, the analysis of clonal richness and genotype diversity revealed 22 groups of clones. Conversely, for *N. xanthographus* there is no linkage disequilibrium and all individuals were genetically different (see Guzmán et al. 2012), as expected for a bisexual species due to both exogamy and recombination.

HABITAT MODELING ANALYSIS

Overall, this analysis indicated that the most suitable areas for the occurrence of *N. cervinus* in South America are in the Delta of the Paraná River. Moderately suitable areas were found in southeastern Brazil, Uruguay, the Argentinean Mesopotamia, and the prairies of central Argentina (see Fig. 6a in Rodríguez et al. 2016).

Areas with optimal environmental conditions are almost coincidental for *N. leucoloma* and *N. xanthographus*, and partially overlapped with that of *N. cervinus*, in the area surrounding the La Plata River (Fig. 1 in Guzmán et al. 2012). Central-western areas of Argentina are moderately suitable for *N. leucoloma* and *N. xanthographus*; conversely *N. cervinus* is predicted to have suitable habitat in northeast Argentina and southeastern Brazil (see Fig. 6a in Rodríguez et al. 2016). Moreover, Central Chile was recorded as highly suitable for *N. xanthographus* (Fig. 2b in Guzmán et al. 2012), whereas in this country, habitat suitability is low (*N. leucoloma*) to null (*N. cervinus*) for both parthenogenetic species, as well as in some areas of other countries where these species were introduced as a byproduct of commercial trade or transportation due to other human activities (see Fig. 2a in Guzmán et al. 2012, and Fig. 6d in Rodríguez et al. 2016).

PHYLOGEOGRAPHIC ANALYSES

The probable original native area of *N. cervinus* is the Paranaense forest (southern Brazil). Subsequent expansion since Pliocene times occurred southward along the gallery forests of the Paraná and Uruguay rivers during the Pleistocene, reaching the mouth of the Paraná River, known as “Delta” (see Fig. 5 in Rodríguez et al. 2016). Climatic oscil-

Table 1. Identity of multi-locus genotypes, sample size, and genetic variation estimates for mitochondrial markers in every area of introduction of *Naupactus cervinus* and *Naupactus leucoloma*.

Species	Country	N	Multi-locus genotype	π	Hd
<i>Naupactus cervinus</i>	Australia	2	B–V	0.0000	0.000
	Chile	22	B–VII, I–VII, J–VII, M–VII, R–XVIII	0.0050	0.747
	Canary Islands	6	B–VII	0.0000	0.000
	Easter Island	7	I–VII	0.0000	0.000
	French Polynesia	4	B–VII	0.0000	0.000
	Hawaii	5	B–V	0.0000	0.000
	New Zealand	2	B–V	0.0000	0.000
	Spain	12	B–VII	0.0000	0.000
<i>Naupactus leucoloma</i>	Australia	3	L1–2, L1–5, L3–8,	0.0010	0.667
	Chile	2	L1–15, L1–19	0.0005	0.523



Fig. 1. Worldwide spatial distribution of mitochondrial and nuclear genetic variation of *Naupactus cervinus* and *Naupactus leucoloma*. The left and right side of the pie chart depicts the mitochondrial and nuclear variants, respectively. Circles are multi-locus genotypes of *Naupactus cervinus* and squares are multi-locus genotypes of *Naupactus leucoloma*. Distribution in Argentina of the colonizer genotypes also is indicated in smaller size.

lations that induced drier conditions in this area led to splitting into 2 lineages, 1 from the northern forests and another from the southern prairies. Diversification in both areas yielded many genotypes in each lineage. One of these genotypes, known as “B-VII” and some of its derivatives, which belong to the lineage of the Argentinean prairies, successfully colonized many continents (B = mitochondrial contribution, and VII = nuclear contribution). Genotype “B-VII,” native from the Argentinean Pampas and spread in marginal areas of western Argentina, also was found in southern Spain, the Canary Islands, Chile, and French Polynesia (Fig. 1), and its derivative “B-V” (1 insertion/deletion event in the internal transcribed spacer 1 sequence with regard to “B-VII”) was found in Australia, Hawaii, and New Zealand (Fig. 1). Genotypes “M-VII,” native from Delta, and the closely related “I-VII” and “J-VII” were found in some locations of Chile, the only place with multiple introductions. Chile aside, genetic diversity estimations in areas of introduction of *N. cervinus* are zero (Table 1). The nuclear genotype “B-VII” is the most frequent in all novel areas and would be related to adaptive capabilities.

For *N. leucoloma*, the analyses of the geographic distribution of genetic variability and landscape genetics revealed that the highest levels of genetic diversity of both mitochondrial and nuclear markers are in northern Buenos Aires, which is the putative area of origin of this weevil. Individuals collected in locations far away from their putative central area, such as Chile and Australia, had the most frequent haplotype (L1), and another (L3) which also was present in western Argentina (marginal area), although each individual has a different multi-locus genotype (Fig. 1; Table 1).

For *N. xanthographus*, the highest levels of mitochondrial and nuclear variation occurred in Buenos Aires Province near the La Plata

River (Guzmán et al. 2012). Outside this range, populations were generally monomorphic, a characteristic of marginal areas. Based on the geographic distribution of variability and the landscape genetic analysis, northern Buenos Aires Province was proposed as the most plausible primary center of diversification for this weevil (Guzmán et al. 2012). The 2 most frequent haplotypes, X1 and X3, also were found in continental and insular Chile (Easter Island) and in western Argentina, all areas of recent expansion or introduction (Guzmán et al. 2012).

Discussion

Phylogeographic and habitat modeling analyses allowed us to identify central and marginal areas for every species. The areas with optimal conditions in South America coincide with those of high genetic variability in all cases, indicating the possible original areas of distribution of the 3 species (Paranaense forest for *N. cervinus*, and northern Buenos Aires Province for *N. leucoloma* and *N. xanthographus*). Those areas with low probability of species occurrence were identified as marginal. Based on these results, we were able to test the hypotheses proposed above.

The bisexual *N. xanthographus* expanded its range westward, from the area of highest environmental suitability in Buenos Aires Province (Guzmán et al. 2012). The single haplotype found in the marginal areas of Argentina, e.g., Mendoza Province, is the same as in the Central Chile area in which the suitability also is high (Guzmán et al. 2012). Mendoza Province is not predicted as optimal by the model; however, its habitats have been highly modified by agricultural activities (e.g., artificial irrigation, intensive crops, and host plants similar to the original area),

and they are probably more suitable than predicted. For *N. leucoloma* the most suitable area and the putative primary center of diversification coincide with that of *N. xanthographus*. There was an expansion to moderately suitable areas of western Argentina (see Fig. 2a in Guzmán et al. 2012), especially individuals with haplotype L1. This weevil colonized not only Chile, but also several countries overseas, e.g., Australia, New Zealand, South Africa, and USA, where its occurrence was predicted by the model of potential distribution (see Guzmán et al. 2012). All multi-locus haplotypes of *N. leucoloma* in these invaded areas are different from each other (Table 1; Fig. 1). Hypothesis “1” predicts that if parthenogenesis per se is enough to guarantee the success of invasion, then every parthenogenetic clone will be capable of colonizing a marginal area with similar environmental requirements, and the range of an invaded area will be larger for parthenogenetic species than for bisexual species. Therefore, parthenogenetic reproduction per se can be invoked as the explanation for the higher invasive capability of *N. leucoloma* compared to the bisexual species.

The other parthenogenetic species analyzed here, *Naupactus cervinus*, seems to fit a different scenario, considering its successful establishment overseas. Originally distributed in the Paranaense forest, this species shows the highest genetic diversity and the broadest geographic distribution. During the 19th and 20th centuries (Chadwick 1965; Germann 2016), clones of *N. cervinus* (“B–VII” and derivatives such as “B–V,” “I–VII,” “J–VII,” and “M–VII”) invaded some areas with low to null probability of establishment and very far from its native range, suggesting that they are able to live and thrive under extreme conditions. The fact that these invaded areas are very distant from each other (Fig. 1) suggests multiple independent introductions from the Buenos Aires port (the most likely foreign source) through commercial

trade. Twelve multi-locus genotypes were found in the area surrounding the Buenos Aires port (Fig. 2), raising the question of why only 1 of them is so prevalent (see sample sizes in Table 1) and succeeded in colonizing outside Argentina (except for Chile). The most probable explanation is provided by the second hypothesis, according to which, if pre-existing adaptations are essential to thrive in novel environments, then a successful invader genotype will be identified (i.e., B–VII and its derivatives) among the clones of the parthenogenetic species from both suitable and unsuitable environments. In this regard, the fact that genotype “VII” invaded and successfully established in marginal areas suggests that there is an invasive lineage of *N. cervinus* with pre-existing adaptations, such as habitat tolerance.

Although Central Chile might be a place with multiple introductions, as many mitochondrial haplotypes were recorded for this country, all of them are closely related and linked to a single nuclear genotype (“VII”). Moreover, mitochondrial variation estimates for this area are lower than the overall estimation for *N. cervinus* (Table 1). We recovered a smaller number of poorly divergent clones and lower estimates of genetic variation in Chile than in the native area. These results do not support the third hypothesis (i.e., local adaptation as a consequence of multiple introductions), because it cannot explain the successful establishment of *N. cervinus* in Chile.

In summary, the geographic distribution and abundance (especially near the Buenos Aires and some Chilean ports) of the bisexual species *N. xanthographus* suggests that it had the same chance of being transported abroad through commercial trade or other human activities as the parthenogenetic species. However, it failed to become established outside South America, supporting the hypothesis that parthenogenesis is one of the reasons behind the higher colonization ability of both

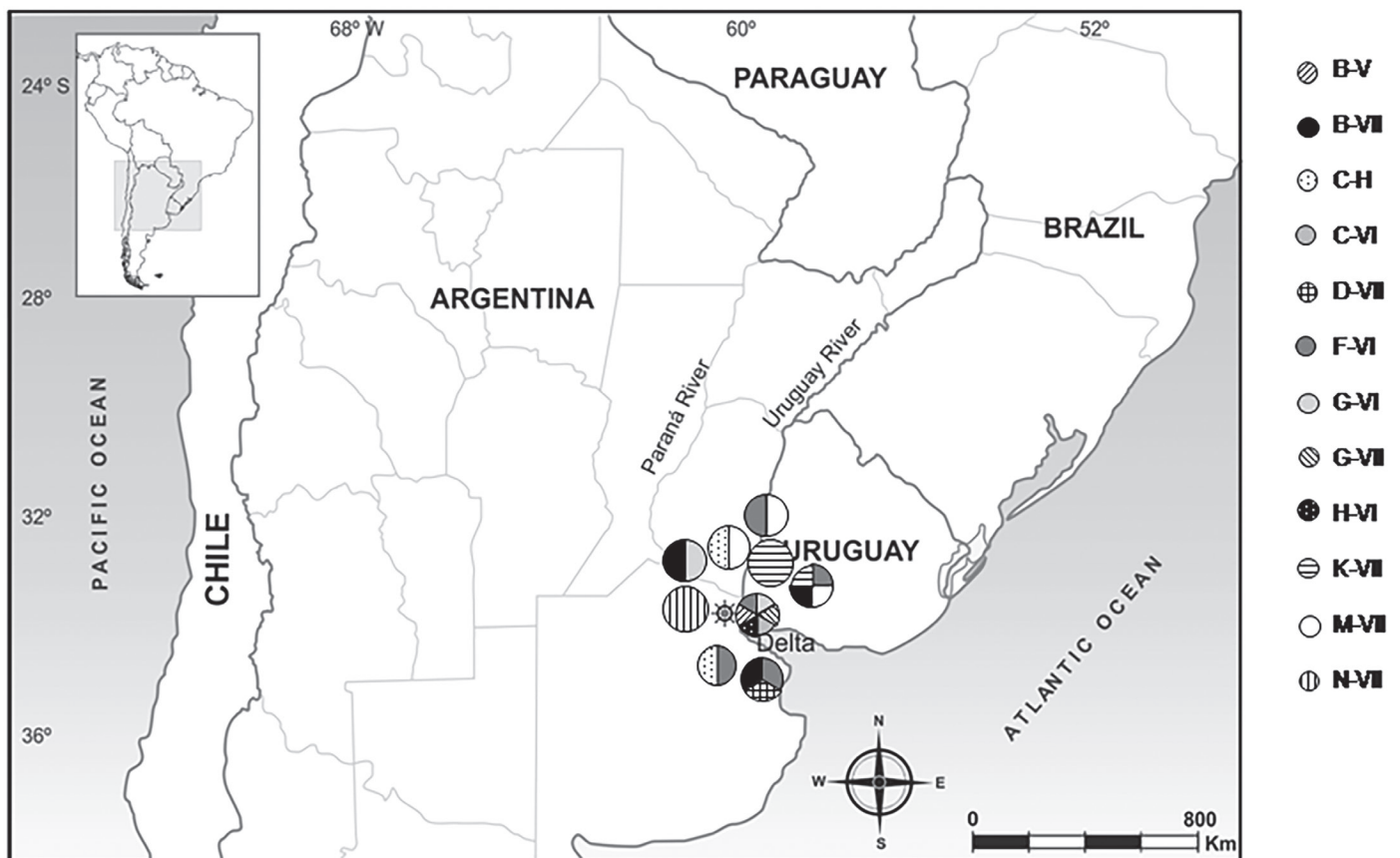


Fig. 2. Multi-locus genotypes of *N. cervinus* in locations surrounding the port of Buenos Aires (indicated by ship's wheel (helm) symbol).

N. cervinus and *N. leucoloma*. Moreover, in the case of *N. cervinus*, parthenogenesis would prevent the breakup of those beneficial allele combinations that are essential for the successful establishment in adverse environments, in addition to the demographic advantages of clonality reported for this species and for *N. leucoloma*.

Genome scan of adaptive loci and experiments in common gardens of native and invasive populations of *N. cervinus* will allow identifying both candidate genes and characters involved in the colonization ability of marginal areas (Sequeira et al. 2017). Then, we will be able to understand the basis of this adaptive process.

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