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Inferring native range and invasion scenarios with mitochondrial DNA: the case of *T. solanivora* successive north–south step-wise introductions across Central and South America

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Abstract *Tecia solanivora* (Lepidoptera: Gelechiidae) is an invasive species that attacks the tubers of the potato *Solanum tuberosum*. It is considered a serious pest of potato crops and stocks in all countries where it occurs. In the present study, we sequenced 541 individuals sampled across the *T. solanivora* distribution range, using the mitochondrial DNA marker Cytochrome b (Cytb) to delimit the area of species origin. We also analyzed the genetic structure of *T. solanivora* in its putative area of origin and described differences in haplotype diversity between samples from different geographic origins affected by the invasion. We observed a gap in the level of genetic diversity between Guatemalan samples (*h* between 0.77 and 0.97) and those from Costa-Rica, Venezuela, Colombia, Ecuador and the Canary Islands (*h* between 0 and 0.56). The number of haplotypes has decreased over the colonization process, ending with the observation of a single haplotype in Colombia, Ecuador and the Canary Islands. Consequently, the invasion of South American countries by *T. solanivora* is likely to have had a front-like step-wise progression, where the most recently invaded country becomes the source of subsequent invasion.

Keywords *Tecia solanivora* · Invasive species · Mitochondrial DNA · Genetic diversity · Invasion scenario

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Introduction

The identification of the geographic source of an invading population and the study of variations in genetic diversity experienced by invasive species during the colonization process are useful means to aid our understanding of the mechanisms that allow establishment and spread of invaders in newly colonized areas (Sakai et al. 2001; Wares et al. 2005; Dlugosch and Parker 2008). Mitochondrial DNA (mtDNA) has proven to be useful for determining both area of origin and population structure of invasive species (Cognato et al. 2005; Grapputo et al. 2005; Simon-Bouhet et al. 2006; Wang et al. 2009). mtDNA can also offer insight into the genetic paradox of biological invasions, which asks how populations that typically have low genetic diversity can experience demographic success and become invasive in a new ecological context (Kolbe et al. 2004; Golani et al. 2007; Puillandre et al. 2008; Ahern et al. 2009). The possibility of using mitochondrial markers to address questions on biological invasions is particularly important for lepidopteran species, in which the development of nuclear molecular markers, such as microsatellites, is a very difficult task (Meglécz et al. 2007).

Tecia solanivora (Povolny 1973), Lepidoptera: Gelechiidae, is commonly named the Guatemalan potato tuber moth or Centro American potato tuber moth (Zhang 1994). These vernacular names do not allow us to delineate the exact origin of the species. Nevertheless it has commonly been assumed that the pest most likely originated from Guatemala (Niño 2004; EPPO 2006).

This invasive species attacks exclusively potato tubers. The adults of *T. solanivora* are nocturnal and present a sexual dimorphism (males are smaller than females). The females usually lay eggs at the bottom of the potato stems in the fields and on the floor or on uncovered tubers in storerooms. The emerging larvae feed inside the potato tubers, where they dig galleries that lead to partial or complete tuber destruction. Pupae can develop within the tuber, in the ground or in bags in storerooms (Niño 2004). Environmental conditions (especially temperature and humidity) strongly influence the development of the insect (Notz 1996; Torres 2003). Dangles et al. (2008) showed that the pest has its highest rates of population increase at fifteen degrees Celsius.

The geographic origin and domestication of the *T. solanivora* host plant, the cultivated potato (*Solanum tuberosum* L.), has long been controversial, (Bonavia 1993; Huaman and Spooner 2002). Wild potatoes (section *Petota*) are widely distributed from Chile and Argentina to Southern USA (Hijmans and Spooner 2001), and were used for human consumption across the whole of this range during the pre-Colombian era. However, several authors trace the origin of the potatoes presently cultivated to Andean and Chilean landraces developed by pre-Colombian cultivators (Grun 1990 in Raker and Spooner 2002; Huaman and Spooner 2002). The identity of the wild species progenitors of these Andean landraces has long been debated, but all hypotheses focus on a group of approximately 20 morphologically similar wild species referred to the *Solanum brevicaule* complex, distributed from central Peru to northern Argentina. A recent study supports a monophyletic origin of these landrace cultivars from the northern component of *Solanum brevicaule* complex in Peru, rather than from multiple independent origins from various northern and southern members of the complex (Spooner et al. 2005). Therefore, domestication of cultivated potatoes probably took place in South America around 8,000 years ago. Cultivated potatoes were transported to Central America by Europeans after the conquest (XVI century) (Hawkes 1989 in Bonavia 1993). The presence of the Darién Gap between Central America (Panama) and South America (Colombia), which historically functioned as an ecological barrier between the two sub-continents, likely impeded contact between the indigenous peoples of Central and South America. Such a barrier would have prevented cultural and commercial exchanges between the two regions and would thus have prevented the transfer of potatoes before the coming of the Europeans.

The pest *T. solanivora* was reported for the first time in Guatemala in 1956 (Gomez de Paz 2008; Niño 2004) when the Inter-American Cooperative Service for Agricultural Development (SCIDA), which was in charge of potato cultivation improvement, first observed the damage caused to potato crops by a small moth (Torres 2003). To improve local production, between 1958 and 1962 the Guatemalan government created an agency for the control and certification of seed potatoes. In 1967 and 1968 most of the certificated potato seed produced in the

Quetzaltenango region of Guatemala, were exported to Central American countries, especially Honduras and Costa Rica (Cifuentes 1980; Christiansen 1980). In the 1970s, potato production in Guatemala increased due to the implementation of new agronomic practices and most of the potatoes produced were exported to Central American countries (94.74 and 67.71% of the total production in 1970 and 1971, respectively; ICTA 1977). At the same time, the presence of *T. solanivora* was reported in other Central American countries. In 1970, the pest destroyed most of the potato crops in Costa Rica (Murillo 1980), although it was not until 1973 that *T. solanivora* was described for the first time from moths and larvae collected in the country (Povolny 1973). In the same year, the pest was recorded in Panama, where it caused 20% losses to the potato harvest. It is possible that an increase of commercial exportation was responsible for the expansion of *T. solanivora* in these countries during this period. The species was also observed in Honduras, where it infected 350 ha in 1982. At this time there were no records of the pest in Salvador, Nicaragua, or Mexico (Murillo 1982). In 1989, the pest was reported in Nicaragua (Leal and Raman 1989). In the 1980s, in parallel with the extension of field irrigation, significant pest damage was reported in Guatemala (Ruano et al. 1984); this was not as great as that reported in other countries during the same period, however. The presence of its natural enemies possibly helped to control the pest in Guatemala (Giron 1984).

T. solanivora had never been reported in South America before the 1980s. In Venezuela at the end of 1983, the importation of infected seed potatoes from Costa Rica was reported (Salazar and Escalante 1984; Torres 2003; Niño 2004). In 1985, the species reached the border area between Venezuela and Colombia and began to colonize the central and southern areas of that country (Rincón and López-Avila 2004). In 1996, *T. solanivora* was reported in Ecuador in the area of the border with Colombia (Gallegos et al. 1997). Finally, in 1999, the presence of the species was recorded in the Canary Islands (Niño 2004). No accurate information is available about the geographic origin of the Canary Island *T. solanivora*; nevertheless, it is thought that the species was introduced into this country through the importation of a bag of infested potatoes from South America (Venezuela, Colombia or Ecuador) (EPPO 2006). *T. solanivora* is now reported as a serious pest of potato crops and stocks in all countries where it is present (EPPO 2006).

Despite these numerous records, historical data is partial and fragmented. The lack of observations of the species at one time in one location does not necessarily mean it was absent. Furthermore, nothing is known about the original host plant of the moth. A previous genetic study based on mitochondrial markers established that Guatemala was part of the area of origin of *T. solanivora* and showed that invaded populations experienced an important decrease in mitochondrial diversity (Puillandre et al. 2008). The aim of the present study is to complement this preliminary study, whose geographic coverage was limited (no samples from Costa-Rica and limited coverage of potato growing areas in Guatemala and other countries where the insect is present). This lack of coverage impeded an accurate delimitation of the area of origin of the species and did not allow relationships between samples from the invaded area and those from Guatemala to be tested. In the present work, using the Cytb marker, we sequenced 541 individuals in order to (1) clarify the area of origin of the species, (2) define the geographic source of samples from invaded areas (3) describe variations in genetic diversity during colonization process.

Materials and methods

Study sites and collection of samples

One of the difficulties in a study dealing with a wide geographical area is to obtain samples from all the countries involved. In the present study, we established a standard protocol using synthetic species-specific pheromone traps (Bosa et al. 2005) to capture spatially distinct collections of insects from almost all the areas where *T. solanivora* has been observed. In general, these areas are located in particular countries. For practical reasons, we will use names of countries to designate specific samples of insects. In Central America, the area of origin of *T. solanivora* probably stretches across more than one country. We chose to take samples in two countries likely to be in this area of origin: Guatemala (Sierra Madre Mountains) and Costa Rica (Central Volcanic cordillera), which could also represent the northern and southern limits.

In Guatemala (Gu), we sampled 8 localities in two regions: Huehuetenango and Quetzaltenango, corresponding to the northern and southern branches of the Sierra Madre Mountains. We sampled between 3 and 7 sites in the each of the other countries studied: Costa Rica (CR), Venezuela (Ve), Colombia (Co), Ecuador (Ec) and the Canary Islands (CI). A total of 541 individuals were collected, sequenced and analysed (see Table 1), of which 72 had already been published by Puillandre et al. (2008). The samples were preserved in 95% ethanol prior to molecular analysis.

DNA extraction and amplification

Genomic DNA samples were extracted from the thorax of *T. solanivora* individuals using the DNeasy Tissue Kit (Qiagen). The remaining body parts were stored in 95% ethanol. Insect genitalia were used to confirm identification of individuals to the species level.

A fragment of the mitochondrial gene, Cytochrome b (Cytb; 770 base pairs) was amplified by polymerase chain reaction. We designed specific primers for the species using PRIMER3 software (Rozen and Skaletsky 2000). PCR reactions with Primer TsF1 (5′-GCTAAYATTGARTTAGCTTTTTAT-3′) and TsR (5′-AAAAATTAGRGTATCTCAAAAT-3′) were performed using a Biometra T1 Thermal cycler with an initial denaturation step at 94°C for 5 min, followed by 35 cycles of the three following steps: denaturation at 94°C for 1 min, annealing at 59°C for 1 min 30 s and extension at 72°C for 1 min 30 s. The final extension was done at 72°C for 5 min. Each amplification (25 µl) contained 1 µl DNA, 5 µl reaction buffer 5X, 3 µl $MgCl_2$ 25 mM, 0.6 µl dNTP 10 mM, 1 µl of each primer at 10 mM and 1 unit Taq polymerase (Promega). PCR products were purified using the PCR clean-up system (Promega). Fragments were sequenced on both DNA strands on an ABI Prism 3130 automatic sequencer using a Big-Dye Terminator Sequencing Kit (Both from Applied Biosystems). Sequences were deposited in GenBank (Accession numbers: GU056361-GU056780).

Because mtDNA geographic variation patterns can be affected by presence of *Wolbachia* endobacteria, we tested the presence of the bacteria in several samples from different geographic locations using primers wsp81F and wsp691R (Zhou et al. 1998).

Data analyses

Sequences were aligned manually with MacClade 4.07 (Maddison and Maddison 2000). Haplotype diversity (h), nucleotide diversity (π) and the number of polymorphic sites (S) within each sample were calculated using ARLEQUIN version 3.01 (Excoffier et al. 2005) for all samples from the supposed origin and invaded areas.

To describe the genetic relationships between haplotypes, a haplotype network was constructed based on statistical parsimony (Templeton et al. 1992), using the program TCS 1.21 (Clement et al. 2000). We used a network approach because this is considered better adapted than traditional phylogenetic methods to representing genealogical relationships at a population level (Clement et al. 2000). Traditional treelike methods make assumptions that are not adequate at the population level, e.g., they assume that ancestral haplotypes are no longer in the population. Moreover, these methods require a large number of variable characters to reconstruct relationships, but sequence variation is usually low at a population level (Clement et al. 2000). Network methods have been developed based on population genetic statistical calculations for the connections between neighboring haplotypes, which allow the occurrence of ancient haplotypes in a present-day population. In our case, the network was built using data from spatially distinct samples.

To analyze the population structure of *T. solanivora* and clarify the area of origin and the region invaded by the species, we used several different approaches. Using molecular variance analysis (AMOVA) we tested the population structure of the species in its reported area of origin (Guatemala). We considered the distribution of the species in this area to define groups of the samples in the study: the first group brought together the samples from the Huehuetenango region and the second group the samples from Quetzaltenango region. In order to estimate whether Costa Rica is part of the native or into the invaded range, we performed three more analyses: in the first, Guatemala, Costa Rica and the remaining invaded countries were considered as three different groups; in the second, we considered Costa Rica as part of the area of origin; and in the third,

Table 1 Genetic diversity of *T. solanivora*

Code	Collection locations and Tukey HSD results	Country	Coordinates	N	Nhp	*h*	π	S	Haplotypes found
Gu1	Paquix	Guatemala	15.63 N 91.68 W	30	10	0.784	0.007	26	H3, H26, H34, H38, H39, H40, H41, H43, H53, H57
Gu2	Chichim	Huehuetenango region	15.56 N 91.58 W	9	8	0.972	0.013	27	H17, H26, H27, H34, H41, H52, H57, H60
Gu3	Madre Selva		15.03 N 91.80 W	10	6	0.867	0.011	25	H2, H16, H36, H54, H55, H56
Gu4	Concepcion 1		15.00 N 91.53 W	73	25	0.885	0.012	40	H1, H2, H3, H4, H5, H16, H18,H19, H20, H21, H23, H24, H25,H28, H29, H30, H31, H32, H33, H44, H45, H48, H49, H50, H51
Gu5	Concepcion 2	Guatemala	14.96 N 91.78 W	9	4	0.778	0.012	20	H1, H2, H16, H50
Gu6	Pachimacho	Quetzaltenango region	14.90 N 91.60 W	22	9	0.775	0.012	29	H1, H2, H16, H35, H37, H44, H46, H47, H48
Gu7	Chiquira		14.86 N 91.62 W	14	9	0.879	0.011	24	H1, H2, H16, H22, H29, H32, H42, H58, H59
Gu8	ICTA Xela		15.87 N 91.52 W	10	8	0.933	0.012	22	H1, H2, H16, H17, H19, H21, H32, H50
GuT	Guatemala all populations (**a**)			177	50	0.914	0.012	58	H1,H2,H3,H4,H5,H16,H17,H18,H19,H20,H21,H22,H23,H24, H25,H26,H27,H28,H29,H30,H31,H32,H33,H34,H35,H36, H37,H38,H39,H40,H41,H42,H43,H44,H45,H46,H47,H48, H49,H50,H51,H52,H53,H54,H55,H56,H57,H58,H59,H60
CR1	Carlos Duran		9.93 N 83.81 W	31	5	0.348	0.003	17	H1, H3, H6, H7, H11
CR2	San Juan de Chicua		9.95 N 83.85 W	24	7	0.558	0.004	21	H1, H2, H6, H8, H9, H10, H12
CR3	Potrero Cerrado		9.93 N 83.88 W	19	3	0.444	0.007	16	H2, H5, H6
CR4	Santa Clara del Guarco	Costa Rica	9.79 N 83.95 W	25	6	0.48	0.004	19	H1, H2, H4, H6, H8, H13
CR5	La fuente Paraizo		9.83 N 83.86 W	12	2	0.303	0.005	13	H2, H6
CR6	Macho Gaff		9.65 N 83.94 W	28	3	0.204	0.0004	4	H4, H6, H8
CRT	Costa Rica all populations (**b**)			139	13	0.392	0.004	30	H1,H2,H3,H4,H5,H6,H7,H8,H9,H10,H11,H12,H13
Ve1	Llanetes Jauregui		8.25 N 71.92 W	27	3	0.145	0.0008	9	H6, H7, H8
Ve2	Pueblo Hondo		8.27 N 71.85 W	6	3	0.733	0.0094	14	H6, H14, H15
Ve3	La Toma Rangel	Venezuela	8.45 N 70.53 W	28	2	0.071	0.0012	13	H2, H6
Ve4	Pueblo Llano		8.91 N 70.65 W	7	1	0	0	0	H6
VeT	Venezuela all populations (**c**)			68	6	0.169	0.0018	21	H2,H6,H7,H8,H14,H15
Ec1	Quito		0.22S 78.52 W	1	1	0	0	0	H6
Ec2	LaPosta		2.53S 78.94 W	9	1	0	0	0	H6
Ec3	San José		0.53S 78.95 W	6	1	0	0	0	H6
Ec4	Riobamba	Ecuador	1.65S 78.56 W	10	1	0	0	0	H6
Ec5	Anchilibi 1		1.06S 78.58 W	5	1	0	0	0	H6

Table 1 continued

Code	Collection locations and Tukey HSD results	Country	Coordinates	N	Nhp	*h*	π	S	Haplotypes found
Ec6	Santa Ana cotopaxi		1.56S 79.10 W	26	1	0	0	0	H6
Ec7	Pumamaqui Bolivar		0.81S 78.92 W	23	1	0	0	0	H6
EcT	Ecuador all populations (d)			79	1	0	0	0	H6
Co1	Cundinamarca		5.23 N 73.55 W	11	1	0	0	0	H6
Co2	Nariño	Colombia	1.9 N 77.56 W	7	1	0	0	0	H6
Co3	Santander		7.36 N 72.65 W	3	1	0	0	0	H6
CoT	Colombia all populations (d)			21	1	0	0	0	H6
CI1	Los Realejos		28.36 N 16.6 W	6	1	0	0	0	H6
CI2	ICOD		28.38 N 16.56 W	6	1	0	0	0	H6
CI3	Santa Ursula	Canary Islands	28.41 N 16.46 W	19	1	0	0	0	H6
CI4	Tacoronte		28.46 N 16.4 W	26	1	0	0	0	H6
CIT	Canary Islands all populations (d)			57	1	0	0	0	H6

Country of sample origin (*Gu* Guatemala, *CR* Costa Rica, *Ve* Venezuela, *Co* Colombia, *Ec* Ecuador, *CI* Canary Islands); name and GPS coordinates of collection locations; sample size (*N*); and measures of genetic diversity: number of haplotypes (Nhp), haplotype diversity (*h*), nucleotide diversity (π) and number of polymorphic sites (*S*). Names of the haplotypes found in each location are listed. Results of Tukey HSD test are shown in *bold* with the collection locations (*different letters* indicate significant differences)

we assumed that Costa Rica was part of the invaded area. Standard AMOVA estimate genetic structure indices using information on the allelic content of haplotypes, as well as their frequencies. The information on the differences in allelic content between haplotypes is entered as a matrix of Euclidean square distances (Excoffier et al. 1992).

To complete our analysis, we performed a spatial analysis of molecular variance (SAMOVA), a method that aims to identify group structure based on genetic data. In SAMOVA, samples are assigned to k (1, 2, 3, *n*…) groups with the constraint that populations within a group must be geographically adjacent and genetically homogeneous. (Dupanloup et al. 2002). The clustering giving the highest Φct value is selected. The molecular distances between pairs of sequences necessary for the computations of Φct values are computed as pairwise differences.

Finally, we calculated pairwise $\Phi_{ST}{}^{values}$. The AMOVA and the pairwise $\Phi_{ST}{}^{values}$ were calculated using ARLEQUIN version 3.01 (Excoffier et al. 2005) and the SAMOVA with SAMOVA 1.0 (Dupanloup et al. 2002).

In order to test for differences in haplotype number between country pairs, we conducted repeated measures ANOVA (analysis of variance) with the different samples from each country as error terms. We then performed post-hoc Tukey HSD tests. To avoid heteroscedasticity (different variances), number of haplotypes per sample was rank-transformed before analyses. Tests were performed using R 2.7.1 (R development core team 2010).

To analyze demographic changes in populations we tested deviations of Tajima's D, Fu's Fs and R2 statistics from a null hypothesis, assuming that these deviations were due to demographic rather than selective effects. Tajima's D (1989) is based on the difference between two alternative estimates of the mutational parameter $\theta = 2Nu$, where N is the effective number of gene copies in the population and u is the mutation rate. Fu's Fs test (Fu 1997) is based on the probability of having a number of haplotypes greater or equal to the observed number of samples drawn for a population of constant size. R2 statistics (Ramos-Onsins and Rozas 2002) are based on the difference between the number of singleton mutations and the average number of nucleotide differences. In order to complete the analyses, we examined the mismatch distribution (based in the analysis of the distribution of pair-wise differences) using ARLEQUIN version 3.01 (Excoffier et al. 2005) and DnaSP version 4.0 (Rozas et al. 2003).

Results

Genetic diversity

A 770 base pair fragment of the Cytb gene was sequenced and analyzed from 541 individuals of *T solanivora*, of which 177 were from Guatemala, the putative native area, and 364 from the remaining locations.

The spatially distinct collections sampled in Guatemala displayed high levels of haplotype and nucleotide diversity compared with samples taken in other areas. Among Guatemalan samples, haplotype diversity (h) ranged from 0.77 to 0.97 and nucleotide diversity (π) from 0.007 to 0.013. A gap in genetic diversity was observed between these Guatemalan samples and the rest of the samples collected in other areas: Costa Rican and Venezuelan samples displayed lower haplotype and nucleotide diversity ($h = 0.392$ and $h = 0.169$, $\pi = 0.004$ and $\pi = 0.0018$, respectively), and samples from Colombia, Ecuador and Canary Islands shared a single haplotype H6 (Fig. 1, Table 1). There is, therefore, a reduction in the number of haplotypes going from the area where the species has been established for the longest time towards the areas where it has most recently become established according to the literature. Sequencing of 177 individuals from Guatemala showed 50 haplotypes, while only 15 haplotypes were found over the rest of the sampled sites, among a total of 364 individuals. Moreover, statistical comparisons between pairs of countries (Tukey HSD test) showed that the mean numbers of haplotypes between country pairs were all significantly different except for the comparisons between Colombia, Ecuador and the Canary Islands (Table 1).

The putative area of origin exhibited 58 polymorphic sites, and 30 polymorphic sites were found among the remaining samples.

Genetic population structure

The relationships between the mitochondrial haplotypes found over the entire distribution area of *T. solanivora* are presented in the haplotype network

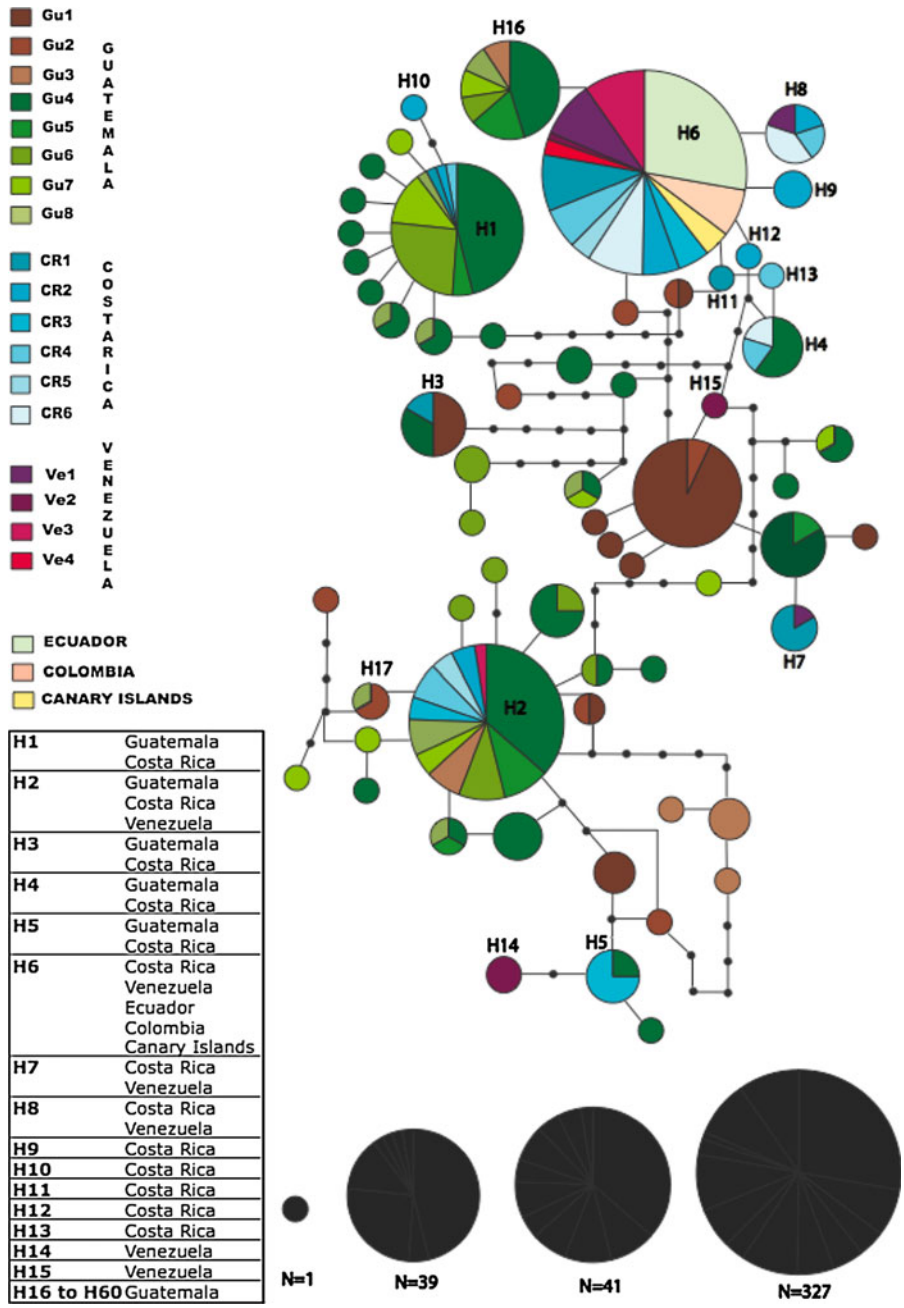

Fig. 1 Cytochrome b haplotype 95% statistical parsimony network from samples collected in two regions of Guatemala: Huehuetenango (*Gu 1*), (*Gu 2*), (*Gu 3*) and Quetzaltenango (*Gu 4*), (*Gu 5*), (*Gu 6*), (*Gu 7*), (*Gu 8*); Costa Rica (*CR*), Venezuela (*Ve*), Colombia, Ecuador and the Canary Islands. Haplotypes H19 to H60 not numbered. Circle area corresponds to number of individuals with a particular haplotype. Collection location names are given in Table 1

(Fig. 1). A total of 60 haplotypes were found overall of which 45 were present exclusively in the Guatemalan samples (Table 1). Only 5 haplotypes were shared between Guatemala and the rest of the sampled locations: haplotypes H1, H3, H4, H5 were shared between Guatemala and Costa Rica; and H2 was shared between Guatemala, Costa Rica and Venezuela. Haplotypes H1 and H2 were the most common haplotypes displayed in Guatemala. Haplotypes H7 and H8 were common to Costa Rica and Venezuela.

Haplotypes H9, H10, H11, H12 and H13 were exclusively found in Costa Rican locations. H14 and H15 were present exclusively in Venezuelan samples. Individuals from Colombia, Ecuador and Canary Islands were fixed in the same single shared

haplotype: H6. This haplotype was also the most commonly found in Costa Rican and Venezuelan samples. Since we have not detected *Wolbachia* in *T. solanivora* samples we can exclude an effect of that bacteria on the haplotype distribution.

Although H6 was not found in any Guatemalan samples, in the network it is closely related to haplotype H16, which was well represented in this area.

The diversity within Guatemala was geographically structured, with only four haplotypes shared between the two sampled regions: Huehuetenango and Quetzaltenango (H2, H3, H16, H17).

AMOVA performed on Guatemalan samples showed significant variation between regions (9.26% of the variance explained). Genetic differentiation within samples was the major component, with 87.75% of the variation explained by the variation between individuals. Results of the AMOVA made in order to define the invaded area, assigned Costa Rica to the invaded zone because significant differentiation among groupings was observed when we included Costa Rica into the colonized area (Table 2).

The spatial analysis of molecular variance SAMOVA, which defines groupings based on genetic data (Table 3), showed that the highest significant value ($\Phi_{CT} = 0.49002$) was obtained when the samples were grouped into five clusters. In this case, the samples from the supposed area of origin were clustered into four groups: the first grouped together all samples from the Quetzaltenango region (Gu4, Gu5, Gu6, Gu7 and Gu8); the following three corresponded to each sample from the Huehuetenango region (Gu1), (Gu2), and (Gu3); and the fifth cluster grouped together the samples from the remaining countries (Costa Rica, Venezuela, Ecuador, Colombia and Canary Islands). Costa Rican samples always clustered into the invaded area group independently of the number of clusters suggested by the SAMOVA.

Pair-wise $\Phi_{ST}{}^{values}$ between Guatemalan samples showed non-significant $\Phi_{ST}{}^{values}$ between Quetzaltenango Gu4, Gu5, Gu6, Gu7 and Gu8 samples. All pair-wise $\Phi_{ST}{}^{values}$ between Guatemalan samples and those of the remaining countries were highly significant (Table 4). $\Phi_{ST}{}^{values}$ between these paired samples are higher as the geographical distance between

Table 2 Analysis of molecular variance (AMOVA) of *Tecia solanivora* Cytb sequences

	Guatemala (Huehue) (Quetzal)	Grouping 1 (GuT) (CRT) (VeT,CoT,EcT,CIT)	Grouping 2 (GuT,CRT) (VeT,CoT,EcT,CIT)	Grouping 3 (GuT) (CRT,VeT,CoT,EcT,CIT)
Percentage of variation				
Among groups	9.26	41.07	26.22	49.98
Among populations within groups	2.99	4.58	19.70	4.42
Within populations	87.75	54.35	54.08	45.60
Variance components				
Va	0.04521	0.14955	0.09595	0.21692
Vb	0.01458	0.01668	0.07208	0.01917
Vc	0.42848	0.19792	0.19792	0.19792
Fixation indices				
FCT	0.09259	0.41069	0.26219	0.49980
FCS	0.03292	0.07773	0.26696	0.08832
FST	0.12246	0.45649	0.45916	0.54398
P-value				
Va and FCT	0.02444 ± 0.00454	0.00000 ± 0.00000	0.01564 ± 0.00340	0.00000 ± 0.00000
Vb and FCS	0.00880 ± 0.00288	0.00000 ± 0.00000	0.00000 ± 0.00000	0.00000 ± 0.00000
Vc and FST	0.00000 ± 0.00000	0.00000 ± 0.00000	0.00000 ± 0.00000	0.00000 ± 0.00000

Huehue Huehuetenango, *Quetzal* Quetzaltenago, *GuT* Guatemala Total, *CRT* Costa Rica Total, *VeT* Venezuela Total, *CoT* Colombia Total, *EcT* Ecuador Total, *CIT* Canary Islands Total

Table 3 Spatial analysis of molecular variance (SAMOVA)

K	Group composition	Φ_{CT}
3	(Gu2,Gu3,Gu4,Gu5,Gu6,Gu7,Gu8) (Gu1) (CRT,VeT,EcT,CoT,CIT)	0.45870***
4	(Gu2,Gu4,Gu5,Gu6,Gu7,Gu8) (Gu1) (Gu3) (CRT,VeT,EcT,CoT,CIT)	0.48675***
5	(Gu4,Gu5,Gu6,Gu7,Gu8) (Gu1) (Gu2) (Gu3) (CRT,VeT,EcT,CoT,CIT)	0.49002***
6	(Gu2,Gu4,Gu5,Gu6,Gu7,Gu8) (Gu1) (Gu3) (CRT,VeT,EcT,CoT,CIT) (VeT1) (VeT2)	0.45356***

Gu1, Gu2, Gu3, Gu4,Gu5,Gu6, Gu7, Gu8 Guatemala 1, 2, 3, 4, 5, 6, 7, 8, *CRT* Costa Rica Total, *VeT* Venezuela Total, *CoT* Colombia Total, *EcT* Ecuador Total, *CIT* Canary Islands Total

Full collection location names are given in Table 1

*** denotes $P < 0.001$

Table 4 Pairwise Φ_{ST}^{values} between *Tecia solanivora* samples taken in its native area and in the remaining countries

	Gu1	Gu2	Gu3	Gu4	Gu5	Gu6	Gu7	Gu8	CRT	VeT
Gu1										
Gu2	0.06^{NS}									
Gu3	0.18***	0.08*								
Gu4	0.22***	0.13**	0.03^{NS}							
Gu5	0.16***	0.07**	0.05*	-0.003^{NS}						
Gu6	0.15***	0.03^{NS}	0^{NS}	0.06^{NS}	-0.01^{NS}					
Gu7	0.17***	0.08*	0.08*	0.01^{NS}	-0.01^{NS}	0.001^{NS}				
Gu8	0.22***	0.14***	0.13**	0.04^{NS}	0.01^{NS}	0.05^{NS}	-0.02^{NS}			
CRT	0.48***	0.45***	0.47***	0.49***	*0.38***	0.45***	0.46***	0.48***		
VeT	0.6***	0.65***	0.67***	0.7***	*0.46***	0.65***	0.63***	0.63***	0.03**	
EcT,CoT,CIT	0.83***	0.92***	0.93***	0.95***	*0.66***	0.92***	0.89***	0.87***	0.13***	0.08***

Gu1, Gu2, Gu3, Gu4, Gu5, Gu6, Gu7, Gu8 Guatemala 1, 2, 3, 4, 5, 6, 7, 8, *CRT* Costa Rica Total, *VeT* Venezuela Total, *CoT* Colombia Total, *EcT* Ecuador Total, *CIT* Canary Islands Total

NS: not significant

* denotes $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Full collection location names are given in Table 1

them broadens, corresponding to the expansion of the invasion: Guatemala-Costa Rica (Φ_{ST}^{values} ranged between 0.38 and 0.49); Guatemala-Venezuela (Φ_{ST}^{values} between 0.46 and 0.7); Guatemala-(Colombia, Ecuador and Canary Island) (Φ_{ST}^{values} between 0.66 and 0.95). The Φ_{ST}^{values} between Costa Rica and Venezuela was lower than the Φ_{ST}^{values} between Costa Rica and the remaining invaded countries.

The lowest pair-wise Φ_{ST}^{values} between a Guatemalan sample and those from the another country were found between Gu5 and Costa Rica ($\Phi_{ST}^{values} = 0.38$), Gu5 and Venezuela ($\Phi_{ST}^{values} = 0.46$), and Gu5 and Colombia, Ecuador + the Canary Islands ($\Phi_{ST}^{values} = 0.66$). There was a gap between the Gu5-Costa Rica distance and the other distances that constituted a mono-modal Φ_{ST} distribution curve.

Historical demography

Both Tajima's D and Fu's neutrality tests showed no significant values for the samples from Guatemala (Table 5). The same tests displayed significant negative values for the whole invaded zone including Costa Rica. These results, which suggest population expansion in the colonized area and a demographic equilibrium in the native range, are supported by the mismatch distribution analyses. The distribution for Guatemala consisted of a multimodal curve (data not shown). The values of the R2 test were also lower in

Table 5 Neutrality test for samples from Guatemala and the remaining countries

Sample site	Tajima's *D*	Fu's *Fs*	R2
Gu1	−0.71516	0.762	0.0992
Gu2	0.20057	−0.974	0.1533
Gu3	−0.10381	1.742	0.1507
Gu4	0.43511	−1.807	0.1145
Gu5	1.39383	4.693	0.2311
Gu6	0.93441	2.863	0.1603
Gu7	0.75367	0.23	0.1657
Gu8	1.08144	−0.409	0.1944
CRT,VeT,CoT,EcT,CIT	−1.82332*	−3.969*	0.025

Gu1, Gu2, Gu3, Gu4, Gu5, Gu6, Gu7, Gu8 Guatemala 1, 2, 3, 4, 5, 6, 7, 8, *CRT* Costa Rica Total, *VeT* Venezuela Total, *CoT* Colombia Total, *EcT* Ecuador Total, *CIT* Canary Islands Total

Full collection location names are given in Table 1

* denotes $P < 0.05$

the colonized area, as would be expected after a recent and strong population growth event (Table 5).

Discussion

Tecia solanivora native range: historical vs molecular data

Although *T. solanivora* is generally reported to be native to Guatemala, little information is available about whether the pest is native or invasive in the remaining countries of Central America. Historical data and vernacular insect names (Guatemalan potato tuber moth or Centro-American potato tuber moth) do not allow the exact origin of the species to be determined. Historically, a South American origin of the pest is very unlikely because it was never signaled on this sub-continent before the 1980s, although other species of the same family have been reported earlier.

Because of their geographic positions, two regions likely to be at the northern and southern limits of the pest origin area were chosen for sampling: the Sierra Madre Mountains in Guatemala, and Central Volcanic cordillera in Costa Rica. These areas have similar ecological characteristics that are favorable for the development of the pest (presence of high-altitude areas and suitable temperatures); furthermore, these are the only two areas and countries in the region that maintain a high level of potato production.

At present, *T. solanivora* attacks exclusively potato tubers. As emphasized in the introduction, origin and domestication of cultivated potatoes probably took place in South America, and Europeans later transported cultivated potatoes races to Central America after the conquest (Hawkes 1989 in Bonavia 1993). Therefore, we hypothesize that the original host plant of *T. solanivora* was a tuber producing Solanaceae, native to Central America. In Central America the number of potential wild Solanaceae host species is small, and almost all are found in Sierra Madre, Guatemala (6 species) (Hijmans and Spooner 2001; CIP 2010). We hypothesize that the pest was associated with one of those plants and that the intensification of potato cultivation in Guatemala may have induced the shift of the species from wild to cultivated Solanaceae. Molecular data is also in agreement with the hypothesis of the pest having a Guatemalan origin (Sierra Madre Mountains). Native populations generally display higher levels of genetic diversity compared with introduced populations (Dlugosch and Parker 2008). This is the case for *T. solanivora*, for which previous results had shown that populations from Guatemala displayed higher levels of genetic diversity (Puillandre et al. 2008) than samples from other areas. In the present study, all the Guatemalan samples analyzed follow the same trend: haplotype diversity (h) among sampled sites ranged from 0.77 to 0.97 and nucleotide diversity (π) from 0.007 to 0.013. Out of the 60 haplotypes found from the whole sampling effort, 50 haplotypes were found in Guatemala and 45 haplotypes were exclusive to this area. The hypothesis of *T. solanivora* having a Guatemalan origin is also supported by the demographic analysis, which showed all Guatemalan populations being in demographic equilibrium rather than in expansion (Table 5).

Molecular data from Costa Rican samples indicates that this country lies in the invaded range of the species. When compared individually with samples from Guatemala, Costa Rican samples indeed showed a markedly lower genetic diversity ($h = 0.392$ and $\pi = 0.004$). In samples containing almost the same number of individuals, genetic diversity was always higher in Guatemalan samples, for example: Gu1: $N = 30$ $h = 078$, CR1: $N = 31$ $h = 0.35$; Gu6: $N = 22$, $h = 0.78$; CR2: $N = 24$, $h = 0.56$; CR4: $N = 25$, $h = 0.48$ (Table 1). Moreover, we took samples across almost the entire potato production

area of Costa Rica in order to cover most of the genetic diversity of the species in this country. Such intensive sampling was not possible for Guatemala, where we focused our sampling effort on the northern production zone, without sampling some secondary production areas where one would expect to find additional haplotypes. In Guatemala, the absence of five haplotypes (H9, H10, H11, H12 and H13) found exclusively in Costa Rica and of one haplotype (H6) shared by all other samples might be explained by the non exhaustive haplotype sampling in Guatemala, considering the high genetic diversity observed in that country.

Such loss of genetic diversity in invasive populations compared to native ones has already been observed in other species (Grapputo et al. 2005; De Walt and Hamrick 2004; Le Roux et al. 2008; Puillandre et al. 2008). These results are congruent with the historical data. The pest was first observed in Costa Rica (Murillo 1980) during a period of increasing importation of potato seeds from Guatemala in the 1970s (Cifuentes 1980; Christiansen 1980).

Natural spread of the pest from Guatemala to Costa Rica could have been limited by an ecological gap between Sierra Madre in Guatemala and the Central Volcanic cordillera in Costa Rica. The gap corresponds to an area including Honduras, Salvador and Nicaragua. The ecological conditions in this zone are not optimal for the development of the pest, and potato cultivation is very limited. Moreover there is only one species of wild Solanaceae as a candidate host plant of the pest in Costa Rica and Honduras, and wild potato species seem totally absent in Salvador and Nicaragua (Hijmans and Spooner 2001; CIP 2010). Despite the lack of *T. solanivora* samples from Honduras, Salvador and Nicaragua in our study, the hypothesis of Costa Rica being an invaded zone is supported by ecological, agronomic and historical data in addition to the genetics results. In agreement with one of the most common vernacular name of the pest (Guatemalan potato tuber moth), we hypothesize that *T. solanivora* was probably introduced to Costa Rica following commercial potato exchange with Guatemala.

Tecia solanivora population structure in the native range

The AMOVA shows a significant differentiation between the two regions analyzed in Guatemala (Huehuetenango and Quetzaltenango), corresponding to the northern and southern branches of the Sierra Madre Mountain. Only four haplotypes out of fifty found in Guatemala were present in both of these sampled regions. The valley between the branches of Sierra Madre Mountain could limit the gene flow between these regions.

SAMOVA results and pairwise $\Phi_{ST}{}^{values}$ show that samples from Quetzaltenango are not significantly genetically differentiated from each other, a result which contrasts with that of the Huehuetenango samples. It is possible that the intensive commercial potato exchanges into the Quetzaltenango area allow greater population homogenization than in the Huehuetenango region.

The haplotype network shows the presence of a few dominant haplotypes in Guatemala. This presence of dominant haplotypes and their recent closely-related haplotypes is associated with multimodal mismatch distribution (a few long branches and many short branches in the haplotype tree), a pattern that is also consistent with population equilibrium.

Inferences on the colonization process

Molecular analysis and historical data lead us to hypothesize that *T. solanivora* was introduced via potato exportations from Guatemala to Costa Rica, (ICTA 1977; Cifuentes 1980; Christiansen 1980). This is in agreement with both AMOVA and SAMOVA results, which always support clustering of Costa Rica with the invaded country samples. Moreover, most of the Costa Rican haplotypes are present within the Guatemalan diversity.

The Costa Rican sample most likely originated from the Quetzaltenango region of Guatemala $\Phi_{ST}{}^{values}$ are low between Quetzaltenango Gu5 sample and those from the invaded countries; the 5 haplotypes shared between the two countries (H1, H2, H3, H4, H5) are found in Quetzaltenango region while only two of them are found in Huehuetenango region (Fig. 1, Table 1).

As indicated earlier, there is no historical evidence of the presence of the pest on the South American continent before 1983. The presence of the Darién Gap, a large swath of forest and swampland between Central America (Panama) and South America (Colombia), likely impeded the natural spread of the pest between the two sub-continents. The northern South American

Andean countries (Venezuela, Colombia and Ecuador) appear to belong to the area invaded by the species. During the invasion process, the pest was likely first introduced to Venezuela via an importation of infected seed potatoes from Costa Rica at the end of 1983 (Salazar and Escalante 1984; Torres 2003; Niño 2004).

In some invasive species, the amount of genetic diversity present in each country can be used to infer the order of colonization of a species (Kawamura et al. 2006; Rollins et al. 2009). In such cases, the level of genetic diversity declines progressively across the introduced range of the species (Clegg et al. 2002; Wares et al. 2005, Hawley et al. 2008). This pattern is observed with *T. solanivora*: diversity decreases from Costa Rica to Venezuela and from Venezuela to Colombia and Ecuador (Table 1). Furthermore, diversity found in an invaded area is included in the diversity of the probable source country. Four of the six haplotypes found in Venezuela (H2, H6, H7, H8) are shared with Costa Rican samples. Haplotype H6, the only one found in Colombia and Ecuador, is the most common haplotype found in Costa Rica (found in 108 individuals out of 139 individuals sequenced, i.e. 77.7%) and in Venezuela (62 individuals out of 68, i.e. 91.2%). Because of the overall lack of genetic diversity, molecular data are not useful to clarify whether the pests in Colombia and Ecuador originate from Costa Rica or Venezuela. Nevertheless, historical data (the absence of records of commercial exchanges of potatoes between Costa Rica and Colombia or Ecuador) and the ecological barrier between Central and South American continents (the Darien Gap) lead us to hypothesize that the invasion most likely came from Venezuela. The pest invaded Colombia and Ecuador by anthropogenic introduction due to commercial exchange between these neighboring countries. Chronological data are congruent with this hypothesis: *T. solanivora* was recorded in Venezuela in 1983, in 1985 the species reached the border area between Venezuela and Colombia (Rincón and López-Avila 2004) and in 1996 *T. solanivora* was reported in Ecuador in the Colombian neighboring zone (Gallegos et al. 1997). The origin of the Canary Islands *T. solanivora* is uncertain and needs to be clarified using more variable molecular markers.

The Φ_{ST} values are also consistent with the same general pattern of *T. solanivora* invasion. The values observed between neighboring countries were always lower than the values between non-neighboring countries in the sequence Guatemala,-> Costa Rica,-> Venezuela,-> Colombia,-> Ecuador,-> Canary Islands. Samples from Costa Rica, Venezuela, Colombia, Ecuador and the Canary Islands exhibit the genetic signature of population expansion, a situation observed in invasive populations (Wang et al. 2009).

According to our results and the chronological data, the *T. solanivora* invasion of these South-American countries appears to be a front-like stepwise process, where the most recently invaded country is the source of the further invasion.

The marked reduction in genetic diversity experienced by *T. solanivora* across the invaded range has not impeded the ecological success of this pest in Central America, Northern Andean countries and the Canary Islands. This paradox has been observed several times in the past for different organisms (Sax et al. 2007; Mooney and Cleland 2001; Frankham 2005) including *T. solanivora* (Puillandre et al. 2008). In the present case it suggests that the cessation of potato importation has not been sufficient to limit the establishment and spread of this pest species in countries where invasion has already started. To prevent the spread of the pest to other South American countries and mainland Europe, monitoring and control measures should be used in addition to a strict blockade to importation.

In our study, mitochondrial DNA data allowed us to delimit the area of origin of *T. solanivora*, and to analyze the genetic structure of the species in its native zone. Inferences about the colonization process were made possible by the combined use of genetic and historical data. The Cytb marker proved useful for the inference of the biological invasion scenario of *T. solanivora*.

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References

Ahern RG, Hawthorne DJ, Raupp MJ (2009) Founder effects and phenotypic variation in *Adelges cooleyi,* an insect pest introduced to the eastern United States. Biol Invasions 11:959–971

Bonavia D (1993) La papa: apuntes sobre sus origenes y su domesticacion. J Soc Am 79:173–187

Bosa CF, Prado AMC, Fukumoto T, Bengtsson M, Witzgall P (2005) Pheromone-mediated communication disruption in Guatemalan potato moth, Tecia solanivora. Entomol Exp Appl 114:137–142

Christiansen JA (1980) Memorias del primer curso nacional de la papa. Sector publico agrícola: ICTA programa regional cooperativo de la papa. Guatemala

Cifuentes JE (1980) Certificación de semilla de papa en Guatemala. Memorias del primer curso nacional de la papa. Sector publico agrícola, ICTA, programa regional cooperativo de la papa. Guatemala 43–46

CIP (2010) Wild potato species catalogue. https://research.cip.cgiar.org/genebankdb/modules/wpsa_old/

Clegg SM, Dignan SM, Kikkawa J, Moritz C, Estoup A, Owens IPF (2002) Genetic consequences of sequential founder events by an island-colonizing bird. PNAS 99:8127–8132

Clement M, Posada D, Crandall K (2000) TCS: a computer program to estimate gene genealogies. Mol Ecol 9:1657–1660

Cognato AI, Sun JH, Anducho-Reyes MA, Owen RD (2005) Genetic variation and origin of red turpentine beetle (*Dendroctonus valens* LeConte) introduced to the People's Republic of China. Agric For Entomol 7:87–94

Dangles O, Carpio C, Barragan AR, Zeddam JL, Silvain JF (2008) Temperature as a key driver of ecological sorting among invasive pest in the tropical Andes. Ecol Appl 18:1795–1809

De Walt SJ, Hamrick JL (2004) Genetic variation of introduced Hawaiian and native Costa Rican populations of an invasive tropical shrub, Clidemia hirta (Melastomataceae). Am J Bot 91:1155–1162

Dlugosch KM, Parker M (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Mol Ecol 17:431–449

Dupanloup I, Schneider S, Excoffier L (2002) A simulated annealing approach to define the genetic structure of populations. Mol Ecol 11:2571–2581

EPPO (2006) *Tecia solanivora*. European and Mediterranean plant protection organization, data sheets on quarantine pests http://www.eppo.org/QUARANTINE/insects/Tecia_solanivora/DSTECASO.pdf

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: applications to human mitochondrial DNA restriction data. Genetics 131:479–491

Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: an integrated software package for population genetics data analysis. Evol Bioinform 1:47–50

Frankham R (2005) Invasion biology—resolving the genetic paradox in invasive species. Heredity 94:385

Fu YX (1997) Statistical tests of neutrality against populations growth?, hitchhiking and background selection. Genetics 133:693–709

Gallegos P, Suquillo G, Chamorro F et al (1997) La palomilla de la papa *Tecia solanivora* en el Carchi, situación actual y perspectives de control. Revista INIAP 9:5–6

Giron LF (1984) Celebran seminario sobre la polilla de la papa. Noticia del Instituto de Ciencia y Tecnología Agrícola, Guatemala

Golani D, Azzurro E, Corsini-Foka M, Falautano M, Andaloro F, Bernardi G (2007) Genetic bottlenecks and successful biological invasions: the case of a recent Lessepsian migrant. Biol Lett 3:541–545

Gomez de Paz R (2008) Recopilacion de investigaciones sobre la polilla de la papa *Tecia Solanivora*, Lepidoptera: Gelechiidae, en Quetzaltenango, Guatemala. Dissertation, Universidad de San Carlos de Guatemala

Grapputo A, Boman S, Lindstrom L, Lyytinen A, Mappes J (2005) The voyage of an invasive species across continent: genetic diversity of North American and European Colorado Potato beetle populations. Mol Ecol 14:4207–4219

Hawley D, Briggs J, Dhondt A, Lovette I (2008) Reconciling molecular signatures across markers: mitochondrial DNA confirms funder effect in invasive North American house finches (*Carpodacus mexicanus*). Conserv Genet 9:637–643

Hijmans R, Spooner DM (2001) Geographic distribution of wild potato species. Am J Bot 88:2101–2112

Huaman Z, Spooner DM (2002) Reclassification of landrace populations of cultivated potatoes (*Solanum* sect. *Petota*). Am J Bot 89:947–965

ICTA (1977) El cultivo de la papa en Guatemala. Folleto técnico Instituto de Ciencia y Tecnologia Agricola no. 6. Instituto de Ciencia y Tecnología Agrícolas, Sector Publico Agropecuario y de Alimentación, Guatemala

Kawamura K, Yonekura R, Katano O, Tanigouchi Y, Sayito K (2006) Origin an dispersal of bluegill sunfish, *Lepomis macrochirus,* in Japan and Corea. Mol Ecol 15:613–621

Kolbe JJ, Glor RE, Schettino LRG, Lara AC, Larson A, Losos JB (2004) Genetic variation increases during biological invasion by a Cuban Lizard. Nature 431:177–181

Le Roux JJ, Wieczorek AM, Meyer JY (2008) Genetic diversity and structure of the invasive tree Miconia Calvescens in pacific Islands. Divers Distrib 14:935–948

Leal H, Raman K (1989) *Scrobipalpoipsis solanivora* (Lepidoptera: Gelechiidae) en Centroamérica. Dissertation, Guatemala

Maddison DR, Maddison WP (2000) MacClade: analysis of phylogeny and character evolution 4.06. Sinauer Associates, Sunderland, MA

Meglécz E, Anderson SJ, Bourguet D et al (2007) Microsatellite flanking region similarities among different loci within insect species. Insect Mol Biol 6:175–185

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. PNAS 98:5446–5451

Murillo R (1980) Memoria del primer seminario internacional sobre polillas de la papa *Scrobipalposis solavivora* Povolny y *Phthorimaea operculella* Zeller. Ministerio de Agricultura y Ganaderia. Costa Rica pp 10–11

Murillo R (1982) Memoria segundo seminario regional sobre investigación y combate de las polillas de la papa *Scrobipalposis solavivora* Povolny y *Phthorimaea operculella* Zeller. Ministerio de Agricultura y Ganaderia (PRECODEPA). Costa Rica pp 10–11

Niño L. (2004) Revision sobre la Polilla de la papa *Tecia solanivora* en Centro y Sur America. Suplemento Revista latinoamericana de la papa:4–21

Notz A (1996) Infliencia de la temperatura sobre la biologia de *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) criadas en tuberculos de papa *Solanum tuberosum*. Bol Entomol Venez NS 11:49–54

Povolny D (1973) *Scrobipalpopsis solanivora* sp. n.—A new pest of potato (*Solanum tuberosum*) from Central America. Acta Universitatis Agriculturae. Facultas Agronomica 21:143–146

Puillandre N, Dupas S, Dangles O, Zeddam JL, Capdevielle-Dulac C, Barbin K, Torres-Leguizamon M, Silvain JF (2008) Genetic bottleneck in invasive species: the potato tuber moth adds to the list. Biol Invasions 10:319–333

R development core team (2010) R: a language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria

Raker CM, Spooner DM (2002) Chilean Tetraploid Cultivated Potato, *Solanum Tuberosum*, is Distinct from the Andean populations: microsatellite data. Crop Sci 42:1451–1458

Ramos-Onsins SE, Rozas J (2002) Statistical properties of new neutrality test against population growth. Mol Biol Evol 19:2092–2100

Rincón F, López-Avila A (2004) Dimorfismo sexual en pupas de *Tecia solanivora*. Revista CORPOICA 5:41–42

Rollins LA, Woolnough AP, Wilton AN, Sinclair R, Sherwing WB (2009) Invasive species can't cover their tracks: using microsatellites to assist management of starling (*Sturnus vulgaris*) populations in Western Australia. Mol Ecol 18:1560–1573

Rozas J, Sanchez-DelBarrio JC, Messeguer X, Rozas R (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19:2496–2497

Rozen S, Skaletsky HJ (2000) Primer3 on the WWW for general users and for biologist programmers. In: Krawetz S, Misener S (eds) Bioinformatics methods and protocols: methods in molecular biology. Humana Press, Totowa, NJ, pp 365–386. Avaible from http://frodo.wi.mit.edu/primer3/

Ruano S, Leal H, Del cid A, Rios E (1984) Generalidades sobre el cultivo de la papa y los efectos causados por polilla en tres areas de Quetzaltenango. Programa Regional Cooperativo de papa PRECODEPA Instituto de ciencia y Tecnología Agrícola. Guatemala

Sakai AK, Allendorf FW, Holt JS et al (2001) The population biology of invasive species. Ann Rev Ecol Syst 32:305–332

Salazar J, Escalante W (1984) La polilla guatemalteca de la papa, *Scrobipalpopsis solanivora*, nueva plaga del cultivo de la papa en Venezuela. Jornadas Agronómicas 9:24–28

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471

Simon-Bouhet B, Garcia-Meunier P, Viard F (2006) Multiple introductions promote range expansion of the mollusc *Cyclope neritea* (Nassariidae) in France: evidence from mitochondrial sequence data. Mol Ecol 15:1699–1711

Spooner DM, McLean K, Ramsay G, Waugh R, Bryan GJ (2005) A single domestication for potato based on multilocus amplied fragment length polymorphism genotyping. PNAS 102(41):14694–14699

Tajima F (1989) Statistical methode for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595

Templeton AR, Crandall KA, Sing CF (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetic 132: 619–633

Torres F (2003) Polilla de la papa *Tecia solanivora* (Povolny). Plagas agrícolas de Venezuela, Ficha técnicas de organismos plaga, Cultivo: Papa. *Solanum tuberosum*. Sociedad Venezolana de Entomología. http://www.plagas-agricolas.info.ve/fichas/cultivo_x_plaga.php?plaga=175

Wang Ch, Li S, Fu C, Gong X, Huang L, Song X, Zhao Y (2009) Molecular genetic structure and evolution in native and colonized populations of the Chinese mitten crab, *Eriocheir sinensis*. Biol Invasions 11:389–399

Wares JP, Hughes AR, Grosberg RK (2005) Mechanisms that drive evolutionary change: insights from species introductionsand invasions. In: Sax DF, Stachowicz JJ, Gaines SD (eds) Species invasions: insights into ecology, evolution and biogeography. Sinauer, Sunderland, pp 229–257

Zhang BC (1994) Index of economically important Lepidoptera. CAB International, UK

Zhou WG, Rousset F, O'Neill S (1998) Phylogeny and PCR-based classification of *Wolbachia* strains using wsp gene sequences. Royal Soc London 265:509–515