## Open Access Articles

The Irish potato famine pathogen Phytophthora infestans originated in central Mexico rather than the Andes

The Faculty of Oregon State University has made this article openly available. Please share how this access benefits you. Your story matters.

| Citation | Goss, E. M., Tabima, J. F., Cooke, D. E. L., Restrepo, S., Fry, W. E., Forbes, G. <br> A.,... \& Grünwald, N. J. (2014). The Irish potato famine pathogen Phytophthora <br> infestans originated in central Mexico rather than the Andes. Proceedings of the <br> National Academy of Sciences, 111(24). doi:10.1073/pnas.1401884111 |
| :--- | :--- |
| DOI | 10.1073/pnas.1401884111 |
| Publisher | National Academy of Sciences |
| Version | Version of Record |
| Terms of Use | http://cdss.library.oregonstate.edu/sa-termsofuse |

# The Irish potato famine pathogen Phytophthora infestans originated in central Mexico rather than the Andes 

Erica M. Goss ${ }^{\text {a }}$, Javier F. Tabima ${ }^{\text {b }}$, David E. L. Cooke ${ }^{\text {c }}$, Silvia Restrepo ${ }^{\text {d }}$, William E. Fry ${ }^{e}$, Gregory A. Forbes ${ }^{\text {f }}$, Valerie J. Fieland ${ }^{\text {b }}$, Martha Cardenas ${ }^{\text {d }}$, and Niklaus J. Grünwald ${ }^{\text {g,h,1 }}$<br>${ }^{\text {a }}$ Department of Plant Pathology and Emerging Pathogens Institute, University of Florida, Gainesville, FL 32611; ${ }^{\text {b }}$ Department of Botany and Plant Pathology,  University of the Andes, 110321 Bogota, Colombia; ${ }^{\text {e Department of Plant Pathology and Plant-Microbe Biology, Cornell University, Ithaca, NY } 14853 ;{ }^{\text {f }} \text { CIP }}$ China Center for Asia and the Pacific, International Potato Center, Beijing 100081, China; ${ }^{9}$ Horticultural Crops Research Laboratory, US Department of Agriculture Agricultural Research Service, Corvallis, OR 97330; and ${ }^{\text {h }}$ Department of Botany and Plant Pathology and Center for Genome Biology and Biocomputing, Oregon State University, Corvallis, OR 97331<br>Edited by Detlef Weigel, Max Planck Institute for Developmental Biology, Tübingen, Germany, and approved May 6, 2014 (received for review January 30, 2014)


#### Abstract

Phytophthora infestans is a destructive plant pathogen best known for causing the disease that triggered the Irish potato famine and remains the most costly potato pathogen to manage worldwide. Identification of $P$. infestan's elusive center of origin is critical to understanding the mechanisms of repeated global emergence of this pathogen. There are two competing theories, placing the origin in either South America or in central Mexico, both of which are centers of diversity of Solanum host plants. To test these competing hypotheses, we conducted detailed phylogeographic and approximate Bayesian computation analyses, which are suitable approaches to unraveling complex demographic histories. Our analyses used microsatellite markers and sequences of four nuclear genes sampled from populations in the Andes, Mexico, and elsewhere. To infer the ancestral state, we included the closest known relatives Phytophthora phaseoli, Phytophthora mirabilis, and Phytophthora ipomoeae, as well as the interspecific hybrid Phytophthora andina. We did not find support for an Andean origin of $P$. infestans; rather, the sequence data suggest a Mexican origin. Our findings support the hypothesis that populations found in the Andes are descendants of the Mexican populations and reconcile previous findings of ancestral variation in the Andes. Although centers of origin are well documented as centers of evolution and diversity for numerous crop plants, the number of plant pathogens with a known geographic origin are limited. This work has important implications for our understanding of the coevolution of hosts and pathogens, as well as the harnessing of plant disease resistance to manage late blight.


biological invasion |coalescent analysis | oomycete | population genetics | stramenopile

The potato pathogen Phytophthora infestans, the causal agent of potato late blight, is the plant pathogen that has most greatly impacted humanity to date. This pathogen is best known for its causal involvement in the Irish potato famine after introduction of the HERB-1 strain to Ireland from the Americas in the 19th century (1). To this day, potato late blight remains a major threat to food security and carries a global cost conservatively estimated at more than $\$ 6$ billion per year (2). In the 1980s, a single asexual lineage named US-1, possibly derived from the same metapopulation as HERB-1 (1), dominated global populations, whereas a genetically diverse and sexual population of $P$. infestans in central Mexico led to formulation of the hypothesis identifying Mexico as this pathogen's center of origin (3, 4). A competing hypothesis argues that the center of origin of the potato, the South American Andes, is the center of origin of $P$. infestans (5). This hypothesis recently gained prominence after an analysis demonstrated ancestral variation in Andean lineages of $P$. infestans (5). Other evidence supporting this hypothesis includes infection of native Solanum hosts and an Andean
distribution for Phytophthora andina, a phylogenetic relative of $P$. infestans (6).

Evidence supporting a Mexican center of origin is substantial, but inconclusive (4). Two close relatives of P. infestans, Phytophthora ipomoeae and Phytophthora mirabilis, are endemic to central Mexico (7, 8). P. ipomoeae and P. mirabilis cause disease on two endemic plant host groups, Ipomoea spp. and Mirabilis jalapa, respectively. Populations of $P$. infestans in the Toluca Valley, southwest of Mexico City, are genetically diverse, are in Hardy-Weinberg equilibrium, and contain mating types A1 and A2 in the expected 1:1 ratio for sexual populations $(9,10)$. Before a migration event from Mexico to Europe in the 1970s (11, 12), only A1 mating types of $P$. infestans were found worldwide outside of central Mexico, limiting other populations to asexual reproduction (13). Tuber-bearing native Solanum species occur throughout the Toluca Valley (14). Of the R genes that have been used to confer resistance to strains of $P$. infestans in potato, the majority described to date originated from Solanum demissum or Solanum edinense in the Toluca Valley, with some discovered in South America (15).

## Significance

The potato late blight pathogen was introduced to Europe in the 1840s and caused the devastating loss of a staple crop, resulting in the Irish potato famine and subsequent diaspora. Research on this disease has engendered much debate, which in recent years has focused on whether the geographic origin of the pathogen is South America or central Mexico. Different lines of evidence support each hypothesis. We sequenced four nuclear genes in representative samples from Mexico and the South American Andes. An Andean origin of P. infestans does not receive support from detailed analyses of Andean and Mexican populations. This is one of a few examples of a pathogen with a known origin that is secondary to its current major host.

[^0]Support for the alternate hypothesis that $P$. infestans originated in the Andes is based on a coalescent analysis conducted by Gómez-Alpizar et al. (5). This analysis used the nuclear RAS locus and the mitochondrial P3 and P4 regions to infer rooted gene genealogies that showed ancestral lineages rooted in the Andes. Furthermore, the Mexico sample harbored less nucleotide diversity than the Andean population. P. andina was identified as the ancestral lineage for the mitochondrial genealogy; however, $P$. mirabilis and $P$. ipomoeae were not included in that study. P. andina has since been shown to be a hybrid species derived from $P$. infestans and a Phytophthora sp. unknown to science (16). Surprisingly, populations of $P$. infestans and $P$. andina are clonal in South America and are not in Hardy-Weinberg equilibrium (6, 1719). Thus, the question of whether $P$. infestans originated in the Andes or central Mexico remained unresolved.
Powerful approaches for determining the demographic and evolutionary history of organisms are now available (20). Many of these approaches rely on the power of coalescent theory for inferring the genealogical history of a species based on a representative population sample (21-23). Bayesian phylogeography uses geographic information in light of phylogenetic uncertainty to provide model-based inference of geographic locations of ancestral strains (24). The isolation with migration (IM) model and associated software uses likelihood-based inference to infer divergence time between evolutionary lineages (25). Approximate Bayesian computation (ABC) makes use of coalescent simulations and likelihood-free inference to contrast complex demographic scenarios. Each of these methods has proven useful in reconstructing the demography of pests and pathogens (24, 26-29).

The objective of the present study was to reconcile the two competing hypotheses on the origin of $P$. infestans using Bayesian phylogenetics and ABC . We sampled key populations of $P$. infestans from central Mexico and the Andes and expanded on the analysis of Gómez-Alpizar et al. (5) by sequencing additional nuclear loci to assess support for the center of origin across multiple loci. To determine ancestral state, we added sequences from the sister taxa P. andina, P. mirabilis, P. ipomoeae, and Phytophthora phaseoli, all of which belong to Phytophthora clade 1c $(30,31)$. Finally, we aimed to reconcile the biology of $P$. infestans in Mexico with the findings of Gómez-Alpizar et al. (5) of ancestral variation in the Andes.

## Results

Population Structure and Mode of Reproduction. Our sample of $P$. infestans included 40 isolates from Colombia, Ecuador, and Peru and 48 isolates from Toluca Valley and Tlaxcala State in central Mexico (SI Appendix, Table S1). We found 30 multilocus simple sequence repeat (SSR) genotypes in the Andes sample and 43 in the Mexico sample. The Mexico sample had slightly higher mean allelic richness per locus compared with the Andes sample ( 6.7 vs . 5.2 ) after correction for sample size by rarefaction. The mean number of private alleles per locus for the Mexico sample was more than twice that for the Andes sample ( 2.1 vs . 0.8 ). In the Mexico sample, clonality was detected in isolates sampled from single patches of the indigenous host S. demissum. The index of association, $I_{A}$, calculated for clone-corrected data for the Mexico isolates accepted the hypothesis of sexual reproduction ( $P=0.25$ ). In contrast, the hypothesis of no linkage among markers was rejected for the Andes sample ( $P<0.001$ ), supporting a clonal mode of reproduction.
We inferred population structure based on SSR genotypes separately for the Mexico and Andes samples of P. infestans, based on a priori knowledge of their sexual and clonal reproduction, respectively, using structure (32). The Mexico sample consisted of admixed subpopulations with at least $K=4$ underlying groups (Fig. $1 A$ and SI Appendix, Figs. S1 and S2), whereas the Andes sample consisted of two distinct clusters with very little admixture (Fig. 1B and SI Appendix, Figs. S1 and S2).

Phylogeographic Root of $\boldsymbol{P}$. infestans. We used Bayesian multilocus phylogeographic analysis to infer the geographic location of the


Fig. 1. Population structure of Mexico and Andes samples of $P$. infestans inferred using structure (32). (A) The Mexico sample shows admixed individuals assigned to $K=4$ clusters. Isolates collected from patches of $S$. demissum are in bold type. Based on the index of association, $I_{A}$, there is no evidence of linkage disequilibrium among loci ( $P=0.25$ ), consistent with a sexually recombining population. (B) The Andes sample clusters into $K=2$ distinct clades with little or no admixture. The hypothesis of no linkage among markers is rejected ( $P<0.001$ ), indicating a clonal population.
root ("root state") of P. infestans and the Phytophthora clade 1c species using BEAST $(24,33)$. For this analysis, we included a representative global sample including isolates from the nowdiverse populations in Europe (SI Appendix, Table S1). Comparison of different molecular clocks for each sequenced nuclear locus showed that three of four loci fit a strict clock, in which the standard deviation of the uncorrelated lognormal relaxed molecular clock indicated no variation in rates among branches. In contrast, the RAS locus (intron Ras and Ras fragments) showed high variation in rates among branches and required a relaxed lognormal molecular clock (SI Appendix, Table S2). The PITG_11126 locus had the highest rate of evolution, whereas $\beta$-tubulin ( $\bar{b}$-tub) had the lowest substitution rate.

Root state reconstruction produced the highest posterior probabilities for Mexico as the root state of both the $P$. infestans and clade 1c datasets (Fig. 2). For each locus independently, posterior probabilities of a Mexico root were $>0.8$ for clade 1c (SI Appendix, Fig. S3). In nearly all of the $P$. infestans clades, there was an inferred ancestral connection to Mexico (SI Appendix, Figs. S4S8). All of the species in Clade 1c were monophyletic with high support, except for the hybrid species $P$. andina as previously demonstrated (16, 34).

Evolution of $\boldsymbol{P}$. infestans in the Andes. We found that three out of four loci had either greater nucleotide diversity or Watterson's theta for the Andes sample compared with the Mexico sample (SI Appendix, Table S3). To better understand the evolution of the Andes lineages and the relationship between $P$. infestans in Mexico and the Andes, we estimated pairwise times since divergence using combined SSR genotypes and nuclear sequence data using the IMa program (25). Divergence times were estimated between each of the clonal lineages in the Andes sample (US-1, EC-1, PE-3, and PE-7) and one another and the Mexico sample (Fig. 3). EC-1, PE-3, and PE-7 produced recent pairwise divergence times. EC-1 showed the most recent divergence from US-1 and the Mexico population. The time since divergence of PE-3 and US-1 was less than that of PE-3 and Mexico. The time since divergence between PE-7 and Mexico was greater than for EC-1 or PE-3 from Mexico. The marginal posterior probability distribution for the divergence time between PE-7 and US-1 was flat, indicating uncertainty in the history of PE-7.
We further explored scenarios for the evolution of the Andes lineages by testing a series of alternative models using ABC as implemented in the DIYABC program (35). We first examined


Fig. 2. Root state probabilities by country inferred using BEAST (33). (A) Summarized maximum clade credibility phylogeny of Phytophthora clade 1c species. Colors of branches indicate the most probable geographic origin of each lineage. Posterior probabilities of major branches supporting the tree topology are shown below each branch. Root state posterior probabilities indicate that Mexico is the most probable origin of clade 1c $(B)$ and $P$. infestans (C).
the relationships among the lineages EC-1, PE-3, and PE-7. Model comparison indicated that the PE-3 and PE-7 lineages have more recent shared ancestry compared with the more widespread EC-1 lineage (SI Appendix, Fig. S9). We next tested the relationships of each of these lineages to the Toluca population in Mexico and the US-1 lineage in the Andes (SI Appendix, Fig. S10). Here we used only isolates from the Toluca Valley, because we know that this population is panmictic (4). Preliminary analyses showed support for the PE-3 and PE-7 lineages being both closely related and distantly related to the other lineages.
To better understand this pattern, we included scenarios containing all possible pairwise admixture events among populations as well as an admixture with an unsampled population (36) (SI Appendix, Fig. S10). There was relatively strong support for PE-3 as an admixed lineage. The scenario in which PE-3 is derived from an admixture event between US-1 and an unsampled population had a posterior probability of 0.67 (Fig. $4 A$ and SI Appendix, Table S4). All other scenarios had posterior probabilities $<0.14$, most $<0.01$. The equivalent scenario for PE-7 also had the highest posterior probability of the tested models at 0.37 , but there was also support for PE-7 emerging from an admixture event between the Toluca population and the unsampled population (Fig. $4 B$ and $C$ and SI Appendix, Table S4). The relationship of EC-1 to US-1 and the Toluca population was uncertain as well, with nearly equal support for two scenarios (Fig. $4 D$ and $E$ and SI Appendix, Table S4). In one scenario, the EC-1 lineage recently diverged from the Toluca population $(P=0.25)$, and in the other, EC-1 was an admixture of the Toluca population and an unsampled population $(P=0.31)$. Our Andes samples were highly clonal; thus, we interpret these results as indicating that the PE-3, PE-7, and perhaps EC-1 lineages formed after a sexual event between two distinct lineages or populations.

We used the most highly supported scenarios to test more complex scenarios including all four Andean lineages and Toluca. Testing all possible admixture events proved to be too complex with support split among scenarios with various combinations of admixture events. Furthermore, the PE-7 results from both IMa and DIYABC analyses suggest that this lineage has a complex ancestry. Therefore, the final scenarios tested admixture in the evolution of EC-1 and PE-3, and excluded PE-7 (Fig. 5). We found that scenario B, in which EC-1 split from the Toluca population and PE-3 originated from an admixture event, had the highest posterior probability of 0.74 (Fig. 4). Notably, there was minimal support for scenario C, with simple ancestral divergence of PE-3 (Fig. 5).

We estimated type I and type II errors for scenario B and found that $65 \%$ of the datasets simulated under scenario B produced the highest posterior probability for scenario B (type I error, 0.352). Pseudo-observed datasets generated under scenarios A and C were wrongly assigned to scenario B at frequencies of 0.210 and 0.096 , respectively (type II error). Posterior distributions for parameters were wide, indicating limited confidence in the parameter estimates.

## Discussion

We found multilocus support for a Mexican origin of $P$. infestans. Bayesian phylogeographic analysis rooted both P. infestans and Phytophthora clade 1c in Mexico for each of four nuclear loci. Our results are consistent with the population biology of $P$. infestans in central Mexico and, taken together, point to Mexico as the origin of this pathogen. These results are supported by the previously noted pathogen and host characteristics. Specifically, Toluca populations are sexual, whereas South American populations of $P$. infestans are clonal ( $6,9,10,17-19$ ). Both mating types of $P$. infestans are known to have been present since at least the 1960s in central Mexico (37, 38).

The genealogical connections between continents that we observed in our phylogeographic analysis are consistent with the movement of $P$. infestans among widespread potato growing regions. Migration estimates using microsatellite variation also support our sequence analysis by showing migration from Mexico to the Andes, but not from the Andes to Mexico (SI Appendix). The commercial potato seed trade can explain much of the current global population structure of $P$. infestans; however, the early movements of $P$. infestans have not been fully reconstructed (1), and examination of the processes underlying the emergence of new, highly successful strains is ongoing $(3,39)$. The diverse population in central Mexico may be the ultimate source for the appearance of new strains worldwide (3, 40), although seed potatoes from Europe are behind recent migrations of virulent strains (41, 42). Detailed genetic reconstruction of global migrations of $P$. infestans may be feasible using population genomic data.

We explored the evolution of the Andean lineages and the relationship between $P$. infestans in Mexico and the Andes by testing a series of alternative models using the ABC technique. Our intention was to determine the timing of divergence of the Andean lineages and their relationship to the Toluca population in Mexico. Surprisingly, we found evidence for diversification of the Andes population as a result of admixture or hybridization. Because of our limited power to discriminate between models, we view this analysis as hypothesis-generating. Nevertheless, even moderate support for hybridization generating novel


Fig. 3. Estimated marginal posterior probabilities of relative divergence times in pairwise comparisons among Andes clonal lineages (EC-1, PE-3, PE-7, and US-1) and the Mexico population estimated using IMa (64). Smaller means and modes of the scaled time since divergence indicate more recent divergence of lineages. Lineages EC-1, PE-3, and PE-7 show more recent divergence from one another than from US-1 and Mexico.


Fig. 4. Scenarios for the evolution of $P$. infestans in the Andes tested using ABC in DIYABC (35). Shown are the scenarios with the highest posterior probabilities out of 15 scenarios testing the relationships of PE-3, PE-7, and EC-1 lineages, in turn, to the US-1 lineage and Toluca Valley population (SI Appendix, Fig. S10). Present-day populations are at the base of the tree schematic. Ancestral relationships among these populations are represented by lines intersecting in the past, with the vertex of the schematic representing the most recent common ancestor of all samples. Horizontal lines indicate admixture events between the ancestral populations connected by the horizontal line. Potential changes in population size over time are indicated by changes in line thickness, but line thickness is not proportional to population size. The dashed line represents an unsampled population that has contributed to the genetic variation observed in sampled populations. (A) For PE-3, the most probable scenario includes an admixture of US-1 and an unsampled population, leading to the PE-3 lineage. ( $B$ and C) For PE-7, support is split between two scenarios containing an admixture event with an unsampled population. ( $D$ and $E$ ) For EC-1, the scenarios with the greatest support showed a simple divergence from the Toluca population or an admixture between Toluca and an unsampled population. Posterior probabilities for all tested scenarios and their $95 \%$ confidence intervals are given in SI Appendix, Table S4.
lineages of $P$. infestans is compelling, given that a new pathogen of Solanum hosts, $P$. andina, has been generated via hybridization (16), and that infrequent hybridization among lineages of $P$. infestans is suspected to be responsible for novel genotypes elsewhere (43).

Considering the diversity of Solanum hosts in the Andes, there is great potential for clonal diversification of $P$. infestans as available niches are colonized and rare events contribute to generation or recombination of variation. There is no evidence of genetic variation among $P$. infestans isolates from potatoes in Peru as recently as the mid-1980s (44). If there were diversity in $P$. infestans or clade 1c in the Andes, it must have been limited to other unsampled hosts. Based on our analyses, we hypothesize that the Andean diversity in P. infestans has been driven by global migration together with hybridization among populations established via independent migration events.

Given our results, why did Gómez-Alpizar et al. (5) infer an Andean origin? First, their mitochondrial coalescent gene tree included the Andean endemic $P$. andina, but not the Mexican sister species, and thus species selection rooted the tree in the Andes. At the time that the work was conducted, $P$. andina was not recognized as a hybrid species with two haplotypes derived from two distinct parental species (16). When we removed $P$. andina from their dataset, the location of the root was ambiguous (SI Appendix); therefore, the mitochondrial loci used in the analysis were not phylogeographically informative. The root of the $P$. infestans mitochondrial genome was recently dated to 460 y ago ( $95 \%$ highestprobability density, 300-643), around the time of the Spanish conquest of the Americas (1). Thus, the two major mitochondrial haplotypes may be the product of movement of the pathogen by humans, resulting in the formation of a new population of $P$. infestans and the evolution of diverged mtDNA haplotypes before global expansion of the pathogen some 200 y later.

Second, the coalescent root of the single nuclear locus used by Gómez-Alpizar et al. is dependent on migration rate (SI Appendix), which was estimated using the same locus. The RAS gene in $P$. infestans has two diverged haplotypes in the first intron. This creates two diverged clades of haplotypes, one of which is not found in the Mexican sample. This might have biased the migration rate estimates for this gene and affected the outcome of the coalescent analysis. Our analysis of this locus required a relaxed molecular clock and took an exceptionally long time to converge. Finally,
explicit treatment of geography in our BEAST analysis did not require us to make assumptions about population structure, but rather incorporated the divergent origins of our isolates into the analysis.
Resolving the origin of $P$. infestans is important to our understanding of the emergence and reemergence of damaging pathogens. $P$. infestans is one of a limited number of agricultural plant pathogens with a well-characterized center of origin (45). An expectation of long-term coevolution between a crop and its host-specific pathogen can mislead one into thinking that the pathogen originates from the crop's center of origin; however, there are other well-documented and suspected instances of host-jumping by crop pathogens (45-47). P. infestans appears to be an example of a pathogen originating from wild relatives in a secondary center of host diversity. Identification of the center of origin also advances our understanding of pathogen evolution outside of this region, that is, how the pathogen has changed after introduction to new environments.

Global populations of $P$. infestans have undergone rapid changes owing to both migration and evolution after migration $(39,48)$. Knowledge of pathogen diversity and evolution both within and outside of the center of origin is critical to crop breeding efforts (49). The long-term success of efforts to breed late blight-resistant potatoes will require breeders to account for geographic and evolutionary sources of novel variation in $P$. infestans and its hosts.

## Materials and Methods

Sampling Individuals. A sampling of the known global diversity in P. infestans was obtained from several collaborators (SI Appendix, Table S1). We focused on assembling two large samples from Mexico $(n=48)$ and the South American Andes ( $n=40$ ) representing the known diversity from each of these regions, and included a more moderate global sample of $P$. infestans for context (SI Appendix, Table S1).

SSR Typing. Isolates were genotyped using 11 SSR markers as described previously $(39,50)$. Given that the individuals varied in ploidy, analysis was restricted to approaches that can accommodate nondiploid genetics (51).

Population Structure (SSR). Allelic richness was calculated using the ADZE program (52). Population composition was inferred using structure 2.3 (32) by testing the number of population clusters (K) between 1 and 20 using the admixture model for the Mexico and Andes samples (53) and the noadmixture model for the Andes sample. The no-admixture model may be more appropriate for the Andean population (i.e., Ecuador, Colombia, and Peru) given a priori knowledge of its clonality (17). Analysis was performed separately for the two different populations. A total of 10 independent runs each of 1,000,000 iterations with a burn-in period of 20,000 Markov chain Monte Carlo (MCMC) iterations were conducted. The results from structure were postprocessed using Structure Harvester (54). The $\Delta K$ method was used to evaluate the rate of change in the log probability of data between successive $K$ values, to infer the number of clusters (55).


Fig. 5. Final three scenarios used to examine the relationships between the Toluca Valley population and EC-1, PE-3, and US-1 lineages in the Andes by ABC. Tree schematics are drawn as in Fig. 4. The three scenarios are simple divergence of populations such that PE-3 is an ancestral lineage (A); emergence of the PE-3 lineage after an admixture of US-1 and an unsampled population (B); and scenario B plus emergence of the EC-1 by an admixture between the Toluca population and an unsampled population (C). Scenario $B$ was the most likely of the three, with a posterior probability of 0.74 . The $95 \%$ confidence intervals for the posterior probabilities are in brackets.

The mode of reproduction was assessed by evaluating observed linkage among loci against expected distributions from permutation using the index of association, $I_{A}$, as proposed by Brown et al. (56) and applied in multilocus (57). $I_{A}$ was calculated using the poppr package (58) in $R(59)$ separately for the Mexico and Andes samples and evaluated with 2,000 permutations using clone-corrected data.

DNA Amplification and Sequencing. Nuclear loci were amplified and directly sequenced as described by Goss et al. (16). A larger fragment of the b-tub gene was sequenced than that sequenced by Gómez-Alpizar et al. (5). Haplotype phases of nuclear gene sequences with multiple heterozygous sites were inferred using PHASE software (51). Inferred haplotypes were confirmed by cloning PCR products for a subset of genotypes and sequencing inserts. In several instances, three distinct alleles were recovered from a given individual; these were the only times when the PHASE-inferred haplotypes were not validated. In some instances, isolates with three alleles at one locus were cloned at another locus, and only two alleles were found; thus, it was not assumed that these isolates had three distinct alleles at other loci.

For the phylogenetic and coalescent-based analyses, we removed indels and recombinant alleles from the datasets. We used the four-gamete test to detect signals of recombination, and found recombination in the b-tub, PITG_11126, and RAS alignments. For PITG_11126, the last 65 nucleotides were excluded owing to recombination in this region relative to the remainder of the fragment. For b-tub, the signal of recombination was removed when an indel was deleted from the alignment and isolate PiEC01 was excluded. For the RAS locus, PiEC07, PiUS11, and PiUS17 were excluded.

The sequences generated have been deposited in GenBank (accession nos. KF979339-KF980878).

Demographic and Phylogeographic History. We adopted a Bayesian coalescent approach to investigate divergence and phylogeographic history using BEAST 1.7.4 (33, 60). BEAST implements a method for sampling all trees that have a reasonable probability given the data. The analysis is based on haplotypes, and two haplotypes in a given individual may or may not share a most common recent ancestor. Furthermore, genealogies obtained from BEAST necessarily estimate how old the common ancestor of these haplotypes might be for each haplotype (even when haplotype sequences are identical), resulting in slight branch length variation among identical haplotypes. This is an expected outcome of coalescent analysis in which identical sequences at a given locus are expected to show divergence at the genome level. Note that although branch length variation is observed among identical haplotypes, there is no support for nodes at this level until different haplotype sequences coalesce to their common recent ancestors, and this branch length variation should not be interpreted.

To initialize BEAST, we obtained the most likely models of nucleotide substitution for each alignment using jModelTest 2.1 (61) and ModelGenerator 0.57 (62), and selected the consensus model from these programs (SI Appendix, Table S5). To ensure adequate sampling of parameters, we conducted the BEAST analyses with independent MCMC simulations of 200 million iterations for each locus both for $P$. infestans only and with the other clade 1 c species. Analyses were conducted at least twice to ensure repeatability. For each MCMC run, we sampled every 10,000 generations and discarded nonstationary samples after $25 \%$ burn-in. Effective sample size estimates were typically greater than 200, and parameter trace plots supported MCMC convergence and good mixing in each independent run. Multilocus analyses were also run for P. infestans only and also for all Phytophthora clade 1c species. For each dataset, models of nucleotide substitution, constant coalescent priors (for the $P$. infestans dataset) or Yule speciation models (for the clade 1c dataset) were used as specified priors to improve the calculation of clock rates, geographic ancestral states, and phylogenetic relationships.

To infer the most likely geographic origin for each clade, we used the discrete phylogeographic approach as implemented by Lemey et al. (24). This method uses the geographic locations of the samples to reconstruct the ancestral states of tree nodes, including estimation of the root state posterior probability. Maximum clade credibility (MCC) trees were obtained using TreeAnnotator and visualized in FigTree 1.3.1. The bar plots for the posterior probability of the root state were created with the ggplot2 package (63) using R statistical computing and graphic language (59). Maximum clade credibility trees were obtained for each locus as well as for multigene analyses.

Divergence Times Under Isolation with Migration. IMa version 2.0 was used to estimate divergence times for each pair of Andean lineages and between Andean lineages and the Mexican population (64). The data used were the 4 nuclear loci and 8 of the 11 SSR loci. Two SSR loci that did not conform to the stepwise mutation model (D13 and G11) and one SSR locus that was nearly
monomorphic (Pi33) were excluded. The infinite sites model was used for all nuclear loci. Initial maxima for uniform prior distributions of the parameters were as follows: population size ( $q$ ), 15.0; divergence time $(t), 0.5$; migration rate ( $m$ ), 1.0. Runs including the Mexican sample were also performed using larger priors for $q$ (20.0) and $t$ (1.0), and similar results were obtained. The option of running the burn-in and recording periods for indefinite durations was chosen to ensure stabilization of likelihoods before the end of the burnin and adequate sampling of the posterior distribution. Metropolis coupling was implemented using the geometric increment model and 80 chains with geometrical increment parameters of 0.97 and 0.3 .

ABC. We evaluated alternative scenarios for the evolution of the Andean $P$. infestans lineages in a systematic stepwise manner using $A B C$ with DIYABC version 1.0.4.45 (35). ABC has been used to estimate parameters for complex evolutionary models for which likelihoods are difficult or practically impossible to compute $(65,66)$. The DIYABC program simulates coalescent genealogies under user-specified evolutionary models using parameters drawn from prior distributions and compares statistics summarizing various aspects of the simulated data with those of the observed data. The similarity of summary statistics between observed and simulated datasets is used to calculate posterior probabilities of competing evolutionary models and posterior distributions of parameters. In effect, models that generate datasets with summary statistics close to the observed data have higher probability. We used this method to evaluate posterior probabilities for alternate scenarios representing different possible evolutionary relationships among P. infestans populations in Mexico and the Andes. The use of $A B C$ to evaluate alternate scenarios has been questioned owing to potential problems with using summary statistics, but DIYABC incorporates tests that address many of these concerns $(67,68)$. In particular, confidence in model choice can be evaluated empirically by calculating type I and II errors using pseudo-observed datasets.

To narrow the number of evolutionary scenarios tested against one another, we used four sets of scenarios to inform a final fifth set of scenarios. We grouped the Andes isolates by clonal lineage to tease apart the evolutionary history of each lineage. Isolates were assigned to a clonal lineage based on a previously determined RG-57 fingerprint (3) and confirmed with SSR genotypes grouped using structure and $k$-means clustering (69). We first simulated the three different possible relationships among the Andean lineages EC-1, PE-3, and PE-7 (SI Appendix, Fig. S9) using the settings in SI Appendix, Table S6A. We next examined 15 alternative relationships for the US-1 lineage, the Toluca population, and each of the Andean lineages in turn (SI Appendix, Fig. S10 and Table S6B). Although the US-1 lineage has had a global distribution, for these analyses we used only US-1 isolates collected in the Andes, because our focus was on the genetic variation and evolution history of the Andes population. Based on the results of preliminary analyses, these scenarios included admixture events between lineages as well as admixture with an unsampled population.

Finally, we used the scenarios with the highest posterior probabilities to construct three final scenarios (Fig. 4 and SI Appendix, Table S6C). This final set tested admixture events generating the EC-1 and PE-3 lineages relative to a scenario with no admixture. We removed the PE-7 lineage from this final analysis, because there were too many plausible admixture events behind the emergence of this lineage.

We tested prior distribution settings with small numbers of simulations by running a principal components analysis on the summary statistics and comparing the overlap of the simulated and observed data. Posterior probabilities and $95 \%$ confidence intervals were estimated by polychotomic weighted logistic regression on $1 \%$ of the simulations, as implemented in DIYABC. Model checking was conducted for the final three scenarios by estimating type I and type II errors. In short, 500 pseudo-observed datasets (pods) were generated according to each evolutionary scenario using parameters drawn from the same prior distributions as used for the simulated genealogies. The posterior probability of each scenario was calculated for each pod. Type I error was estimated as the proportion of pods for which the correct scenario did not receive the highest posterior probability. Type II error was calculated as the proportion of pods erroneously assigned to a given scenario.

ACKNOWLEDGMENTS. We are grateful to the many colleagues who provided isolates for this study. We thank Karan Fairchild, Kevin Myers, Caroline Press, and Naomi Williams for maintenance of the cultures and general technical support. This research is supported in part by US Department of Agriculture (USDA) Agricultural Research Service Grant 5358-22000-039-00D, USDA National Institute of Food and Agriculture Grant 2011-68004-30154 (to N.J.G.), and the Scottish Government (D.E.L.C.).

1. Yoshida K, et al. (2013) The rise and fall of the Phytophthora infestans lineage that triggered the Irish potato famine. eLife 2:e00731.
2. Haverkort AJ, et al. (2008) Societal costs of late blight in potato and prospects of durable resistance through cisgenic modification. Potato Res 51:1871-4528.
3. Goodwin SB, Cohen BA, Fry WE (1994) Panglobal distribution of a single clonal lineage of the Irish potato famine fungus. Proc Natl Acad Sci USA 91(24):11591-11595.
4. Grünwald NJ, Flier WG (2005) The biology of Phytophthora infestans at its center of origin. Annu Rev Phytopathol 43:171-190.
5. Gómez-Alpizar L, Carbone I, Ristaino JB (2007) An Andean origin of Phytophthora infestans inferred from mitochondrial and nuclear gene genealogies. Proc Natl Acad Sci USA 104(9):3306-3311.
6. Oliva RF, et al. (2010) Phytophthora andina sp nov., a newly identified heterothallic pathogen of solanaceous hosts in the Andean highlands. Plant Pathol 59(4):613-625.
7. Flier WG, et al. (2002) Phytophthora ipomoeae, a new homothallic species causing late blight on Ipomoeae longipedunculata in the Toluca Valley of central Mexico. Mycol Res 106(7):848-856.
8. Goodwin SB, Legard DE, Smart CD, Levy M, Fry WE (1999) Gene flow analysis of molecular markers confirms that Phytophthora mirabilis and $P$. infestans are separate species. Mycologia 91(5):796-810.
9. Grünwald NJ, et al. (2001) Population structure of Phytophthora infestans in the Toluca Valley region of Central Mexico. Phytopathology 91(9):882-890.
10. Flier WG, et al. (2003) The population structure of Phytophthora infestans from the Toluca Valley in central Mexico suggests genetic differentiation between populations from cultivated potato and wild Solanum species. Phytopathology 93(4):382-390.
11. Fry WE, et al. (1993) Historical and recent migrations of Phytophthora infestans: Chronology, pathways, and implications. Plant Dis 77(7):653-661.
12. Niederhauser JS (1991) Phytophthora infestans: The Mexican connection. Phytophthora, eds Lucas JA, Shattock RC, Shaw DS, Cooke LR (Cambridge Univ Press, Cambridge, UK), pp 25-45.
13. Fry WE, et al. (1992) Population genetics and intercontinental migrations of Phytophthora infestans. Annu Rev Phytopathol 30:107-130.
14. Hijmans RJ, Spooner DM (2001) Geographic distribution of wild potato species. Am J Bot 88(11):2101-2112.
15. Vleeshouwers VGAA, et al. (2011) Understanding and exploiting late blight resistance in the age of effectors. Annu Rev Phytopathol 49(1):507-531.
16. Goss EM, et al. (2011) The plant pathogen Phytophthora andina emerged via hybridization of an unknown Phytophthora species and the Irish potato famine pathogen, P. infestans. PLoS ONE 6(9):e24543.
17. Adler NE, et al. (2004) Genetic diversity of Phytophthora infestans sensu lato in Ecuador provides new insight into the origin of this important plant pathogen. Phytopathology 94(2):154-162.
18. Chacon MG, et al. (2006) Genetic structure of the population of Phytophthora infestans attacking Solanum ochranthum in the highlands of Ecuador. Eur J Plant Pathol 115(2):235-245.
19. Forbes GA, et al. (1997) Population genetic structure of Phytophthora infestans in Ecuador. Phytopathology 87(4):375-380.
20. Grünwald NJ, Goss EM (2011) Evolution and population genetics of exotic and reemerging pathogens: Novel tools and approaches. Annu Rev Phytopathol 49:249-267.
21. Tavare $S$ (1984) Lines-of-descent and genealogical processes, and their applications in population-genetics models. Adv Appl Prob 16(1):471-491.
22. Kingman JFC (1982) The coalescent. Stochastic Process Appl 13:235-248.
23. Wakeley J (2009) Coalescent Theory: An Introduction (Roberts \& Company, Greenwood Village, CO).
24. Lemey P, Rambaut A, Drummond AJ, Suchard MA (2009) Bayesian phylogeography finds its roots. PLOS Comput Biol 5(9):e1000520.
25. Hey J, Nielsen R (2004) Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of Drosophila pseudoobscura and D. persimilis. Genetics 167(2):747-760.
26. Miller N, et al. (2005) Multiple transatlantic introductions of the western corn rootworm. Science 310(5750):992.
27. Stukenbrock EH, Banke S, Javan-Nikkhah M, McDonald BA (2007) Origin and domestication of the fungal wheat pathogen Mycosphaerella graminicola via sympatric speciation. Mol Biol Evol 24(2):398-411.
28. Lombaert $E$, et al. (2010) Bridgehead effect in the worldwide invasion of the biocontrol harlequin ladybird. PLoS ONE 5(3):e9743.
29. Dutech C, et al. (2012) The chestnut blight fungus world tour: Successive introduction events from diverse origins in an invasive plant fungal pathogen. Mol Ecol 21(16):3931-3946.
30. Cooke DEL, Drenth A, Duncan JM, Wagels G, Brasier CM (2000) A molecular phylogeny of Phytophthora and related oomycetes. Fungal Genet Biol 30(1):17-32.
31. Blair JE, Coffey MD, Park S-Y, Geiser DM, Kang S (2008) A multi-locus phylogeny for Phytophthora utilizing markers derived from complete genome sequences. Fungal Genet Biol 45(3):266-277.
32. Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945-959.
33. Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol Biol Evol 29(8):1969-1973.
34. Blair JE, Coffey MD, Martin FN (2012) Species tree estimation for the late blight pathogen, Phytophthora infestans, and close relatives. PLoS ONE 7(5):e37003.
35. Cornuet JM, Ravigné V, Estoup A (2010) Inference on population history and model checking using DNA sequence and microsatellite data with the software DIYABC (v1.0). BMC Bioinformatics 11:401.
36. Guillemaud T, Beaumont MA, Ciosi M, Cornuet J-M, Estoup A (2010) Inferring introduction routes of invasive species using approximate Bayesian computation on microsatellite data. Heredity (Edinb) 104(1):88-99.
37. Gallegly ME, Galindo J (1958) Mating types and oospores of Phytophthora infestans in nature in Mexico. Phytopathology 48:274-277.
38. Flier WG, Grünwald NJ, Fry WE, Turkensteen LJ (2001) Formation, production and viability of oospores of Phytophthora infestans isolates from potato and Solanum demissum in the Toluca Valley, central Mexico. Mycol Res 105(8):998-1006.
39. Cooke DEL, et al. (2012) Genome analyses of an aggressive and invasive lineage of the Irish potato famine pathogen. PLoS Pathog 8(10):e1002940.
40. Spielman LJ, et al. (1991) A second world-wide migration and population displacement of Phytophthora infestans? Plant Pathol 40(3):422-430.
41. Li Y, et al. (2012) Population structure of Phytophthora infestans in China: Geographic clusters and presence of the EU genotype Blue_13. Plant Pathol 62:932-942.
42. Chowdappa P, et al. (2012) Emergence of 13_A2 blue lineage of Phytophthora infestans was responsible for severe outbreaks of late blight on tomato in south-west India. J Phytopathol 161:49-58.
43. Goodwin SB, et al. (1998) Genetic change within populations of Phytophthora infestans in the United States and Canada during 1994 to 1996: Role of migration and recombination. Phytopathology 88(9):939-949.
44. Tooley PW, Therrien CD, Ritch DL (1989) Mating type, race composition, nuclear DNA content, and isozyme analysis of Peruvian isolates of Phytophthora infestans. Phytopathology 79:478-481.
45. Stukenbrock EH, McDonald BA (2008) The origins of plant pathogens in agro-ecosystems. Annu Rev Phytopathol 46:75-100.
46. Zaffarano PL, McDonald BA, Linde CC (2008) Rapid speciation following recent host shifts in the plant pathogenic fungus Rhynchosporium. Evolution 62(6):1418-1436.
47. Couch BC, et al. (2005) Origins of host-specific populations of the blast pathogen Magnaporthe oryzae in crop domestication with subsequent expansion of pandemic clones on rice and weeds of rice. Genetics 170(2):613-630.
48. Goodwin SB, Sujkowski LS, Fry WE (1995) Rapid evolution of pathogenicity within clonal lineages of the potato late blight disease fungus. Phytopathology 85:669-676.
49. McDonald BA, Linde C (2002) Pathogen population genetics, evolutionary potential, and durable resistance. Annu Rev Phytopathol 40:349-379.
50. Lees AK, et al. (2006) Novel microsatellite markers for the analysis of Phytophthora infestans populations. Plant Pathol 55:311-319.
51. Stephens M, Smith NJ, Donnelly P (2001) A new statistical method for haplotype reconstruction from population data. Am J Hum Genet 68(4):978-989.
52. Szpiech ZA, Jakobsson M, Rosenberg NA (2008) ADZE: Allelic Diversity Analyzer, version 1.0. http://rosenberglab.bioinformatics.med.umich.edu/adze.html.
53. Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. Genetics 164(4):1567-1587
54. Earl DA, Vonholdt BM (2012) STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4(2):359-361.
55. Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Mol Ecol 14(8):2611-2620.
56. Brown AHD, Feldman MW, Nevo E (1980) Multilocus structure of natural populations of Hordeum spontaneum. Genetics 96(2):523-536.
57. Agapow P-M, Burt A (2001) Indices of multilocus linkage disequilibrium. Mol Ecol Notes 1(1-2):101-102.
58. Kamvar ZN, Tabima JF, Grünwald NJ (2014) Poppr: An R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. PeerJ 2:e281.
59. R Development Core Team (2013) R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria).
60. Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol 7:214.
61. Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. Nat Methods 9(8):772.
62. Keane TM, Creevey CJ, Pentony MM, Naughton TJ, McInerney JO (2006) Assessment of methods for amino acid matrix selection and their use on empirical data shows that ad hoc assumptions for choice of matrix are not justified. BMC Evol Biol 6:29.
63. Wickham H (2009) ggplot2: Elegant Graphics for Data Analysis (Springer, New York), p 212.
64. Hey J (2010) Isolation with migration models for more than two populations. Mol Biol Evol 27(4):905-920.
65. Beaumont MA (2010) Approximate Bayesian computation in evolution and ecology. Annu Rev Ecol Evol Syst 41(1):379-406.
66. Csilléry K, Blum MGB, Gaggiotti OE, François O (2010) Approximate Bayesian Computation (ABC) in practice. Trends Ecol Evol 25(7):410-418.
67. Robert CP, Cornuet JM, Marin JM, Pillai NS (2011) Lack of confidence in approximate Bayesian computation model choice. Proc Natl Acad Sci USA 108(37):15112-15117.
68. Bertorelle G, Benazzo A, Mona S (2010) ABC as a flexible framework to estimate demography over space and time: Some cons, many pros. Mol Ecol 19(13):2609-2625.
69. Meirmans P, Van Tienderen P (2004) Genotype and Genodive: Two programs for the analysis of genetic diversity of asexual organisms. Mol Ecol Notes 4:792-794.

## Supporting Information

Supporting Methods. ..... 1
Supporting Results ..... 2
References Cited ..... 3
Supporting Tables ..... 4
Supporting Figures. ..... 19

## Supporting Methods

Genetree analysis. We revisited the coalescent analysis of Gómez-Alpizar et al. (1) using their data and ours to investigate the sensitivity of root inference to estimates of migration rates. Our concern was that there is little power to estimate migration rates with only a single locus, yet these rates were used to infer the rooting of structured coalescent trees in the program Genetree (2). Furthermore, Gómez-Alpizar et al. considered migration to and from South America, which confounds migration from Mexico and other global populations. P. infestans is transported transcontinentally and intercontinentally via infected seed tubers, and there is a vibrant commercial seed tuber trade from Northwest Europe with known pathways of migration from Europe to South America.

We revised the Genetree analysis of the P3 and P4 mtDNA regions using sequences from Gómez-Alpizar et al. (1) for isolates from Mexico and the Andes but removing the haplotypes representing the $P$. andina isolates (haplotype 1c). The topology and rooting of the coalescent tree for the $P$. infestans haplotypes remained the same. We inferred the maximum likelihood value of theta and a symmetric migration rate for the revised data set. We then used $1 \times 10^{7}$ simulations to examine the inferred subpopulation of the most common recent ancestor (MRCA) of the sample while varying theta and symmetric migration rates using three sets of runs, each set using a different starting seed.

For the RAS nuclear gene, we repeated the Gómez-Alpizar et al. (1) analysis while varying migration rates. We used their data set and value of theta. We conducted two runs of $1 \times 10^{7}$ simulations for each set of migration rates. We varied migration rates from low and symmetric to the values used by Gómez-Alpizar et al. We also examined the coalescent history of the RAS locus using our sequences from Mexico and the Andes. The tree was rooted using ancestral states obtained from $P$. ipomoeae, $P$. mirabilis, and $P$. phaseoli. We used four runs of $1 \times 10^{6}$ or $1 \times 10^{7}$ simulations and three symmetric migration rates using two different values of theta (1.5 and 2.0) and four starting seeds.

Migration scenarios from SSR genotypes. The program Migrate version 3.3 was used to examine recent migration between the Andes and Mexico, using SSR genotypes. Three migration models were compared (3): bidirectional migration, migration from Mexico to the Andes only, and migration from the Andes to Mexico only. The runs used Brownian motion approximation for the stepwise mutation model, initial parameter values from $\mathrm{F}_{\text {ST }}$, and mutation rates per locus estimated from the data. Bayesian inference across 10 replicates used slice sampling, uniform prior distributions from 0 to 1000 for both theta and $M$ parameters, and four chains (temperatures: $1,000,000,3.0,1.5,1.0$ ) in which the cold chain was sampled at 10,000
steps at 200 step increments after a burnin of 500,000 steps. Models were evaluated using Bezier approximation of $\log$ marginal maximum likelihoods.

## Supporting Results

Dependence of Genetree results on migration rates. When we removed $P$. andina from the Gómez-Alpizar et al. mitochondrial data set and included only the Mexican and South American isolates, the root location was uncertain such that there was equal probability of rooting in Mexico or South America when migration rates were symmetric (Table S7A). Asymmetric migration rates increased the probability of the root in the population that was the source of migration to around 0.95 , irrespective of which population was assigned the higher emigration rate.

For the RAS locus, the location of the coalescent root was dependent on migration rates as well (Table S7B). When we used the Gómez-Alpizar et al. data under low symmetric migration rates the rooting was uncertain, and asymmetric migration rates affected the inferred population of origin. The migration rates used by Gómez-Alpizar et al. produced a high probability for a South American root, which replicates their result. The opposite condition produced a similarly high probability for a non-South American root. Therefore, both mitochondrial and RAS analyses were highly dependent on choice of migration parameters.

We used our data set to examine the root location of RAS for Mexican and Andean isolates only. Using RAS sequences from P. andina, P. mirabilis, P. ipomoeae, and P. phaseoli, we were able to unambiguously assign ancestral states to each segregating site and these ancestral states were used to root the $P$. infestans RAS tree. The coalescent history of the gene was simulated on the rooted topology to infer the location of the root in Mexico or the Andes. Moderate and inconclusive probabilities for root location were observed under nearly all conditions examined, including three symmetric migration rates and two values of theta (Table S8).

Key to the Gómez-Alpizar et al. analysis was their finding of a higher migration rate from South America to non-South American populations (i.e. Mexico, USA, and Ireland) than vice-versa using the nuclear RAS locus. Given this result, we used our SSR data to test among models of migration between the Andes and Mexico using the program Migrate (3). Multiple loci are expected to provide more robust estimates of migration rates for the nuclear genome than can be obtained from a single locus. This analysis revealed a higher migration rate from Mexico to the Andes than from the Andes to Mexico ( $\mathrm{M}=11.7$ vs. 0.3 , respectively). Bayesian comparison of migration models strongly supported unidirectional migration from Mexico to the Andes (Bezier approximation of the log marginal likelihood $=-11,055$ ) compared to the opposite scenario of migration from the Andes to Mexico $(-12,243)$ or bidirectional migration $(-52,357)$. This result is consistent with the known directions of trade in commercial seed tubers.

## References Cited

1. Gómez-Alpizar L, Carbone I, \& Ristaino JB (2007) An Andean origin of Phytophthora infestans inferred from mitochondrial and nuclear gene genealogies. Proc Natl Acad Sci U S A 104(9):3306-3311.
2. Griffiths RC \& Tavaré S (1994) Ancestral inference in population genetics. Statistical science 9(3):307-319.
3. Beerli P \& Palczewski M (2010) Unified framework to evaluate panmixia and migration direction among multiple sampling locations. Genetics 185(1):313-U463.
4. Nei M (1987) Molecular Evolutionary Genetics (Columbia University Press, New York) p 512
5. Watterson GA (1975) On the number of segregating sites in genetic models without recombination. Theoretical Population Biology 7:256-276.
6. Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123(3):585-595.
7. Fu Y-X \& Li W-H (1993) Statistical tests of neutrality of mutations. Genetics 133(3):693-709.

## Supporting Tables

Table S1. Isolates used in the study.

| ID | Original name | Year sampled | Country | State | Host | Source ${ }^{1}$ | Lineage |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P. infestans |  |  |  |  |  |  |  |
| PiCO01 | 1011 |  | Colombia | Cundinamarca | S. tuberosum | Restrepo | EC-1 |
| PiCO02 | 1063 |  | Colombia | Cundinamarca | S. tuberosum | Restrepo | EC-1 |
| PiCO03 | 1064 |  | Colombia | Cundinamarca | S. tuberosum | Restrepo | EC-1 |
| PiCO04 | 1068 |  | Colombia | Cundinamarca | S. tuberosum | Restrepo | EC-1 |
| PiCO05 | 4084 |  | Colombia | Cundinamarca | Physalis peruviana | Restrepo | US-8 |
| PiEC01 | EC_3843 | 2004 | Ecuador |  | potato | Forbes | EC-1 |
| PiEC02 | EC_3527 | 2002 | Ecuador |  | S. andreanum | Forbes | EC-1 |
| PiEC03 | EC_3626 | 2003 | Ecuador |  | potato | Forbes | EC-1 |
| PiEC06 | EC_3841 | 2004 | Ecuador |  | S. habrochaites | Forbes | US-1 |
| PiEC07 | EC_3921 | 2006 | Ecuador |  | S. jugandifolium | Forbes | US-1 |
| PiEC08 | EC_3774 | 2004 | Ecuador |  | S. ochanthum | Forbes | US-1 |
| PiEC10 | EC_3378 | 2001 | Ecuador |  | S. lycopersicum | Forbes | US-1 |
| PiEC11 | EC_3381 | 2001 | Ecuador |  | S. lycopersicum | Forbes | US-1 |
| PiEC12 | EC_3150 | 1997 | Ecuador |  | S. muricatum | Forbes | US-1 |
| PiEC13 | EC_3520 | 2002 | Ecuador |  | S. muricatum | Forbes | US-1 |
| PiEC14 | EC_3809 | 2004 | Ecuador |  | S. caripense | Forbes | US-1 |
| PiES01 | 2005_10 | 2005 | Estonia |  | potato | Fry |  |
| PiES02 | 2005_17 | 2005 | Estonia |  | potato | Fry |  |
| PiES03 | 2005_19 | 2004 | Estonia |  | potato | Fry |  |
| PiES04 | 2004_4 | 2004 | Estonia |  | potato | Fry |  |
| PiES05 | 2004_16 | 2004 | Estonia |  | potato | Fry |  |
| PiHU02 | Josze_S32 |  | Hungary |  | potato | Bakonyi |  |


| PiMX03 | MX980211 | 1998 | Mexico |  | potato |
| :--- | :--- | :--- | :--- | :--- | :--- |
| PiMX04 | MX980230 | 1998 | Mexico |  | pry |
| PiMX05 | MX980317 | 1998 | Mexico |  | potato |
| PiMX06 | MX980352 | 1998 | Mexico |  | pry |
| PiMX07 | MX980400 | 1998 | Mexico |  | Fry |
| PiMX10 | PIC97008 | 1997 | Mexico | Toluca | potato |
| PiMX11 | PIC97066 | 1997 | Mexico | Toluca | pry |
| PiMX12 | PIC97106 | 1997 | Mexico | Toluca | potato |


| PiMX45 | PIC97749 | 1997 | Mexico | Toluca | S. demissum | Flier/Grünwald/PRI |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| PiMX46 | PIC97750 | 1997 | Mexico | Toluca | S. demissum | Flier/Grünwald/PRI |  |
| PiMX47 | PIC97751 | 1997 | Mexico | Toluca | S. demissum | Flier/Grünwald/PRI |  |
| PiMX48 | PIC97785 | 1997 | Mexico | Toluca | S. demissum | Flier/Grünwald/PRI |  |
| PiMX49 | PIC97791 | 1997 | Mexico | Toluca | S. demissum | Flier/Grünwald/PRI |  |
| PiMX50 | PIC97793 | 1997 | Mexico | Toluca | S. demissum | Flier/Grünwald/PRI |  |
| PiMX61 | Tlax 701 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX62 | Tlax 715 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX63 | Tlax 722 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX64 | Tlax 728 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX65 | Tlax 740 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX66 | Tlax 748 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX67 | Tlax 756 | 2007 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX71 | T48 | 2003 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiMX72 | T68 | 2003 | Mexico | Tlaxcala | potato | Fernández Pavia |  |
| PiNL01 | NL_01096 | 2001 | Netherlands |  | potato | Kessel |  |
| PiNL02 | NL_96259 | 1996 | Netherlands |  | potato | Kessel |  |
| PiPE01 | BTLM 004 | 1997 | Peru | Lima | NA | Forbes | PE-7 |
| PiPE02 | PHU 076 | 2003 | Peru | Huánuco | potato | Forbes | EC-1 |
| PiPE03 | PHU 079 | 2003 | Peru | Huánuco | potato | Forbes | EC-1 |
| PiPE04 | PPI 015 | 2000 | Peru | Piura | S. huancabambense | Forbes | EC-1 |
| PiPE05 | PTS 031 | 1998 | Peru | Cajamarca | S. caripense | Forbes | EC-1 |
| PiPE06 | 1696 | 1995 | Peru | Arequipa | potato | Forbes | PE-3 |
| PiPE07 | PCA 004 | 1999 | Peru | Cajamarca | potato | Forbes | PE-3 |
| PiPE08 | PCZ 024 | 1997 | Peru | Cuzco | potato | Forbes | EC-1 |
| PiPE09 | PCZ 080 | 1997 | Peru | Cuzco | potato | Forbes | EC-1 |
| PiPE10 | PSR 001 | 2005 | Peru | Junín | NA | Forbes | EC-1 |
| PiPE11 | PCA 020 | 1999 | Peru | Cajamarca | NA | Forbes | PE-7 |
| PiPE12 | PLI 003 | 1999 | Peru | Lima | NA | Forbes | PE-7 |
| PiPE13 | PLI 036 | 2000 | Peru | Lima | S. wittmackii | Forbes | PE-7 |


| PiPE14 | POX 100 | 2003 | Peru | Pasco | potato | Forbes | PE-7 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| PiPE20 | PCA 025 | 1999 | Peru | Cajamarca | NA | Forbes | US-1 |
| PiPE21 | PPI 009 | 2000 | Peru | Piura | S. caripense | Forbes | US-1 |
| PiPE22 | PPI 013 | 2000 | Peru | Piura | S. caripense | Forbes | US-1 |
| PiPE23 | PPI 014 | 2000 | Peru | Piura | S. caripense | Forbes | US-1 |
| PiPE24 | PPI 023 | 2000 | Peru | Piura | S. caripense | Forbes | US-1 |
| PiPE25 | PPI 028 | 2000 | Peru | Piura | S. caripense | Forbes | US-1 |
| PiPE26 | PPU 048 | 1997 | Peru | Puno | potato | Forbes | PE-3 |
| PiPE27 | PPU 097 | 1997 | Peru | Puno | potato | Forbes | US-1 |
| PiPE28 | PCA 006 | 1999 | Peru | Cajamarca | potato | Forbes | PE-3 |
| PiPE29 | PCA 010 | 1999 | Peru | Cajamarca | potato | Forbes | PE-3 |
| PiPO01 | MP_618 | 2005 | Poland |  | potato | Lebecka |  |
| PiPO02 | MP_622 | 2005 | Poland |  | potato | Lebecka |  |
| PiSA01 | SA960008 | 1996 | South Africa |  | potato | Fry | US-1 |
| PiSW01 | SE_03058 | 2003 | Sweden |  | potato | Andersson |  |
| PiSW02 | SE_03087 | 2003 | Sweden |  | potato | Andersson |  |
| PiUK01 | 2006_3984C | 2006 | UK |  | potato | Cooke | EU_1_A1 |
| PiUK02 | 2006_4012F | 2006 | UK |  | potato | Cooke | EU_3_A2 |
| PiUK03 | 2006_3928A | 2006 | UK |  | potato | Cooke | EU_13_A2 |
| PiUK04 | 2006_4132B | 2006 | UK |  | potato | Cooke | EU_13_A2 |
| PiUK05 | 2006_3888A | 2006 | UK |  | potato | Cooke | EU_2_A1 |
| PiUK06 | 2007_5866B | 2007 | UK |  | potato | Cooke | EU_5_A1 |
| PiUK07 | 2006_4388D | 2006 | UK |  | potato | Cooke | EU_17_A2 |
| PiUK08 | 2006_4100A | 2006 | UK |  | potato | Cooke | EU_6_A1 |
| PiUK09 | 2006_4440C | 2006 | UK |  | potato | Cooke | EU_10_A2 |
| PiUK10 | 2006_4232E | 2006 | UK |  | potato | Cooke | EU_8_A1 |
| PiUS08 | US040009 | 2004 | USA |  | potato | Fry | US-8 |
| PiUS11 | US050007 | 2005 | USA |  | tomato | Fry | US-11 |
| PiUS12 | US940494 | 1994 | USA |  | tomato | Fry | US-12 |
| PiUS17 | US970001 | 1997 | USA |  | tomato | Fry | US-17 |
| PiVT01 | Vn02-076 | 2002 | Vietnam |  | tomato | Le | US-1 |


| PiVT02 | Vn02-106 | 2002 | Vietnam | tomato | Le | US-1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| PiVT03 | Vn03-416 | 2003 | Vietnam | potato | Le | US-1 |
| PiVT04 | Vn03-590 | 2003 | Vietnam | potato | Le | US-1 |
| P. mirabilis |  |  |  |  |  |  |
| PmMX01 | CBS 136.86 |  | Mexico | NA | CBS |  |
| PmMX02 | CBS 678.85 |  | Mexico | NA | CBS |  |
| PmMX03 | DF 409 |  | Mexico | NA | Fernández Pavia |  |
| PmMX04 | G 11-3 | 1998 | Mexico | NA | Flier/Grünwald/PRI |  |
| PmMX05 | 00M 410 | 2000 | Mexico | NA | Fernández Pavia |  |
| PmMX06 | P 3001 |  | Mexico | NA | Flier/Grünwald/PRI |  |
| PmMX07 | P 3006 |  | Mexico | NA | Flier/Grünwald/PRI |  |
| PmMX08 | P mirabilis DF 07 | 2007 | Mexico | NA | Fernández Pavia |  |
| PmMX09 | P. mirabilis Mich | 2003 | Mexico | NA | Fernández Pavia |  |
| PmMX10 | WF014/PIC99114 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| PmMX11 | WF035/PIC99135 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| P. ipomoeae |  |  |  |  |  |  |
| PoMX01 | 00Ip5 | 2000 | Mexico | NA | Fernández Pavia |  |
| PoMX02 | Ipom1-2 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| PoMX03 | Ipom2-1 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| PoMX04 | Ipom2-4 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| PoMX05 | Ipom3-3 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| PoMX06 | Ipom6 | 1999 | Mexico | NA | Flier/Grünwald/PRI |  |
| PoMX07 | P. ipomoeae | 1999 | Mexico | NA | Fernández Pavia |  |
| $P$. andina |  |  |  |  |  |  |
| PaEC01 | EC_3189 | 1998 | Ecuador | Anarrichomenum | Forbes |  |
| PaEC02 | EC_3399 | 2001 | Ecuador | Anarrichomenum | Cooke |  |
| PaEC03 | EC_3818 | 2004 | Ecuador | Anarrichomenum | Cooke |  |
| PaEC04 | EC_3821 | 2004 | Ecuador | Anarrichomenum | Forbes |  |
| PaEC05 | EC_3780 | 2004 | Ecuador | S. hispidum | Forbes |  |
| PaEC06 | EC_3655 | 2003 | Ecuador | S. hispidum | Forbes |  |


| PaEC07 | EC_3163 | 1998 | Ecuador |  | Anarrichomenum | Forbes |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| PaEC08 | EC_3510 | 2002 | Ecuador |  | S. betaceum | Forbes |
| PaEC09 | EC_3540 | 2002 | Ecuador |  | Anarrichomenum | Forbes |
| PaEC10 | EC_3561 | 2002 | Ecuador |  | S. quitoense | Forbes |
| PaEC11 | EC_3563 | 2002 | Ecuador |  | S. quitoense | Forbes |
| PaEC12 | EC_3678 | 2003 | Ecuador |  | Anarrichomenum | Forbes |
| PaEC13 | EC_3836 | 2004 | Ecuador |  | S. betaceum | Forbes |
| PaEC14 | EC_3860 | 2005 | Ecuador |  | Torva | Forbes |
| PaEC15 | EC_3864 | 2005 | Ecuador |  | Torva | Forbes |
| PaEC16 | EC_3865 | 2005 | Ecuador |  | S. jugandifolium | Forbes |
| PaEC17 | EC_3936 | 2006 | Ecuador |  | S. ochanthum | Forbes |
| PaPE01 | POX 102 | 2003 | Peru |  | S. betaceum | Forbes |
| PaPE02 | POX 103 | 2003 | Peru |  | S. betaceum | Forbes |
| P. phaseoli |  |  |  |  |  |  |
| PpUS01 | CBS 556.88 |  |  |  |  | CBS |
| PpUS02 | P10150 |  | USA | Delaware |  | Coffey |

Isolates were contributed by the authors and the following colleagues: Sampled by W. G. Flier and N. J. Grünwald and curated by Geert Kessel, Plant Research International (PRI), Netherlands; Geert Kessel, Plant Research International (PRI), Netherlands; Silvia Fernández Pavia, Universidad Michoacana de San Nicolás de Hidalgo, Mexico; Michael Coffey, University of California Riverside, USA; Vihn Hong Le and Arne Hermansen, Norwegian Institute for Agricultural and Environmental Research, Norway; Björn Andersson, Swedish University of Agricultural Sciences, Sweden; Renata Lebecka Młochow Research Centre, Poland; Jozsef Bakonyi, Academy of Agricultural Sciences, Hungary.

Table S2. Molecular clock and mutation rates obtained in this study for each locus for (A) Clade 1c and (B) P. infestans datasets. See Table S3 for indices of nucleotide variation at each locus.
A. Clade 1c

| Locus | Clock | Clock Rate | UCLD stdev |
| :--- | :--- | :--- | :--- |
| $\beta$-tubulin | Strict | 0.824 | 0.04 |
| RAS | Log Normal | 1.839 | 2.2 |
| Trp1 | Strict | 1.73 | 0.03 |
| PITG_11126 | Strict | 4.09 | 0.02 |

B. P. infestans

| Locus | Clock | Clock Rate | UCLD stdev |
| :--- | :--- | :--- | :--- |
| $\beta$-tubulin | Strict | 0.54 | 0.02 |
| RAS | Log Normal | 2.25 | 1.94 |
| Trp1 | Strict | 1.73 | 0.012 |
| PITG_11126 | Strict | 3.03 | 0.01 |

Table S3. Nucleotide variation by locus, species, and sampling location. Statistics given are number of individuals ( $\mathrm{N}_{\mathrm{ind}}$ ), number of sequences ( $\mathrm{N}_{\text {seq }}$ ), length of alignment excluding gaps (L), segregating sites (S), number of heterozygous sites (Het), number of haplotypes (Hap), average pairwise nucleotide diversity ( $\pi$ ), Watterson's theta ( $\theta_{\mathrm{w}}$ ), Tajima's D, and Fu and Li's D* and F* (4-7).

| Locus | Species/Popn | $\mathbf{N}_{\text {ind }}$ | $\mathbf{N}_{\text {seq }}$ | L | S | Het | Hap | $\pi$ | $\theta_{\text {w }}$ | $\begin{aligned} & \text { Tajima's } \\ & \text { D } \end{aligned}$ | Fu \& Li's D* | $\begin{aligned} & \hline \text { Fu \& } \\ & \text { Li's F* } \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| PITG_11126 |  |  |  |  |  |  |  |  |  |  |  |  |
|  | $P$. infestans | 119 | 242 | 764 | 13 | $13^{\#}$ | 10 | 0.00286 | 2.144 | 0.04 | 0.79 | 0.61 |
|  | Europe | 22 | 46 | 764 | 7 | $7{ }^{\text {\# }}$ | 5 | 0.00294 | 1.593 | 1.10 | 1.25 | 1.41 |
|  | Mexico | 48 | 96 | 764 | 9 | $9{ }^{\#}$ | 6 | 0.00154 | 1.752 | -0.82 | -0.17 | -0.47 |
|  | S. America | 40 | 82 | 764 | 11 | $11^{\#}$ | 8 | 0.00394 | 2.210 | 0.97 | 0.79 | 1.01 |
|  | United States | 4 | 8 | 779 | 2 | 2 | 2 | 0.00138 | 0.771 | 1.45 | 1.11 | 1.30 |
|  | Africa/Asia | 5 | 10 | 779 | 3 | 3 | 2 | 0.00214 | 1.060 | 2.06* | 1.15 | 1.53 |
|  | P. andina | 19 | 38 | 748 | 16 | $16^{\#}$ | 3 | 0.01040 | 3.808 | 3.39*** | 1.58** | 2.56** |
|  | P. ipomoeae | 7 | 14 | 787 | 2 | 1 | 3 | 0.00052 | 0.629 | -0.96 | -0.45 | -0.66 |
|  | P. mirabilis | 11 | 22 | 778 | 11 | 11 | 3 | 0.00593 | 4.610 | 1.83 | 1.44* | 1.80** |
|  | P. phaseoli | 2 | 4 | 779 | 0 | 0 | 1 | 0 | 0 | NA | NA | NA |
| $\beta$-tubulin |  |  |  |  |  |  |  |  |  |  |  |  |
|  | P. infestans | 118 | 238 | 1590 | 9 | $9^{\#}$ | 8 | 0.00138 | 1.488 | 1.06 | -0.43 | 0.13 |
|  | Europe | 22 | 44 | 1590 | 6 | $6^{\#}$ | 3 | 0.00061 | 1.379 | -0.79 | 1.18 | 0.67 |
|  | Mexico | 48 | 96 | 1590 | 7 | $7{ }^{\#}$ | 3 | 0.00185 | 1.363 | 2.75** | 1.20 | 2.03** |
|  | S. America | 39 | 80 | 1590 | 9 | $9^{\#}$ | 7 | 0.00113 | 1.817 | -0.03 | -0.84 | -0.67 |
|  | United States | 4 | 8 | 1590 | 5 | $5^{\#}$ | 3 | 0.00124 | 1.928 | 0.08 | 0.75 | 0.65 |
|  | Africa/Asia | 5 | 10 | 1590 | 0 | 0 | 1 | 0 | 0 | NA | NA | NA |
|  | P. andina | 19 | 38 | 1590 | 23 | 23 | 2 | 0.00743 | 5.474 | 3.92*** | 1.70** | 2.89** |
|  | P. ipomoeae | 7 | 14 | 1590 | 2 | 2 | 2 | 0.00018 | 0.629 | -1.48 | -1.83 | -1.97 |
|  | P. mirabilis | 11 | 22 | 1590 | 16 | $15^{\#}$ | 6 | 0.00469 | 4.389 | 2.54** | 1.54** | 2.14** |
|  | P. phaseoli | 2 | 4 | 1590 | 0 | 0 | 1 | 0 | 0 | NA | NA | NA |
| Trp1 |  |  |  |  |  |  |  |  |  |  |  |  |
|  | P. infestans | 117 | 234 | 813 | 9 | 7 | 9 | 0.00183 | 1.492 | -0.004 | 0.42 | 0.32 |
|  | Europe | 22 | 44 | 813 | 4 | 3 | 4 | 0.00185 | 0.920 | 1.48 | -0.06 | 0.47 |
|  | Mexico | 48 | 96 | 813 | 6 | 4 | 5 | 0.00144 | 1.168 | -0.20 | 1.12 | 0.81 |
|  | S. America | 38 | 76 | 813 | 6 | 6 | 6 | 0.00211 | 1.224 | 0.95 | 0.22 | 0.54 |
|  | United States | 4 | 8 | 813 | 4 | 4 | 4 | 0.00180 | 1.543 | -0.22 | -0.18 | -0.21 |
|  | Africa/Asia | 5 | 10 | 813 | 3 | 3 | 2 | 0.00205 | 1.060 | 2.06* | 1.15 | 1.53 |
|  | P. andina | 19 | 38 | 813 | 10 | 10 | 3 | 0.00293 | 2.380 | 3.48*** | 1.40* | 2.42** |
|  | P. ipomoeae | 7 | 14 | 812 | 0 | 0 | 1 | 0 | 0 | NA | NA | NA |
|  | P. mirabilis | 11 | 22 | 813 | 1 | 1 | 2 | 0.00011 | 0.274 | -1.16 | -1.57 | -1.68 |
|  | P. phaseoli | 2 | 4 | 813 | 0 | 0 | 1 | 0 | 0 | NA | NA | NA |
| RAS |  |  |  |  |  |  |  |  |  |  |  |  |
|  | $P$. infestans | 117 | 234 | 762 | 15 | $15^{\#}$ | 13 | 0.00364 | 2.487 | 0.290 | 0.311 | 0.364 |
|  | Europe | 21 | 42 | 766 | 10 | 10 | 6 | 0.00569 | 2.324 | 2.585* | 1.40 | 2.096** |
|  | Mexico | 47 | 94 | 766 | 11 | $11^{\#}$ | 8 | 0.00164 | 2.150 | -1.09 | -2.51* | -2.39* |
|  | S. America | 40 | 80 | 762 | 10 | 10 | 5 | 0.00377 | 2.019 | 1.12 | 1.38 | 1.53 |
|  | United States | 4 | 8 | 766 | 11 | 11 | 4 | 0.00643 | 4.242 | 0.808 | 1.52** | 1.50 |
|  | Africa/Asia | 5 | 10 | 766 | 1 | 1 | 2 | 0.00205 | 1.060 | 2.06* | 1.15 | 1.53 |
|  | P. andina | 17 | 34 | 765 | 23 | $23^{\#}$ | 4 | 0.01433 | 5.625 | 3.28*** | 1.39 | 2.37** |
|  | P. ipomoeae | 7 | 14 | 768 | 3 | 0 | 2 | 0.00103 | 0.943 | -0.49 | 1.07 | 0.76 |
|  | P. mirabilis | 10 | 20 | 766 | 6 | $6^{\#}$ | 3 | 0.00091 | 1.973 | -2.13* | $-3.08 * *$ | -3.25** |
|  | P. phaseoli | 1 | 2 | 764 | 0 | 0 | 1 | 0 | 0 | NA | NA | NA |

\#Also heterozygous for one or more indel.

* $\mathrm{P}<0.05$
** $\mathrm{P}<0.02$
*** $\mathrm{P}<0.001$

Table S4. Results from testing relationships among Toluca population, US1 and Andean lineages as illustrated in Figure S10.

| Andean lineage | Scenario | Admixed population | Probability | 95\% CI |
| :---: | :---: | :---: | :---: | :---: |
| PE3 | 1 | - | 0.0040 | [0.0028,0.0052] |
|  | 2 | - | 0.0071 | [0.0058,0.0084] |
|  | 3 | - | 0.0066 | [0.0055,0.0077] |
|  | 4 | PE3 | 0.0014 | [0.0010,0.0017] |
|  | 5 | Toluca | 0.0062 | [0.0051,0.0073] |
|  | 6 | US1 | 0.0009 | [0.0008,0.0011] |
|  | 7 | PE3 | 0.6709 | [0.6478,0.6939] |
|  | 8 | PE3 | 0.1094 | [0.0994,0.1194] |
|  | 9 | US1 | 0.0023 | [0.0011,0.0034] |
|  | 10 | US1 | 0.0052 | [0.0034,0.0070] |
|  | 11 | Toluca | 0.0020 | [0.0009,0.0032] |
|  | 12 | Toluca | 0.1302 | [0.1093,0.1511] |
|  | 13 | PE3 | 0.0474 | [0.0410,0.0537] |
|  | 14 | US1 | 0.0011 | [0.0004,0.0017] |
|  | 15 | Toluca | 0.0053 | [0.0034,0.0073] |
| PE7 | 1 | - | 0.0089 | [0.0055,0.0124] |
|  | 2 | - | 0.0327 | [0.0265,0.0389] |
|  | 3 | - | 0.0141 | [0.0107,0.0176] |
|  | 4 | PE7 | 0.0038 | [0.0025, 0.0051$]$ |
|  | 5 | Toluca | 0.0093 | [0.0073,0.0112] |
|  | 6 | US1 | 0.0191 | [0.0148,0.0234] |
|  | 7 | PE7 | 0.3656 | [0.3393,0.3919] |
|  | 8 | PE7 | 0.2893 | [0.2656,0.3131] |
|  | 9 | US1 | 0.0016 | [0.0003, 0.0030$]$ |
|  | 10 | US1 | 0.0248 | [0.0145,0.0350] |
|  | 11 | Toluca | 0.0121 | [0.0032,0.0211] |
|  | 12 | Toluca | 0.0880 | [0.0673,0.1087] |
|  | 13 | PE7 | 0.1242 | [0.1069,0.1416] |
|  | 14 | US1 | 0.0012 | [0.0003, 0.0022 ] |
|  | 15 | Toluca | 0.0050 | [0.0021,0.0079] |
| EC1 | 1 | - | 0.2524 | [0.2335,0.2713] |
|  | 2 | - | 0.0293 | [0.0260,0.0326] |
|  | 3 | - | 0.0575 | [0.0519,0.0631] |
|  | 4 | EC1 | 0.0908 | [0.0830,0.0987] |
|  | 5 | Toluca | 0.0843 | [0.0773,0.0913] |
|  | 6 | US1 | 0.0216 | [0.0192,0.0239] |
|  | 7 | EC1 | 0.0320 | [0.0276,0.0364] |
|  | 8 | EC1 | 0.3060 | [0.2811,0.3309] |
|  | 9 | US1 | 0.0071 | [0.0053,0.0088] |
|  | 10 | US1 | 0.0234 | [0.0188,0.0280] |
|  | 11 | Toluca | 0.0177 | [0.0144,0.0210] |
|  | 12 | Toluca | 0.0140 | [0.0116,0.0163] |
|  | 13 | EC1 | 0.0088 | [0.0069,0.0106] |
|  | 14 | US1 | 0.0517 | [0.0420,0.0614] |
|  | 15 | Toluca | 0.0035 | [0.0026,0.0043] |

Table S5. Nucleotide substitution model for each locus as inferred from jModelTest and ModelGenerator. The appropriate most similar model available in BEAST was used for each analysis.
A. Clade 1c

| Locus | jModeITest | ModelGenerator | Model Used |
| :--- | :--- | :--- | :--- |
| $\beta$-tubulin | HKY | HKY | HKY |
| RAS | JC | JC | JC |
| Trp1 | K80 | HKY | HKY |
| PITG_11126 | HKY | HKY | HKY |

B. P. infestans

| Locus | jModeITest | ModelGenerator | Model Used |
| :--- | :--- | :--- | :--- |
| $\beta$-tubulin | HKY | HKY | HKY |
| RAS | F81 | JC | JC |
| Trp1 | HKY | HKY | HKY |
| PITG_11126 | HKY | HKY | HKY |

Table S6. Settings used for DIYABC analyses. All runs used the same summary statistics: within population statistics were number of segregating sites, mean of pairwise differences, variance of pairwise differences, and number of private segregating sites; between population statistics were number of segregating sites, mean of pairwise differences, and $\mathrm{F}_{\text {ST }}$. Posterior probabilities of scenarios were calculated using the closest $1 \%$ of simulated datasets using logistic regression.
A. Prior distributions for scenarios in Figure S9.

| Parameter | Shape | Min.-Max. | Increment |
| :---: | :---: | :---: | :---: |
| Population size |  |  |  |
| EC-1 | Uniform | 1-200000 | 1 |
| PE-3 | Uniform | 1-200000 | 1 |
| PE-7 | Uniform | 1-200000 | 1 |
| Ancestor of two lineages | Uniform | 1-500000 | 1 |
| Ancestor of three lineages | Uniform | 1-1000000 | 1 |
|  |  |  |  |
| Time since divergence ${ }^{1}$ |  |  |  |
| t1: two lineages | Uniform | 1-300000 | 1 |
| t2: all three lineages | Uniform | 1-500000 | 1 |
|  |  |  |  |
| Nucleotide sequence evolution ${ }^{2}$ |  |  |  |
| Mean mutation rate | Uniform | $\begin{aligned} & 1.00 \times 10^{-10}- \\ & 1.00 \times 10^{-8} \end{aligned}$ |  |
| Gamma distribution | Uniform | $\begin{aligned} & 1.00 \times 10^{-11}- \\ & 1.00 \times 10^{-7} \end{aligned}$ | 2.00 |

${ }^{1}$ An additional condition was put on the prior distributions such that $\mathrm{t} 2>\mathrm{t} 1$.
${ }^{2}$ The Kimura 2-parameter nucleotide substitution model was used with invariant sites=90 and gamma rate variation parameter $\alpha=0.050$.
B. Prior distributions for scenarios in Figure S10.

| Parameter | Shape | Min.-Max. | Increment |
| :---: | :---: | :---: | :---: |
| Population size |  |  |  |
| Toluca | Uniform | 1-1000000 | 1 |
| EC-1 | Uniform | 1-300000 | 1 |
| PE-3 | Uniform | 1-200000 | 1 |
| PE-7 | Uniform | 1-200000 | 1 |
| US-1 | Uniform | 1-500000 | 1 |
| Unsampled population | Uniform | 1-2000000 | 1 |
| Ancestor of two lineages | Uniform | 1-2000000 | 1 |
|  |  |  |  |
| Time since divergence ${ }^{3}$ |  |  |  |
| t1: two populations (scenarios 1-3) | Uniform | 1-200000 | 1 |
| t2: two or three populations | Uniform | 1-500000 | 1 |
| t3: sampled \& unsampled populations (scenarios 7-15) | Uniform | 1-10000000 | 1 |
|  |  |  |  |
| Admixture events |  |  |  |
| Proportion from parent population | Uniform | 0.001-0.999 | 0.001 |
| ta1: timing since admixture event (scenarios 4-12) | Uniform | 1-300000 | 1 |
| ta2: timing since admixture event (scenarios 13-15) | Uniform | 1-1000000 | 1 |


|  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- |
| Nucleotide sequence evolution ${ }^{4}$ |  |  |  |  |
|  | Mean mutation rate | Uniform | $1.00 \times 10^{-10}-$ |  |
|  | Gamma distribution | Uniform | $1.00 \times 10^{-8}$ |  |
|  |  | $1.00 \times 10^{-11}-$ | 2.00 |  |

${ }^{3}$ Additional conditions were put on the prior distributions to force the timing of events into the tree structure shown in Figure S9, including placing admixture events before or after population splits and ordering of the population splits such that $\mathrm{t} 2>\mathrm{t} 1, \mathrm{t} 2>\mathrm{ta} 1, \mathrm{t} 3>\mathrm{ta} 1, \mathrm{ta} 2>\mathrm{t} 2$, and $\mathrm{t} 3>\mathrm{ta} 2$.
${ }^{4}$ The Kimura 2-parameter nucleotide substitution model was used with invariant sites=90 and gamma rate variation parameter $\alpha=0.050$.
C. Prior distributions for scenarios in Figure 5.

| Parameter | Shape | Min.-Max. | Increment |
| :---: | :---: | :---: | :---: |
| Population size |  |  |  |
| Toluca | Uniform | 1-1000000 | 1 |
| EC-1 | Uniform | 1-400000 | 1 |
| PE-3 | Uniform | 1-200000 | 1 |
| US-1 | Uniform | 1-400000 | 1 |
| Unsampled population | Uniform | 1-1000000 | 1 |
| Ancestor to Toluca \& EC-1 | Uniform | 10-1000000 | 1 |
| Ancestor to Toluca \& US-1 | Uniform | 10-1000000 | 1 |
|  |  |  |  |
| Time since divergence ${ }^{5}$ |  |  |  |
| t1: Toluca-EC-1 | Uniform | 1-200000 | 1 |
| t2: Toluca-US-1 | Uniform | 1-600000 | 1 |
| t3: All populations | Uniform | 1-1000000 | 1 |
|  |  |  |  |
| Admixture events |  |  |  |
| Proportion from parent population | Uniform | 0.001-0.999 | 0.001 |
| Timing since admixture event | Uniform | 1-200000 | 1 |
|  |  |  |  |
| Nucleotide sequence evolution ${ }^{6}$ |  |  |  |
| - ${ }^{\text {Mean mutation rate }}$ | Uniform | $\begin{aligned} & 1.00 \times 10^{-10}- \\ & 1.00 \times 10^{-8} \end{aligned}$ |  |
| Gamma distribution | Uniform | $\begin{aligned} & 1.00 \times 10^{-11}- \\ & 1.00 \times 10^{-7} \end{aligned}$ | 2.00 |

${ }^{5}$ Additional conditions were put on the prior distributions to force the timing of events into the tree structure shown in Figure 5, including placing admixture events before or after population splits and ordering of the population splits such that $\mathrm{t} 3>\mathrm{t} 1, \mathrm{t} 3>\mathrm{t} 2$.
${ }^{6}$ The Kimura 2-parameter nucleotide substitution model was used with invariant sites=90 and gamma rate variation parameter $\alpha=0.050$.

Table S7. Inferred root subpopulation using three starting seeds for (A) the mitochondrial P3 and P4 regions using only isolates from Mexico and the Andes, and (B) the nuclear RAS locus, using the data from Gómez-Alpizar et al. (1).
A. P3 and P4

| Theta | Migration | Seed 1 |  | Seed 2 |  | Seed 3 |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  | Root <br> location | Prob. | Root <br> location | Prob. | Root <br> location | Prob. |
| 1.8 | $0.3,0.3$ | Mexico | 0.505 | Mexico | 0.500 | Andes | 0.501 |
|  | $1.0,1.0$ | Andes | 0.501 | Andes | 0.505 | Mexico | 0.508 |
|  | $5.0,5.0$ | Mexico | 0.559 | Mexico | 0.556 | Mexico | 0.510 |
|  | $10.0,10.0$ | Mexico | 0.587 | Mexico | 0.577 | Andes | 0.669 |
| 2.0 | $1.0,1.0$ | Andes | 0.504 | Andes | 0.501 | Mexico | 0.503 |
|  | $5.0,5.0$ | Andes | 0.513 | Andes | 0.531 | Andes | 0.562 |
|  | $10.0,10.0$ | Andes | 0.689 | Mexico | 0.727 | Andes | 0.549 |

B. RAS

| Theta | Migration | Seed 1 |  | Seed 2 | Seed 3 |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  | Root <br> location | Prob. | Root <br> location | Prob. | Root <br> location | Prob. |  |
| 2.0 | $0.5,0.5$ | SA | 0.515 | NSA | 0.537 | SA | 0.535 |
|  | $5.0,5.0$ | SA | 0.514 | SA | 0.582 | SA | 0.847 |
|  | $10.0,10.0$ | NSA | 0.889 | NSA | 0.875 | SA | 0.686 |
|  | $5.0,10.0$ | SA | 0.916 | SA | 0.949 | SA | 0.985 |
|  | $10.0,5.0$ | NSA | 0.679 | NSA | 0.902 | SA | 0.935 |
|  | $4.3,14.6 *$ | SA | 0.965 | SA | 0.992 | SA | 0.970 |
|  | $14.6,4.3$ | NSA | 0.939 | NSA | 0.996 | NSA | 0.979 |

[^1]Table S8. Root population inferred using RAS sequences from Mexico and Andean samples from this study. Migration rates were symmetric for all runs.

|  |  | Seed 1 |  | Seed 2 |  | Seed 3 |  | Seed 4 |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Simulations | $\mathbf{1 \times 1 0}^{\mathbf{6}}$ |  | $\mathbf{1}^{\times 10}{ }^{\mathbf{6}}$ |  | $\mathbf{1 \times \mathbf { 1 0 } ^ { 7 }}$ |  | $\mathbf{1 0 1 0}^{7}$ |  |  |
| $\boldsymbol{\theta}$ | M | Root | Prob. | Root | Prob. | Root | Prob. | Root | Prob. |
| 1.5 | 0.5 | Mexico | 0.541 | Mexico | 0.584 | Andes | 0.510 | Mexico | 0.521 |
|  | 5.0 | Mexico | 0.638 | Mexico | 0.703 | Mexico | 0.564 | Mexico | 0.583 |
|  | 10.0 | Andes | 0.723 | Mexico | 0.975 | Mexico | 0.612 | Andes | 0.794 |
| 2.0 | 0.5 | Andes | 0.676 | Andes | 0.638 | Mexico | 0.513 | Mexico | 0.514 |
|  | 5.0 | Mexico | 0.883 | Andes | 0.614 | Mexico | 0.590 | Andes | 0.794 |
|  | 10.0 | Mexico | 0.714 | Andes | 0.688 | Mexico | 0.663 | Mexico | 0.939 |

## Supporting Figures

Figure S1. Structure plots for K from 2 to 10 for the Andes (with and without admixture) and Mexico samples of $P$. infestans.

Figure S2. Delta K values obtained from Structure Harvester for (A) Mexico and (B) Andes (with admixture) samples of $P$. infestans. Note the highest delta K value corresponds to $\mathrm{K}=4$ for Mexico and $\mathrm{K}=2$ for the Andes.

Figure S3. Root state posterior probabilities for each location for (A) Clade 1c and (B) $P$. infestans. Independent analysis of each locus produced high probabilities for the root of both Clade 1c and $P$. infestans in Mexico (green bar).

Figure S4. Maximum clade credibility genealogy for the $\boldsymbol{\beta}$-tubulin locus. Colors of branches indicate the most probable geographic origin of each lineage.

Figure S5. Maximum clade credibility genealogy for the PITG_11126 locus. Colors of branches indicate the most probable geographic origin of each lineage.

Figure S6. Maximum clade credibility genealogy for the RAS locus. Colors of branches indicate the most probable geographic origin of each lineage.

Figure S7. Maximum clade credibility genealogy for the Trp1 locus. Colors of branches indicate the most probable geographic origin of each lineage.

Figure S8. Maximum clade credibility phylogeny of Phytophthora Clade 1c from all four loci. Colors of branches indicate the most probable geographic origin of each lineage and taxon colors represent species (purple: P. phaseoli; blue: P. ipomoeae; green: P. mirabilis; red: P. andina; black: $P$. infestans).

Figure S9. Scenarios used to test evolutionary relationships among Andes lineages EC-1, PE-3, and PE-7 using DIYABC. Present day populations are at the base of the tree schematic. Ancestral relationships among these populations are represented by lines intersecting in the past, with the vertex of the schematic representing the most recent common ancestor of all samples. Horizontal lines indicate admixture events between the ancestral populations connected by the horizontal line. Change in line thickness indicates a potential change in population size, such that all branches in scenarios D, E, and F had independently estimated population sizes. The scenarios in which PE-3 and PE-7 diverged more recently from each other than from EC-1 produced high posterior probabilities.

Figure S10. Scenarios used to test evolutionary relationships of EC-1, PE-3, and PE-7 lineages to US-1 in the Andes and to the Toluca, Mexico population. The 15 scenarios were compared against each other, using three independent sets of scenarios with EC-1, PE-3, and PE-7, in turn, substituted for population ' X '. Present day populations are at the base of the tree schematic. Ancestral relationships among these populations are represented by lines intersecting in the past, with the vertex of the schematic representing the most recent common ancestor of all samples.

Horizontal lines indicate admixture events between the ancestral populations connected by the horizontal line. Potential changes in population size over time are indicated by changes in line thickness, but line thickness is not proportional to population size. The dashed line represents an unsampled population that has contributed to the genetic variation observed in sampled populations.
A. Andes (No admixture model)

Delta K $=69.862747$


Delta K = 0.070747


Delta K $=0.718652$


Delta K = 4.446202


Delta K = 0.830527


Delta K = 3.058297


Delta K $=0.647233$


Delta K $=0.556458$

B. Andes (Admixture model)

Delta K $=240.274178$


Delta K = 0.070147


Delta K $=0.636815$


Delta K $=0.995806$


Delta K = 0.701862


Delta K = 14.273424


Delta K = 10.087991


Delta K = 0.637663

C. Mexico (Admixture model)

Delta K $=0.253093$


Delta K = 0.439997


Delta K $=3.887928$


Delta K $=2.839755$


Delta $K=1.360291$


Delta K $=0.272208$


Delta K $=0.746226$


Delta K = 1.004472


Delta K $=1.687174$





## A) Clade 1c

B) P. infestans


Figure S3. Root state posterior probability values for each location after 300 millions MCMC generations by locus for (A) Clade 1c species and (B) P. infestans. The posterior probability for a Mexico root (green bar) is higher than for any of the other countries for each locus independently and both datasets.

Figure S4. Maximum clade credibility genealogy for the $\boldsymbol{\beta}$-tubulin locus. Colors of branches indicate the most probable geographic origin of each lineage.


Figure S5. Maximum clade credibility genealogy for the PITG_11126 locus. Colors of branches indicate the most probable geographic origin of each lineage.


Figure S6. Maximum clade credibility genealogy for the RAS locus. Colors of branches indicate the most probable geographic origin of each lineage.


Figure S7. Maximum clade credibility genealogy for the Trp1 locus. Colors of branches indicate the most probable geographic origin of each lineage.

4.0E-5 substitutions per site


B.



E.
73.5 [71.1, 75.8]




[^0]:    Author contributions: E.M.G., D.E.L.C., S.R., G.A.F., and N.J.G. designed research; E.M.G., J.F.T., D.E.L.C., S.R., W.E.F., G.A.F., V.J.F., M.C., and N.J.G. performed research; D.E.L.C., S.R., W.E.F., G.A.F., and N.J.G. contributed new reagents/analytic tools; E.M.G., J.F.T., D.E.L.C., V.J.F., M.C., and N.J.G. analyzed data; and E.M.G., J.F.T., D.E.L.C., S.R., W.E.F., G.A.F., M.C., and N.J.G. wrote the paper.

    The authors declare no conflict of interest.
    This article is a PNAS Direct Submission.
    Data deposition: The sequences reported in this paper have been deposited in the GenBank database (accession nos. KF979339-KF980878).
    ${ }^{1}$ To whom correspondence should be addressed. E-mail: grunwaln@science.oregonstate. edu.
    This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10. 1073/pnas. 1401884111/-/DCSupplemental.

[^1]:    * Migration rates used by Gómez-Alpizar et al. (1)

