Global climate change increases risk of crop yield losses and food insecurity in the tropical Andes

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Abstract
One of the greatest current challenges to human society is ensuring adequate food production and security for a rapidly growing population under changing climatic conditions. Climate change, and specifically rising temperatures, will alter the suitability of areas for specific crops and cultivation systems. In order to maintain yields, farmers may be forced to change cultivation practices, the timing of cultivation, or even the type of crops grown. Alternatively, farmers can change the location where crops are cultivated (e.g., to higher elevations) to track suitable climates (in which case the plants will have to grow in different soils), as cultivated plants will otherwise have to tolerate warmer temperatures and possibly face novel enemies. We simulated these two last possible scenarios (for temperature increases of 1.3°C and 2.6°C) in the Peruvian Andes through a field experiment in which several traditionally grown varieties of potato and maize were planted at different elevations (and thus temperatures) using either the local soil or soil translocated from higher elevations. Maize production declined by 21%–29% in response to new soil conditions. The production of maize and potatoes declined by >87% when plants were grown under warmer temperatures, mainly as a result of the greater incidence of novel pests. Crop quality and value also declined under simulated migration and warming scenarios. We estimated that local farmers may experience severe economic losses of up to 2,300 US$ ha\(^{-1}\) yr\(^{-1}\). These findings reveal that climate change is a real and imminent threat to agriculture and that there is a pressing need to develop effective management strategies to reduce yield losses and prevent food insecurity. Importantly, such strategies should take into account the influences of non-climatic and/or biotic factors (e.g., novel pests) on plant development.

KEYWORDS
agricultural production, future climatic scenarios, global warming, herbivores, maize, novel interactions, Peru, potato, small-scale agriculture

1 | INTRODUCTION

There is broad consensus that climate change represents a major threat to agricultural production and to food security (Alexandratos & Bruinsma, 2012; Challinor et al., 2014; Godfray et al., 2010; IPCC, 2014; Lobell et al., 2008; Wheeler & von Braun, 2013). Empirical data indicate that the productivity of many crops worldwide has already declined markedly as a result of rising temperatures. In the case of maize, for example, global production has declined by 3.8%–12.5% over the past three decades (Lobell & Field, 2007; Lobell, Schlenker, & Costa-Roberts, 2011). The negative effects of climate change on crop production are likely to be even more severe in the future as global temperatures are predicted to increase from 2.6 to 4°C before the end of this century (IPCC, 2014; Rogelj et al., 2016).
Current estimates indicate that an increase of 1°C can cause a 10%–20% decrease in the global production of maize (Challinor et al., 2014; Lobell et al., 2011; Rose, Osborne, Greatrex, & Wheeler, 2016); likewise, an increase of 1.6–3°C could reduce global potato yields by 18%–32% (Hijmans, 2003). Decreases in the production of these and other staple crops represent a major challenge to food security, especially in the face of rapid population growth (Alexandratos & Bruinsma, 2012).

In addition to temperature, precipitation and CO2 concentrations are also projected to change in the future (IPCC, 2014). Many studies have evaluated the influence of these three factors, individually or in combination, on plant development under projected future climatic conditions (reviewed in Challinor et al., 2014; Kimball, 2016). However, most of these previous studies were based on models or experiments performed under controlled conditions and, therefore, they could not account for the potential influence of non-climatic or biotic factors on plant development. This is one of the reasons why the effectiveness of many potential adaptation and mitigation strategies proposed to reduce the negative impacts of climate change on food production are considered highly uncertain (Howden, Tubiello, & Meinke, 2007; Lobell, 2014).

As already evident in some parts of the world, climate change and the consequent changes in the suitability of areas for certain crops and/or cultivation systems (Machovina & Feeley 2013) can force farmers to change the timing of cultivation (Hijmans, 2003; Howden et al., 2007; Rose et al., 2016), or the type of crop grown (Meng et al., 2014). Alternatively, farmers may maintain their current crops and cultivations system but change locations (e.g., to higher, cooler elevations; Skarbe & VanderMolen, 2016). In the latter case, crops may be in the proper climate but they will potentially have to grow in different soil conditions that can affect growth and yield (Barker & Pilbeam, 2015).

Here, we evaluated the potential impact of global warming on maize and potato production in the Peruvian Andes. We contrasted two possible scenarios: one in which farmers move their crops to cooler, higher elevation areas (with new soils) and the other in which farmers are unwilling or unable to move production into new land, and in which case crops will have to tolerate the new climatic conditions as well as potential concomitant increases in the incidence of pests and pathogens (Bebber, Holmes, & Gurr, 2014; Bebber, Ramotowski, & Gurr, 2013; Crespo-Pérez, René, Chuine, Rebaudo, & Dangles, 2015; Dangles, Carpio, Barragan, Zeddam, & Silvain, 2008; Dangles, Herrera, Mazoyer, & Silvain, 2013). More specifically, we performed a field experiment in which several traditional varieties of potato (Solanaceae: Solanum tuberosum) and maize (Poaceae: Zea mays) were planted at different elevations (and thus temperatures) using either the local soil or soil translocated from higher elevations (Figures 1 and 2). The experiment was designed to simulate future climatic scenarios for the tropical Andes where temperatures are expected to rise by approximately 0.3°C per decade (Vuille & Bradley, 2000). We simulated conditions expected to be found in the study area (southern Peru) within the next ~35–70 years under increases of 1.3°C and 2.6°C in mean temperatures, considering that climate change continues as currently projected. We chose to study maize and potato because these are staple foods that provide basic nutrition to millions of people in the world, especially in developing countries, and the demand for which is rapidly increasing (Alexandratos & Bruinsma, 2012; FAOSTAT, 2014; Hijmans, 2003; Shiferaw, Prasanna, Hellin, & Bänziger, 2011). In addition, maize is widely used for animal feed and as raw material for industrial products, including biofuels (Alexandratos & Bruinsma, 2012; Shiferaw et al., 2011). The tropical Andes is one of the main regions for the production of potato and maize (FAOSTAT, 2014; Hijmans, 2003) and in this region most producers are small-scale farmers (Halloy, Ortega, Yager, & Seimon, 2005).

For maize, we simulated a "migration" scenario in which plants are grown in their current climate but on soils from higher elevations (i.e., as would occur under an upward shift of crop cultivation areas), and a "tolerance" scenario in which plants experience warmer temperatures (+1.3°C and +2.6°C) while remaining on the current soil (Figure 1). For potatoes, we simulated future "tolerance" scenarios in which plants experience warmer temperatures (+1.3°C and +2.6°C) while remaining on the current soil (Figure 1). We did not simulate an upward shift in the cultivation of potatoes because the varieties we studied are already being cultivated at or near the tops of the local mountains. In other words, it will be impossible for farmers in this region to shift the production of potatoes, or other similar high-elevation crops, to cooler elevations in the future.

Through these experiments, we addressed the following questions: (1) considering an eventual upward migration of crop production areas, what are the effects of soils from higher elevations on maize survivorship, production, and yield? (2) What are the effects of future, warmer conditions on potato and maize development and the susceptibility of these crops to pests and pathogens? (3) What are the estimated economic losses on maize and potato production associated with the projected climatic changes?

2 | MATERIALS AND METHODS

2.1 | Study area and species

The study was conducted in the remote Andean region of Huamboque, near the town of Chincheros, in southern Peru (between coordinates 13°21′–13°24′S and 73°35′–73°36′W) and at an elevation varying from ~2,100 to 4,100 m above sea level (m asl; Fig. S1). The dominant soil in this region is classified as Lithosol (FAO, 1971). The average annual rainfall in our study region varies from 905 mm at 2,750 m asl to 856 mm at 4,150 m asl, with most of the rain falling from October to April (Condom, Rau, & Espinoza, 2011). Mean daily temperatures at our study sites range from 19.3°C (+1.2) at 2,135 m asl to 7.6°C (+0.8) at 3,812 m asl and decrease with an adiabatic lapse rate of 7.4°C (+0.3) for every 1 km of elevation (Fig. S2). This climatic variability allows the local farmers (~300 families) to cultivate dozens of varieties of agricultural species, thus maintaining an important source of germplasm diversity. In our study area, about 30 varieties of potato and 15 varieties of maize are grown at different elevations. Farmers produce the majority of these...
crop varieties for their own consumption. Only eight varieties of potato and four of maize are produced for commercial purposes. From the commercial varieties, we chose three native potatoes (locally known as *asunapu runtun*, *ka* Akas, and *peruanita*; hereafter referred to as var.1, var.2, and var.3, respectively) and two maize varieties (locally known as *almidón* and *morocho amarillo*; hereafter referred to as white and yellow varieties, respectively) to use in our experimental studies. These varieties were chosen because they are commonly cultivated by most farmers.

The local farmers typically cultivate maize or potato in small (~4 ha) patches of land. Most farmers own several patches of land (each of them usually located at a different elevation), and in each year they cultivate a different patch. In this way, the two maize varieties are cultivated anywhere from 2,500 to 3,400 m asl (i.e., at current mean temperatures ranging from 18.1 to 11.3°C), whereas the potato varieties are grown anywhere from 3,700 m to the top of the mountain (located at ~4,100 m of elevation; <8.6°C; Figure 1). Maize and potato are cultivated without agricultural machinery, with limited use of chemicals, and generally using only natural fertilizers (e.g., manure). Such small-scale and low input agriculture is typical for most of the Andean regions of Peru (Halloy et al., 2005). During the design, implementation, and maintenance of our experiment, we tried to follow as close as possible the agronomic practices employed by local farmers.

### 2.2 Experimental setup

Our experiment was designed to simulate two possible future scenarios: (1) one in which the varieties will be cultivated at higher elevations [i.e., farmers “migrate” upwards; cf. (Skarbø & VanderMolen, 2016)], in which case plants will face temperatures similar to those that they are currently experiencing but will have to grow in a different soil, and (2) one in which the varieties remain being cultivated at the same range of elevations as today, in which case soil conditions will not change but plants will have to “tolerate” higher temperatures (Figure 1). For the first scenario, we collected soil from 3,590 and 3,780 m asl (i.e., 190 and 380 m above the upper altitudinal limit of cultivation of the two maize varieties), and then transported this soil to 2,900 m asl (Figure 1). Thus, maize seeds were planted at 2,900 m in the local soil (hereafter control plants), or in soil collected at 3,590 or at 3,780 m of elevation (hereafter plants from the “migration” treatment; Figures 1 and 2). Chemical and physical analyses of these soils (*n* = 6 soil samples per elevation) were performed following the standard procedures adopted by the Brazilian Agricultural Research Corporation (EMBRAPA Solos, 2011). The soil was transported on horseback (as access by roads was nonexistent) and in total over 4 tons of soil were moved into our experimental plots (Fig. S3a). Our intention was to test the influence of higher elevation soils on plant performance. This experiment was performed only with maize as the three varieties of potato we studied are already being cultivated up to the mountaintop.

To simulate the second scenario, we intended to compare the performance of maize and potato plants growing at temperatures 1.3°C and 2.6°C higher than where they are being currently cultivated; i.e., the average temperature at 2,500 m asl for maize and at 3,700 m asl for potato. For this, we planted and grew the two

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**FIGURE 1** Schematic representation of the experiment. The experiment evaluated: (1) the performance of three varieties of potato and two varieties of maize under temperatures 1.3°C and 2.6°C higher than the highest temperatures currently experienced by these varieties, and (2) the performance of two maize varieties growing in soils collected from higher elevations where current temperatures are 1.3°C and 2.6°C lower than the lowest temperature currently experienced by these varieties. The maize varieties are currently cultivated at elevations between 2,500 and 3,400 m asl; the potato varieties are cultivated between 3,700 and 4,100 m (current areas of cultivation depicted in green). In the study area, every 190 m of elevation corresponds to a difference of 1.3°C. Semi-circles with different colors represent soil from different origins (elevations). Black and gray arrows represent experimental treatments to simulate an upward shift (“migration”) of cultivation areas in order to avoid elevated temperatures. Yellow and red arrows represent experimental treatments to simulate the tolerance scenario in which plants experience warmer temperatures while remaining on the current area of cultivation. The green arrows represent control treatments [Colour figure can be viewed at wileyonlinelibrary.com]
varieties of maize at 2,310 and at 2,120 m asl with soil collected at 2,900 m asl, and the three varieties of potato at 3,590 and at 3,780 m elevation with soil brought from 3,900 m of elevation (hereafter plants from the “tolerance” treatment; Figures 1 and 2)—in our study area, each 190 m of elevation corresponds to a 1.3°C change in temperature (Fig. S2). These treatments allowed us to compare the performance of plants growing at higher temperatures with those growing at the “average current temperature.” As average current temperature, we denote the mean temperature along the altitudes 2,500–3,400 m for maize and 3,700–4,100 m for potato. Given the logistical difficulties of establishing control plots across this entire area, we set our control plots at approximately the middle of the current range of cultivation for each crop. As such, we set our control plots at ~2,900 and 3,900 m asl for maize and potato, respectively.

Seeds from the two maize varieties were obtained from three different farmers, and they originated from plants that grew during the previous year at elevations ranging from ~2,600 to 3,300 m asl. Similarly, “seed tubers” (20–30 g each) from the different potato varieties were obtained from different farmers and from plants that grew during the previous year at elevations ranging from ~3,700 to 4,000 m asl.

Plants were grown following local farming practices. The soil of our study plots (n = 8 plots) was plowed to a depth of ~25 cm before planting. Plots located in the same elevation were located ≥50 m apart. Each maize variety was planted in a different plot to prevent cross-pollination between varieties. The different potato varieties were planted in the same plot (Figure 2). Therefore, in each elevation, we established a total of 16 “maize plots” (8 for each variety) and 8 “potato plots”. For maize plots located at 2,310 or 2,120 m asl, six seeds were planted in the soil brought from 2,900 m elevation, whereas for those located at 2,900 m asl, seeds were planted either in the local soil, or in soil brought from 3,590 or from 3,780 m asl (5–6 seeds in each soil; Figure 2). Seeds were planted in soil pits of ~25 cm of diameter and 25 cm deep (that were subsequently filled with local soil or with soil from higher elevations). Five to six soil pits were set at 40 cm distances along “planting rows” keeping a space of 80 cm between any two rows (i.e., 3 plants/m²; Figure 2).
In each potato plot, 21 soil pits (~35 cm of diameter and 25 cm deep), arranged in a 1.6 × 4 m grid, were excavated and then filled with the same soil (in the case of plots located 3,900 m asl), or with soil brought from 3,900 m of elevation (in the case of plots located 3,510 or 3,320 m asl; Figure 2). Seven "seed tubers" from each variety were planted within each plot (3 plants/m²).

When plants attained a height of 10–15 cm, we piled up ~1 kg (dry weight) of soil (from different elevations, depending on the treatment) around the base of each maize plant and ~2 kg of soil around each potato plant (Figure 2). This same procedure was repeated when plants were about 30-35 cm in height. This technique, known as hilling, is commonly employed by the local farmers to facilitate the development of adventitious roots and stolons. No fertilizers were added to our experimental plots. Similarly, no pesticides were applied onto the experimental plants (of maize or potato).

We performed weed control by removing weeds manually from the study plots at 2-month intervals in accord with local practice.

### 2.3 Data collection

We recorded plant survival and the incidence of plant pathogens and herbivores at the following phases of development: (1) emergence (~15 days after planting for maize, and 35–40 days for potato), (2) juvenile phase (~50 days after planting for maize and potato), and (3) reproductive/tuberization phase (~110 and 134 days after planting for both potato and maize, respectively). Observations on herbivore or pathogen attacks were also performed during the weed control events. Identification of the potential agents of damage was performed by a local trained expert on potato/maize pests and pathogens. Identifications were based on photographs and descriptions of the structures damaged, and whenever possible, of the agent of damage.

Harvesting of the potato tubers and of the maize spikes was performed during plant senescence (~160 days after planting). Potato tubers were first sorted according to their sizes as: (1) large, (2) medium, (3) small, or (4) non-commercial (including rotten tubers and tubers of very small size), using the same criteria adopted by local producers (Table S1). All commercial tubers were cleaned and then weighed. In order to determine maize production, we first recorded the total number of intact grains (i.e., excluding those that have been damaged by pathogen or herbicides) produced per plant. Following the procedure adopted by local producers, undamaged grains were left to sun dry for 10 days and then weighed. After a period of 10 days, grains have ~75% of humidity and can be stored.

Considering the economic importance of maize and potato, we estimated the economic value of production based on commodity prices at the place of production as of December 2015. The estimated values were derived considering that local farmers sell one kilogram of maize for 0.68 (yellow variety) to 0.85 (white variety) US$, and potato for 0.12–0.38 (var.1 and var.2) to 0.24–0.60 (var.3) US$. The ranges in the selling prices of potatoes are due to the variation in the tuber size (i.e., larger tubers are more expensive than small tubers).

### 2.4 Statistical analyses

We evaluated differences in survival for plants growing in soils from different elevations using a generalized linear mixed effect model (GLMM). Soil origin was included as explanatory variable in the model, and plot was included as random effect. Differences in survival for plants growing in different elevations (but in the same soil) were evaluated using a generalized linear model (GLM). For both analyses, we used the “cbind” function and a binomial error distribution with logit link function. The “cbind” function allows including two columns of variables (in our case one with the number of plants alive and the other with the number of dead plants) to create the dependent variable used in the analysis. The analyses were carried out with the statistic software R version 3.2 (www.r-project.org), using either the “glm” or the “glmmer” functions from lme4 package (Bates, Maechler, Bolker, & Walker, 2014)).

A generalized linear model with a Gaussian distribution was used to evaluate differences in crop yield (biomass produced) in relation to differences in soil or elevation. Data were square-root transformed when necessary to meet the assumptions of data normality and homoscedasticity. Separate analyses were performed for evaluating production per plant or per unit of planted area. When the assumptions of the model were not met, the Kruskal–Wallis test was performed.

### 3 RESULTS

#### 3.1 Elevational variation in soil properties

The soil analyses revealed that soils collected from the area where maize is currently cultivated (2,900 m asl) have more clay and less coarse sand than those located 3,590 or 3,780 m asl (i.e., 190 and 380 m above the current upper elevational limit of maize cultivation). In addition, soils located at 2,900 m asl had less organic matter, a lower content of calcium, and a higher content of magnesium than those located at higher elevations (Table S2). The content of phosphorous and potassium was higher in soil located 3,590 m asl than those located at 2,900 or at 3,780 m asl (Table S2).

#### 3.2 Soil effects on maize

Despite the observed differences in the chemical and physical properties of soil from different elevations, there was no difference in survival among maize plants growing in different soils (white variety: $\chi^2 = 32.8$, df = 2, $p > .05$; yellow variety: $\chi^2 = 42.1$, df = 2, $p > .05$; Figure 3a,b). Nevertheless, for the white variety of maize, production (kg/ha) at current temperatures was greater when plants were grown in the control soil (i.e., from 2,900 m asl) than when grown in soils from higher elevations (i.e., from 3,590 and 3,780 m asl; Figure 3e). For the yellow variety, production was greater when plants were grown in control soils than in those from 3,780 m elevation (Figure 3f). Overall, maize production declined by 21%–29% when
grown in higher elevation soils with equivalent losses of 142–246 US$ ha$^{-1}$ yr$^{-1}$ (Figure 3e,f).

### 3.3 Effects of elevation on maize

We observed a strong and significant effect of elevation (temperature) on plant survival (white variety: $\chi^2 = 116.7$, df = 2, $p < .001$; yellow variety: $\chi^2 = 87.3$, df = 2, $p < .001$). Mortality was lower for plants growing in the control plots (at 2,900 m asl) than for those growing at lower, warmer elevations (at 2,310 m asl $= +1.3^\circ C$, or 2,120 m asl $= +2.6^\circ C$) but in control soils (Figure 3a,b). The number of maize plants reaching the reproductive phase was 5–21 times higher in the control plots than in plots located at lower elevations. Observed differences in crop production (kg/ha) were even stronger. For the white variety of maize, mean production was 32–58 times higher in control plots than in those located at 2,310 or 2,120 m asl (Kruskal–Wallis test: $H = 18.3$, df = 2, $p < .001$, Figure 3e), whereas for the yellow variety production was 11–56 times higher in the
control plots (Kruskal–Wallis test: $H = 17.3$, $df = 2$, $p < .001$, Figure 3f). Overall, the commercial production of maize declined by 91%–98% in response to elevated temperatures. In terms of current market values, this is equivalent to losses of 617–1,102 US $ ha^{-1} \text{yr}^{-1}$ (Figure 3e,f).

Herbivores—and most notably granivorous birds of the genera *Nothoprocta* sp. (“tinamous”) and *Zenaida* sp. (“doves”)—were the main cause of mortality for maize seedlings growing at low elevations (2,310 or 2,120 m asl), causing 87%–96% of the observed mortality. *Nothoprocta* sp. and *Zenaida* sp. did not attack the control plants (2,900 m asl) even though individuals were observed foraging near the plots. Deer (*Hippocamelus* sp.) and *Acromyrmex* leaf-cutter ants also occasionally attacked maize seedlings but only at 2,310 or 2,120 m elevation (3%–18% of the plants growing at these elevations were attacked). Attacks by an unknown virus caused the death of 3%–20% of the juvenile and reproductive plants growing at 2,120 m elevation. Similarly, the inflorescences of most plants growing at 2,120 m elevation were infested with aphids (Fig. S3b). The level of aphid infestation was lower on plants growing at 2,310 m, and aphids did not occur on plants in control plots.

### 3.4 Effects of elevation on potatoes

We found that elevation (temperature) affected the survival of just one of the three varieties of potatoes (var.1: $\chi^2 = 8.1$, $df = 2$, $p = .017$; Figure 4a–c). Only for var.1, plant survival was higher in control plots (3,900 m asl) than in plots located at 3,320 m elevation. However, for all three varieties, there was a significant negative effect of higher temperatures on crop production (var.1: $F_{2,21} = 43.8$, $p < .001$; var.2: $F_{2,21} = 35.1$, $p < .001$; var.3: $F_{2,21} = 91$, $p < .001$). Production of potato tubers (both on a per plant basis, as well as per unit of planted area) was 5–21 times higher in the control plots than in plots located at lower elevations (Figure 4d–i). Overall, production declined by 87%–97% when plants were grown in warmer temperatures, and the associated economic losses are estimated to approximate 805–2,304 US$ ha^{-1} \text{yr}^{-1}$ under current market values (Figure 4g–i; Table S3).

Several species of insect herbivores were recorded damaging the leaves, stems, or tubers of the potatoes. The most common were *Diabrotica* sp. (Chrysomelidae), *Epitrix* sp. (Chrysomelidae), *Phtorimaea operculella* (Gelechiidae), and *Symmetrischema tangolias* (Gelechiidae). The latter, which is a stem borer that strongly damaged potato

![](image)

**FIGURE 4** Effects of different elevations (temperatures) on the performance of three potato varieties. (a–c) Plant survival at different growth stages. (d–f) Biomass of marketable tubers produced per plant. (g–i) Biomass of marketable tubers produced per unit of planted area and corresponding market values in US$. Market value was calculated based on commodity prices in the production zone as of December 2015. Shown are means ± SE. Different letters represent significant differences in mean values [Colour figure can be viewed at wileyonlinelibrary.com]
plants during the tuberization phase (Fig. S3c), was never recorded in plants in the control plots.

4 | DISCUSSION

4.1 | Effects on maize

For maize, we experimentally simulated two possible future scenarios: one in which plants are grown in the same climate as today but on soils from higher elevations (i.e., as predicted under an upward migration of crop cultivation), and the other in which plants experience warmer temperatures while remaining on the current soil. Our results show that in both cases, production will decline. Maize production declined by 21%-29% in response to changed soil conditions and by 91%-98% in response to elevated temperatures. In terms of current values, this is equivalent to losses of 142-246 US $ ha⁻¹ yr⁻¹ and of 617–1,102, respectively.

The exact reason(s) for the decline in maize production on higher elevation soils are not clear but likely involves an imbalance in nutrient concentrations. We found that the concentration of calcium increases strongly with elevation whereas the concentration of magnesium decreases (the Ca:Mg ratio increased from 3:1 in control soil to 8:1 in soils at 3,590 m asl and 13:1 in soils at 3,780 m asl). As Ca and Mg are antagonist nutrients, the greater concentration of Ca at higher elevations reduces the availability and absorption of Mg (Barker & Pilbeam, 2015). Magnesium is essential for many biochemical and physiological processes in plants, including a structural role as a key component of the chlorophyll molecule. Mg deficiency can, therefore, have a negative effect on photosynthesis and, consequently, on plant productivity (Dechen, Carmello, Monteiro, & Nogueiro, 2015; Hernandez & Silveira, 1998) of crops migrating into higher elevations. In agreement with this hypothesis, previous studies have shown that a ratio of Ca:Mg of 2:1–3:1 is suitable for maize plant development, but that higher ratios decrease productivity due to Mg deficiency (Dechen et al., 2015; Hernandez & Silveira, 1998).

The effect of elevation (temperature) on maize yields was largely an indirect effect. Plants growing in sites with temperatures 1.3–2.6°C higher than the highest current temperature were heavily attacked by herbivores. These herbivores caused severe plant mortality, most notably during the seedling phase. In addition, maize plants growing at temperatures 2.6°C warmer had their reproductive performance negatively impacted by the high number of aphids attacking their inflorescences. These results indicate that if farmers continue to cultivate maize at the same current elevations under future warmer temperatures, plant productivity is likely to decline significantly as result of the increased incidence of pests and pathogens. Our results are consistent with results from several other studies that have shown that agricultural pests and pathogens have already expanded their area of occurrence, and will continue to do so as global temperatures increase (Bebber et al., 2013, 2014; Crespo-Pérez et al., 2015; Dangles et al., 2008, 2013). Furthermore, for most of these pest organisms, warmer temperatures increase the rate of population growth and thus the pressure on their host plants (Bale et al., 2002).

4.2 | Effects on potatoes

For the potato varieties, production declined by 87%-97% when plants were grown under warmer temperatures, and the associated economic losses are estimated to be in the order of 805–2,304 US $ ha⁻¹ yr⁻¹. As with maize, the observed decreases in potato production were due largely to the greater incidence of pests in plants grown at lower, hotter elevations. However, in contrast to maize, we did not detect differences in plant survival until the reproductive phase for two of the three potato varieties studied. Furthermore, for potato var.1, differences in survival among sites with different temperatures were restricted to the sprouting phase and were comparatively much smaller than differences observed for the two varieties of maize. Yet, for all three potato varieties, there were strong and significant differences in plant production between plants growing in the control plots and those growing in warmer temperatures. Part of this difference is likely due to the high incidence of stem borers (Symmetrictera tangolica) in juvenile and reproductive plants in the treatment (higher temperature) plots. As various studies have previously shown (Stieha & Poveda, 2015), potato plants are highly sensitive to stem damage, especially during tuberization, because damage to the vascular tissues affects sap flow causing the production of fewer and smaller tubers (as in our case, see Fig. S4). In addition, it is likely that the elevated temperatures directly decreased tuber production. This is because elevated temperatures can negatively affect both the synthesis of plant hormones that stimulate tuber initiation and formation, and reduce the allocation of plant assimilates for tuber formation (Ewing & Struik, 1992; Hancock et al., 2014; Jackson, 1999).

4.3 | Conclusions and implications

A strategy commonly suggested to counter the effects of climate change is for farmers to switch to other crops or crop varieties that can better tolerate warmer temperatures and/or pests (Eyshi Rezaei, Gaiser, Siebert, & Ewert, 2015; Howden et al., 2007; IPCC, 2014). However, a potential downside to this strategy is the loss of local or native varieties with unique features (including taste, texture, and nutrient content). For example, compared to the other varieties growing at lower elevations, the high-elevation varieties of potato and maize studied here are valued more by local buyers due to their desirable properties for human consumption (INEI, 2016). Furthermore, many local farmers may lack the resources or knowledge required to switch production to other crops or crop varieties.

Shifting cultivation of crops to higher, cooler elevations (or latitudes) is another potential strategy to reduce production losses under rising temperatures (Meng et al., 2014; Skarbø & VanderMolen, 2016). However, as shown here, this is a not a possibility for crops that are already being cultivated at or near mountain tops. Furthermore, the effectiveness of this "migration" strategy may be
limited by soil nutrient conditions, potentially ameliorated through fertilization. Even if fertilization is economically feasible, shifting cultivation locations may still not prevent production declines due to the inevitable reduction in arable land as elevation increases. For example, even moderate warming would restrict farming of the potato varies studied here to just the very tops of mountains and a warming of approximately 3°C would make potato production in our study area entirely unfeasible as no land with suitable temperatures would remain. Likewise, warming will rapidly shrink the extent of land with temperatures suitable for the production of maize and other local crops.

Development of pest management strategies focused on current and novel pests are also needed. As shown here, novel pest and diseases will very likely become a damaging threat under warmer conditions (Bebber et al., 2014; Dangles et al., 2008, 2013). Laboratory experiments, for instance, have shown that the survival and developmental rates of stem borer S. tangolias increases at temperatures warmer than those found within their current area of occurrence (Dangles et al., 2008). This indicates that this pest species is likely to expand its distribution and prevalence in response to global warming (Crespo-pérez et al., 2013; Crespo-Pérez et al., 2015). A suitable and ideally "environmentally friendly" control management will be important to maintain reasonably healthy conditions for consumers and the environment (Foley et al., 2011). Studies show that the use of pesticides has increased over recent decades and rising trends will likely continue (Bourguet & Guillemaud, 2016; Oerke, 2006). In this sense, the valorization of farmer’s skills and traditional knowledge should be encouraged. In our study site, some farmers plant maize in association with beans and cucumber in order to minimize the damage caused by granivorous birds.

In short, our experimental findings clearly demonstrate that climate change, and specifically rising temperatures, is a real and imminent threat to small-scale agriculture in the Peruvian Andes, as it will very likely cause severe declines in the production of two locally and globally important crops. We show that plant survival and crop production are markedly affected by planting soil and especially by planting elevation (temperature). Such dramatic declines in crop yields will likely translate into large economic losses for the farmers as well as increased risk of food insecurity in a region that depends heavily on local food production. As such, there is a pressing need to develop more effective management strategies to mitigate the impacts of decreasing yields and help prevent food insecurity, not just for the benefit of farmers and rural communities, but also for the wider population that depends on these crops. Importantly, such strategies should take into account the influences of non-climatic and/or biotic factors on plant development. These factors are often overlooked in models projecting future crop production in response to climate change. However, as our field experiments indicate, a major driver of mortality and production declines of both maize and potatoes when grown at lower elevations (higher temperatures) was increased incidence of novel herbivores and pathogens. This finding highlights that the dangers of climate change for crops is not only the direct effects of rising temperatures but also the indirect effects of changing biotic conditions.

Future studies should evaluate the isolated and combined effects of soil, temperature, and CO2 concentration on crop production. There is strong evidence that elevated atmospheric concentrations of CO2 can enhance the production of the crops we studied (with this effect being stronger for potatoes than for maize; Finnan, Donnelly, Jones, & Agency, 2013; Kimball, 2016; Korres et al., 2016; Streck, 2005). However, there is also evidence that temperature and CO2 act antagonistically, indicating that higher concentrations of atmospheric CO2 will not mitigate the negative effects of global warming on crop production (Ruiz-vera, Siebers, Drag, & Ort, 2015).

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