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BRIEF REPORT

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The importance of conserving Mexico's tomato agrodiversity to research plant biochemistry under different climates

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Societal Impact Statement

Tomatoes are important to agriculture, human nutrition and cuisines globally. However, many commercial tomato varieties, including the saladette that dominates the North American market, are highly sensitive to environmental changes that impact yields and critical biochemical pathways including carotenoids and isoprenoids that influence nutritional content and flavour. We highlight the potential of tomato agrodiversity, notably its genetic diversity, as an undervalued research tool for understanding environmental regulation of plant biochemistry under different climates. Yet, tomato genetic diversity in Mexico, the major centre of tomato domestication, is not formally described or protected. We propose that transdisciplinary efforts are essential to identify, conserve and research these globally significant genetic resources.

KEYWORDS

carotenoids, conservation, genetic resources, Mexico, transdisciplinary

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1 | INTRODUCTION

The tomato is the world's most cultivated horticultural crop and fourth most economically valuable food crop produced in low- and middle-income countries, with a global production worth ~US$88 billion (FAOSTAT, 2019). Amongst the most widely used culinary ingredients globally (Long, 2000), it is culturally significant and an important dietary source of carotenoids, including provitamin A (ß-carotene) and other antioxidants (i.e., lycopene and tocopherols). Related deficiencies amongst undernourished populations cause childhood blindness, nutrient malabsorption and higher risks of mortality and poor health (WHO Global Database on Vitamin A deficiency, 2021).

Mexico—the global centre of tomato domestication—hosts unique tomato agrodiversity (Lobato-Ortiz et al., 2012), including genetic diversity and associated traditional agro-ecosystems and knowledge. We consider the underexplored research potential of these resources, including as a unique model for exploring the environmental regulation of carotenoid biosynthesis and accumulation under different climatic regimes, and put forward preliminary evidence that locally adapted Mexican varieties may demonstrate higher carotenoid accumulation across temperature regimes compared with the major commercial cultivar in Mexico. However, we highlight that such promising lines of research are reliant on first establishing transdisciplinary efforts to better identify, characterise and conserve Mexico's tomato agrodiversity.

2 | EMERGING THREATS TO TOMATO AGRODIVERSITY

Although native to the Andean region (Blanca et al., 2012), Mexico is the centre of tomato domestication (Razifard et al., 2020) hosting hundreds of varieties (Lobato-Ortiz et al., 2012). These include diverse red, yellow and orange varieties (*Solanum lycopersicum and Solanum lycopersicum var cerasiforme*) that have been bred and adapted to a range of temperatures, rainfall conditions, soil types and biotic stressors over centuries, linked to Mexico's diverse climates, cultures and agricultural traditions (Peralta & Spooner, 2007).

These varieties were the source of the 17th century introductions into Europe that made tomatoes mainstays of farms and diets globally (Blanca et al., 2012, 2015; Foolad, 2007) and are origins for the diverse varieties planted worldwide (e.g., UC Davis, 2020). However, from the 1930s, commercial breeders centred efforts on increasing yields and fruit shelf-life, often relegating to the margins traits linked to fruit nutritional quality, flavour, aroma, input demands and climatic resilience (Bai & Lindhout, 2007; Cebolla-Cornejo et al., 2012). As with other crops (Orozco-Ramírez et al., 2017), commercial tomato production also transitioned to large-scale monocultures of a reduced number of varieties. Notably, the "saladette" variety represented 86% of Mexican production and 25.11% of the global export market in 2016 (SAGARPA, 2017). In Mexico, this has aligned with market pressures, government programmes promoting greenhouse-dependent varieties (Amaro-Rosales & de Gortari-Rabiela, 2016; SAGARPA, 2017), alongside large-scale migration and farm abandonment (Villarreal, 2010). These factors are driving decreased production of traditional varieties; farmers and chefs across Mexico can readily describe the disappearance of landraces, whose production is relegated to small scale and self-consumption. These trends are resulting not only in agrodiversity loss but also the loss of associated agricultural practices, culinary traditions, knowledge and values that have often been passed on amongst communities and across generations (see FAO, 2009, 2020).

Shifts in agricultural practices and genetic erosion are increasing concerns under global warming (Blanca et al., 2015; Cebolla-Cornejo et al., 2012). Many mass-produced commercial varieties, including "saladette," are less adaptable to adverse environmental conditions, threatening yields, fruit nutritional quality and taste (FAO et al., 2018; Morton, 2007). Low resilience has been driven by its limited genetic variability, resulting from founder effects and selective breeding that characterises much contemporary agriculture (Foolad, 2007). By 2030, projected environmental changes are estimated to reduce yields by 10% in Southern Italy, with similar or higher losses expected in Greece, Spain, southern France, Cyprus and Turkey (Georgopoulou et al., 2017; Ventrella et al., 2012). There are, however, a growing number of modern tomato hybrids developed for tolerance to diverse stressors (Schouten Schouten et al., 2019). Notably, such efforts often involve introgression of genes from locally-adapted landraces.

3 | PROOF OF CONCEPT STUDY: TOMATO GENETIC DIVERSITY TO RESEARCH PLANT BIOCHEMISTY IN DIFFERENT CLIMATIC ENVIRONMENTS

There is growing appreciation of the importance of tomato genetic diversity for breeding varieties that are more resistant to adverse environments and climates (Chávez-Servia et al., 2011; Cortes-Olmos et al., 2014). Less widely recognised are their potential research values, including for understanding environmental regulation and effects of global warming. In particular, tomatoes accumulate very high concentrations of carotenoids and other isoprenoids, making the crop a unique model system for exploring their biosynthesis and accumulation (Figure 1a). These multifunctional pigments derive from the methylerythritol 4-phosphate (MEP)-isoprenoid pathway (Figure 1a) and are essential for plant photosynthesis and growth and for human nutrition as antioxidants (i.e., lycopene) and precursors of vitamins (pro-vitamin A).

Molecular data generated in plant model systems have singled out environmental inputs such as light and temperature as important modulators of the production of carotenoids and other isoprenoids (Liu et al., 2004; Toledo-Ortiz et al., 2010, 2014). In particular, the phytochrome photoreceptors and their signalling components that act as thermosensors regulate plant metabolism, including the transcription of the phytoene synthase gene

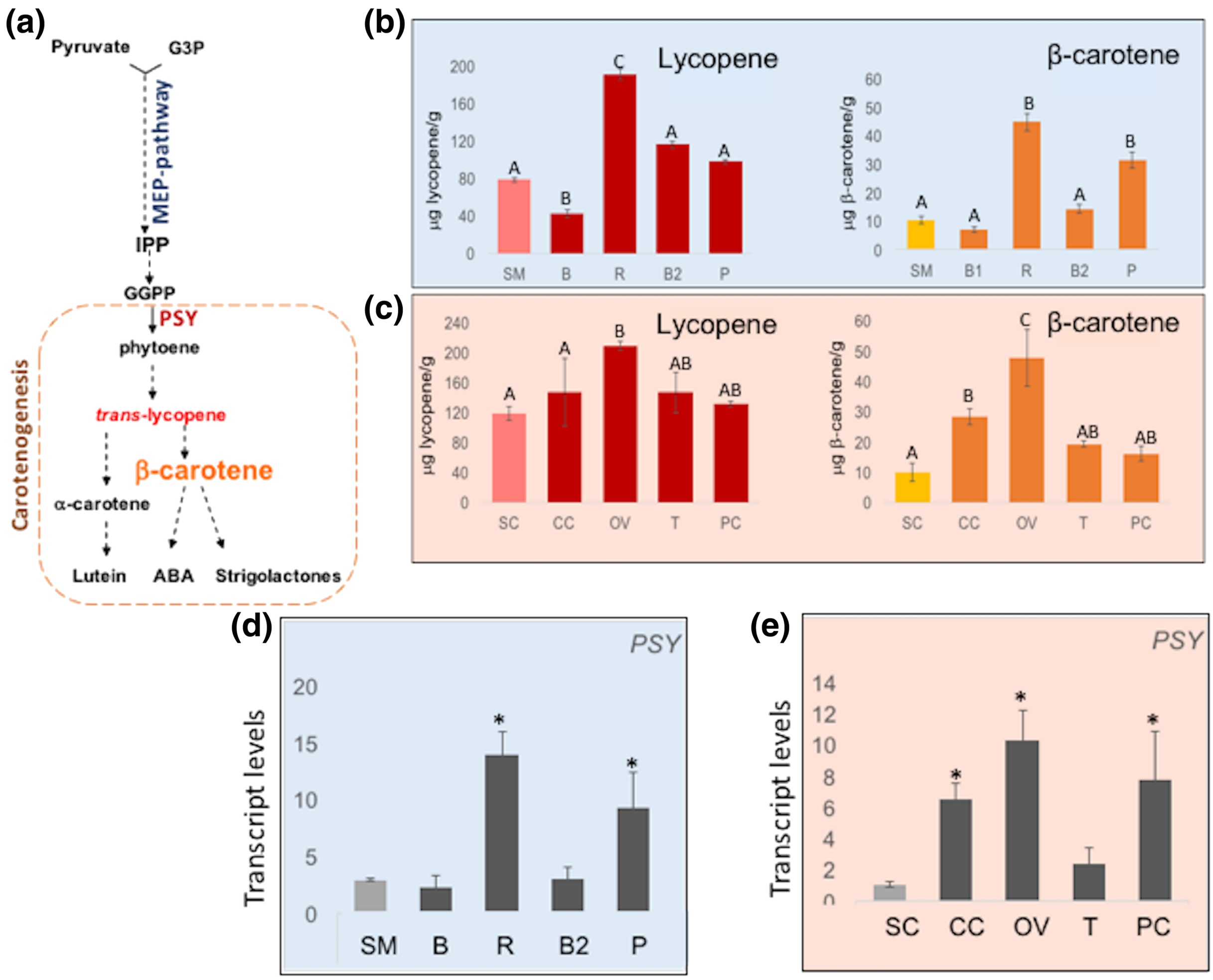

FIGURE 1 (a) Overview of the carotenoid biosynthesis pathway. HPLC quantification of lycopene and ß-carotene in selected tomato varieties from Oaxaca State from (b) cool temperatures (average 14°C) Mixteca Region (M) or (c) warm Costa region (average 34.4°C Mixteca tomatoes include SM: saladette mixteca commercial control; B: bola tomato; R: rinon tomato, B2: bola II, P: pajarito tomato. Costa tomatoes include SC, saladette costa; commercial control; CC: criollo; OV: Ojo de venado tomato; T: tinana tomato; and PC: pajarito costa tomato. Data represent the average of three biological replicas, and error bars indicate standard error. Statistical significance was calculated with one way Anova ($p < .05$). Data that do not share a letter are statistically significant. (d) Relative Gene expression profiles by qPCR of *PSY* (phytoene synthase) gene that encodes for the rate-limiting step enzyme from carotenogenesis, in cool temperatures grown Mixteca tomatoes and (e) in warm temperature grown Costa tomatoes. Transcript levels are relative to *ACT4* used as reference gene. Graphs represent average of biological triplicates; error bars indicate SE and statistical significance *t*-test ($p < .05$) compared with saladette that is indicated by asterisks (see SI methods section for sampling sites and experimental conditions). Abbreviations: ABA, abscisic acid; G3P, glyceraldehyde 3-phosphate; GGPP, geranylgeranly pyrophosphate; IPP, isopentenyl pyrophosphate PSY, phytoene synthase

(*PSY*), encoding the first committed enzyme in carotenogenesis (Figure 1a) (Llorente et al., 2016; Toledo-Ortiz et al., 2010, 2014). At present our knowledge of how carotenogenesis and isoprenoid biosynthesis are affected by environmental inputs is still limited.

In an initial proof of concept study, we explored the research potential of locally adapted tomato varieties, cultivated in their sites of origin in regions with wide climate gradients in Mexico's Oaxaca State (Figure 2a,b). We used varieties grown by traditional farmers using local seed stock aiming to survey in two selected areas germplasm that grows in temperature extremes (Costa and Mixteca, Figure 2b) the performance of carotenogenesis for local tomatoes compared with the commercial "saladette" variety (Figure 1b,c). We observed that some of these locally adapted varieties to either low temperatures (Figures 1b; 2a and S1) or high temperatures (Figures 1c; 2a and S1) accumulated higher levels of lycopene and β-carotene, when compared with the "saladette" variety (Figure 1b, c) at least in the two study regions. This illustrates that locally adapted varieties in their native environments can potentially have higher levels of compounds important to human nutrition than dominant tomato cultivars grown in the study regions. Interestingly, this higher carotenoid accumulation correlated with a higher accumulation of the transcript levels for the enzyme involved in the rate-limiting step of carotenogenesis and phytoene synthase (PSY) (Figure 1a,d,e). This is particularly clear in the "riñón" and "ojo de venado" varieties, adapted, respectively, to warmer and cooler environments, for which the increased transcript levels of *PSY* correlated

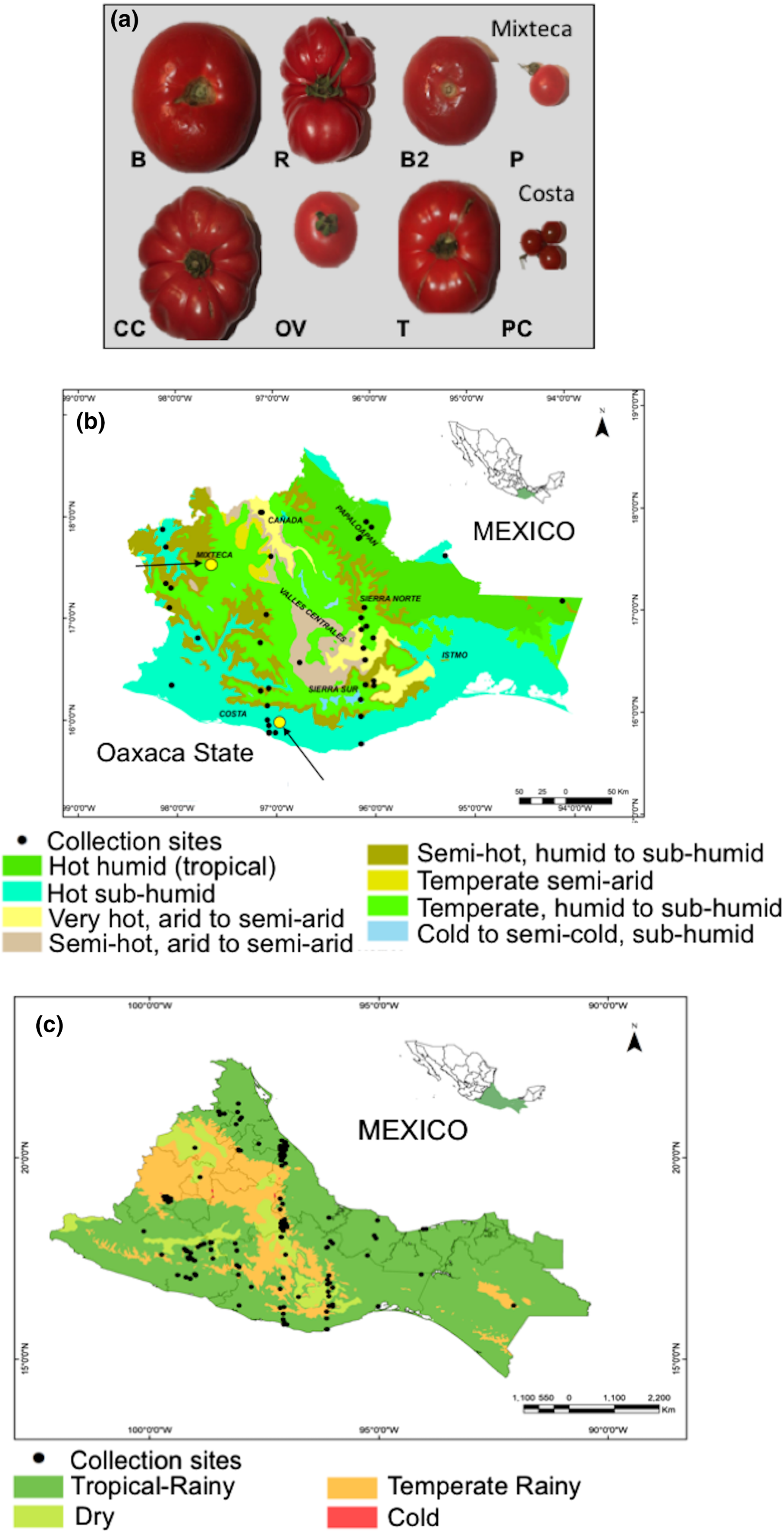

FIGURE 2 (a) Photographs of Oaxaca State tomato agrodiversity cultivated in the Mixteca and the Costa regions. Mixteca tomatoes include B: bola tomato; R: rinon tomato, B2: bola II, P: pajarito tomato. Costa tomatoes illustrated are as follows: CC: costa criollo; OV: Ojo de venado tomato; T: tinana tomato; PC: pajarito costa tomato. (b) Map of Oaxaca State cultivated tomato agrodiversity sampled in climate diverse regions. Arrows indicate the areas in the Mixteca region and Costa region sampled for this work. Black dots indicate extra collection sites for the ex situ COLPOS national collection that includes 105 accessions from Oaxaca State. (c) Map of cultivated tomato agrodiversity collected from diverse climatic regions in Southern-Central Mexico for the ex situ national collection from COLPOS. The collection includes 628 accessions from the areas indicated by black dots

with a higher carotenoid content (Figure 1b–e). Whilst at present, the exact mechanisms of high accumulation are unknown; the preliminary results highlight the potential to use genetics to investigate the responsiveness of essential biosynthetic pathways to different environments in crops. Such mechanisms may involve differential modulation of key flux-controlling transcription factors that lead to altered gene regulation of essential carotenogenenic-enzymes or epigenetic mechanisms. Their dissection might lead to "climate-smart cultivars" that are low-inputs, high-nutrition and palatable, via targeted breeding programmes, and possibly biotechnological approaches based on cisgenic CRISPR-CAS9 technology. Properly managed (see Montenegro de Wit, 2017), such advances could be designed to benefit farmers and improve nutrition.

4 | CONSERVING AGRODIVERSITY AS A PRECONDITION FOR PLANT SCIENCE RESEARCH

Further exploring these research opportunities requires work to first identify, characterise and conserve Mexico's tomato varieties. Mexico's tomato resources are expected to be vast, as its main centre of domestication over >1300 years (Razifard et al., 2020) and given the prevalence of varieties known to have adapted to specific regions across Mexico's 15 Koppen–Geiger climates (Kottek et al., 2006), including drought, excessive rain and sharp weather changes. Several research groups have started sampling (Lobato-Ortiz et al., 2012), including in the state of Oaxaca and southern Mexico. Sites sampled by COLPOS for their ex situ collection are illustrated in Figure 1b,c. These initial efforts indicate the scale of Mexican tomato diversity; however, most of the country has yet to be surveyed and clear estimates are awaiting, including in high-biodiversity states such as Puebla, Oaxaca and Michoacan. Overall, few Mexican traditional varieties have been documented or characterised in terms of their agronomic traits and nutritional content and genetic diversity (Pacheco-Triste et al., 2014). Moreover, there are no evaluations of their in situ conservation status on farms (e.g., Chávez-Servia et al., 2011; Lobato-Ortiz et al., 2012), and few are in ex situ conservation. The two largest collections in Mexico include 628 accessions (COLPOS, for collection sites see Figure 2b,c) and 491 accessions (SNICS, Lobato-Ortiz et al., 2012), representing 11 of Mexico's 32 states. Whilst at present little genetic characterisation work has been conducted for these collections, preliminary surveys of the COLPOS ex situ collection landraces show a broad range of desirable agronomic and nutritional traits, including flower morphology (Figure S2) and fruit locule number and shape (Figure S3), as well as shelf life associated parameters such as postharvest respiration rate and fruit weight loss (S4-S5) and accumulation of total antioxidants (Figure S6) and vitamin E (Figure S7). These preliminary studies illustrate the potential of the germplasm for use in novel research programmes including their use as starting material for new breeding programmes. Yet, these seedbanks are insecure due to a lack of funds for seed maintenance under refrigerated conditions and for active management involving systematic planting and recollection to maintain high viability. Outside of Mexico, the Tomato Genetics Resource Centre holds the world's largest collection of tomato wild relatives and miscellaneous genetic stocks, including only 51 Mexican landrace accessions in their collection of 4405 stocks (https://tgrc.ucdavis.edu). The USDA-ARS Germplasm Resources Information Network includes 124 Mexican accessions *of S. lycopersicum* and *S. lycopersicum var cersiforme*, but not all include information on origin or genetic characterisation, and the collection is biassed towards specific areas (i.e., State of Puebla). Other efforts, such as TradiTom (http://www.traditom.eu/), have focused on European varieties. Meanwhilst, large-scale studies that have used diverse tomato samples (e.g., Lin et al., 2014; Zhu et al., 2018) have lacked significant sampling from Mexico. These highlight gaps in efforts to identify and study Mexican tomato agrodiversity.

There is also a need for ex situ and on-farm conservation in the sites where natural and selective pressures have shaped tomato adaptation, including in order to study the molecular genetic basis of those adaptations. This requires interventions to promote continued production of tomato varieties in their niches (see Lobato-Ortiz et al., 2012). Maintaining on-farm agrodiversity conservation can present significant challenges because it is crop and context specific and involves diverse economic and non-financial motives (see Wood & Lenne, 1997). Tangible conservation actions can include rekindling local subsistence and market use, alongside the careful establishment of new networks that link farmers to novel and high-value markets, including gourmet restaurants and organic markets (see Baker, 2008; Pallante et al., 2016). There is also scope for farmer-driven seed sharing programmes and agricultural extension that facilitate on-farm conservation and use (see Pautasso et al., 2013). In addition, there is a need for cooperation and education amongst farmers, researchers, chefs and consumers about the benefits, characteristics and traditions associated with tomato diversity. Mexico has previously demonstrated that these types of broad, cooperative agro-food movements can rekindle traditional agriculture by facilitating market access, building recognition of traditional agriculture and motivating consumers (i.e., with traditional maize varieties, Baker, 2008; FAO, 2020, Globally Important Agricultural Heritage Systems; FAO, 2009, FAO & Traditional Knowledge: the linkages with sustainability, food security and climate change impacts; Intangible Cultural Heritage (ICH), 2010). Such efforts are incipient for Mexican tomatoes, including the pending consolidation of a Mexican tomato network and the establishment of the authors' Tomatoes for Tomorrow initiative that fosters transdisciplinary collaborations to protect and research traditional tomato varieties (www.tomatoes4tomorrow.com).

There is growing recognition of the importance of Mexican tomato agrodiversity, including for research that could deliver benefits for small and industrial farmers and consumers globally. Efforts to further explore this research potential rely on parallel, transdisciplinary efforts to identify and conserve these resources in their centres of origin.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

MGSC, NK, JHCG and RMP performed the experiments; GMG conducted the fieldwork; GTO, JP, VAGH, IRR, PL, NCH, LM, RGS, CB, LM and JLCS analysed the data and wrote the manuscript; GTO, VAGH, IRR, NCH, PL, MGSC, JLCS and RMP prepared the figures.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available from the corresponding authors upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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