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THE GENETICS OF INSECTICIDE RESISTANCE IN RELATION TO CLIMATE CHANGE

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ABSTRACT

Due to climate change, many animal species are experiencing rapid evolutionary transformations, including agricultural pests and disease carriers. This, in turn, causes changes in the prevalence of certain gene variants related to heat tolerance and desiccation resistance. Since some of these genes also influence resistance to insecticides, it is probable that climate change will affect the development of insecticide resistance in natural environments. The purpose of this review is to provide a real-world analysis of the effects of climate change and insecticide resistance. We illustrate this through examples involving plant-feeding and hematophagous pests, with a specific focus on the effects of rising temperatures and increased aridity. We propose that trade-offs or synergistic interactions between adaptation to climate change and resistance to insecticides can modify the frequencies of alleles responsible for insecticide resistance in natural environments. It is crucial to consider the dynamics of these interactions when devising strategies for managing agricultural pests and disease vectors in the face of a changing climate.

Keywords: Insect resistance, climate change, heat stress

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1. INTRODUCTION

Climate change, a pressing concern of our era, is having far-reaching effects on our planet. The global climate is experiencing various transformations, such as rising temperatures, heightened levels of CO2, fluctuations in UV radiation, and unpredictable alterations in precipitation patterns caused by extreme weather events (Ahmed et al. 2022; Nadeem et al. 2023). These changes are significantly impacting numerous habitats and ecosystems, resulting in increased area of drylands in many regions (Stott 2016). As organisms adapt to these shifting environmental conditions, rapid evolutionary changes are occurring, particularly among animal species, including insects. As a result, geographic patterns of agricultural insect pests and disease vectors are changing, as are their metabolic rates, potentially leading in a faster rate of generational turnover (Razzaq et al. 2023). It is predicted that a changing climate will result in a decrease in crop productivity because due to increased damage inflicted by insect pests. Additionally, there is a predicted rise in the occurrence of vector-borne diseases, presenting new challenges in pest management. The conventional approach of using synthetic insecticides for the control of agricultural insect pests and disease vectors has been in practice for several decades and has generally yielded positive results (Zafar et al. 2020). However, with the changing climate variables, the effectiveness of these chemical-based strategies may diminish. One hypothesis suggests that the modifications in environmental conditions caused by climate change can potentially reduce the efficacy of insecticides (Razzaq et al. 2021). Studies have shown that temperature variations can affect the toxicity of many insecticides commonly employed in pest management, leading to a decline in their effectiveness. According to another theory, the allele frequencies of genes linked to pesticide resistance may quickly shift as a result of evolutionary responses to climatic change. This is because the genes responsible for insecticide resistance can have pleiotropic effects on other characteristics, such as tolerance to higher temperatures or resistance to desiccation. Consequently, the development of insecticide resistance and adaptation to climate conditions would occur in a co-evolutionary manner (Deutsch et al. 2018).

The alteration of a single trait can have either positive or negative repercussions on another trait, which can occur through tradeoffs or facilitation. In this comprehensive analysis, we will delve into various studies that shed light on

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the impact of climate change on insecticide resistance among plant-feeding (phytophagous) and blood-feeding (hematophagous) pest insects. Specifically, our focus will be on the impacts of increased temperature and aridity.

2. Climate Change and Insecticide Resistance

Climate change has emerged as a significant driver of ecological and evolutionary dynamics, affecting various aspects of organisms' biology and interactions with their environment. One area of concern is the potential impact of climate change on insecticide resistance in pest insects. Understanding the relationship between climate change and insecticide resistance is crucial for effective pest management strategies in agriculture and public health. Insecticide resistance refers to the ability of certain insects to withstand the toxic effects of insecticides that were once effective in controlling them. It is a result of genetic changes in insect populations over time. These genetic changes can occur through several mechanisms, including mutations, gene amplification, and changes in gene expression, leading to alterations in metabolic pathways and target site insensitivity (Zafar et al. 2020).

Climate change can influence insecticide resistance in multiple ways. One major factor is the alteration of environmental conditions, such as temperature and moisture levels, which directly impact the biology and physiology of insects. For instance, increased temperatures can accelerate the metabolic rates of insects, potentially affecting the detoxification mechanisms that break down insecticides within their bodies. This increased metabolic rate may result in faster detoxification and elimination of insecticides, rendering them less effective in controlling the pests (Aleem et al. 2023). As a result, research on the correlation between long-term climatic data and insecticide use or resistance data in particular places has produced proof that the influence of climate on the evolution of resistance in the field. Investigations into pyrethroid resistance in the red legged earth mite, Halotydeus destructor, a serious pest affecting Australia's grain and pastoral industries, in various regions of Western Australia, for instance, revealed that regional differences in aridity, temperature seasonality, and precipitation patterns contributed to spatial variations in resistance patterns. This finding underscores the involvement of climate in the distribution of resistance (Maino et al. 2018). Similarly, a study focusing on the development of deltamethrin resistance in Triatoma infestans, a vector of Chagas disease, suggested that climate might play a role in the emergence of resistance within a specific region in Argentina. Modeling approaches have helped elucidate the potential influence of climate on resistance evolution by considering factors such as temperature, aridity, and precipitation patterns (Fronza et al. 2019).

Another way climate change can affect insecticide resistance is through its influence on the evolutionary dynamics of pest populations. Climate change can act as a selective pressure, favoring certain genetic variants or alleles associated with insecticide resistance. Insects that possess genes conferring resistance to insecticides may have a higher survival and reproductive advantage in altered climatic conditions. This selective advantage can lead to an increase in the frequency of resistant individuals within the population over time (Zafar et al. 2020). The impact of climate change in the development of insecticide resistance can be classified into two main groups. The first category pertains to the fitness costs imposed by climatic adaptation on insecticide resistance, leading to tradeoffs in fitness and a reduction in the prevalence of insecticide resistance alleles in natural populations. Invitro studies investigating the impacts of climatic factors, such as increased temperatures, on insecticide resistance alleles can provide valuable insights into the potential evolutionary trajectories of insecticide resistance under climate change scenarios. For instance, a laboratory study conducted on the diamondback moth, *Plutella xylostella*, demonstrated that higher temperatures impose a fitness cost on the chlorpyrifos-resistant strain of the species. In comparison to the susceptible strain, the resistant strain had higher rates of wing vein damage and decreased survival when subjected to heat stress (Fig. 1). This data implies that in this species, there is a trade-off between heat tolerance and pesticide resistance (Zhang et al. 2015). Similar findings from studies on the brown planthopper, *Nilaparvata lugens*, showed that at higher temperatures, a chlorpyrifos-resistant strain exhibits reduced fitness relative to its susceptible counterparts. This indicates that a shared genetic mechanism may underlie both chlorpyrifos resistance and tradeoffs with thermotolerance, even in distantly related species (Yang et al. 2018). By elucidating these fitness tradeoffs (Haroon et al. 2023) and the effects of temperature on insecticide resistance, laboratory studies provide valuable insights into the potential impacts of climate change on the evolution and prevalence of resistance in pest populations. Understanding these dynamics can inform pest management strategies by considering the interactive effects of climatic factors and resistance development (Haroon et al. 2023). Moreover, climate change can indirectly impact insecticide resistance by altering the ecological interactions between pests and their natural enemies. Changes in temperature, precipitation patterns, and habitat availability can disrupt the natural balance of predator-prey relationships and disrupt the effectiveness of biological control agents that naturally suppress pest populations. This disruption can lead to increased reliance on insecticides, potentially driving the evolution and spread of resistance (Zafar et al. 2020). While research on the specific effects of climate change on insecticide resistance is still evolving, studies have demonstrated its potential impact in various pest insect species. For example, research on mosquitoes, which are vectors for diseases such as malaria and dengue fever, has shown that temperature variations can influence the expression of genes associated with insecticide resistance. Similarly, studies on agricultural pests have indicated

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that increased temperature and aridity can affect the detoxification mechanisms and metabolic pathways involved in insecticide resistance (Akbar et al. 2023).

The second category involves the facilitation of insecticide resistance development through climatic adaptation, leading to an increase in the prevalence of insecticide resistance alleles. This facilitation occurs because both climatic adaptation and insecticide resistance share a common molecular basis, meaning that selection for one trait will also promote the other trait. This mutual reinforcement between climatic adaptation and insecticide resistance can contribute to the rapid emergence and spread of resistance in pest populations. An example of such facilitation can be observed in the small brown planthopper, *Laodelphax striatellus*. Studies have reported a positive association between resistance to the insecticide buprofezin and thermotolerance in this species. This indicates that individuals possessing buprofezin resistance alleles also exhibit enhanced tolerance to higher temperatures, suggesting a shared genetic basis for both traits (Li et al. 2017).

Another case highlighting the facilitation between climatic adaptation and insecticide resistance is found in the major malaria vector, *Anopheles arabiensis*. Research has shown that at elevated temperatures, resistant individuals tend to have a longer lifespan compared to their susceptible counterparts. This suggests that insecticide resistance confers a fitness advantage at higher temperatures, potentially contributing to the increased prevalence of resistance in populations experiencing warmer climates (Oliver and Brooke 2017).

The facilitation of insecticide resistance through climatic adaptation underscores the complex interplay between environmental factors and the evolution of resistance in pest species. By favoring the simultaneous development of traits related to both climatic adaptation and insecticide resistance, climatic conditions can accelerate the spread of resistance alleles within populations. Understanding these interactions is crucial for developing effective pest management strategies that account for the influence of climate on resistance dynamics. In order to comprehend the reasons behind the occurrence of tradeoffs between climate change and insecticide resistance in certain cases, while in others climate change facilitates resistance, it is essential to delve into the genetic and molecular mechanisms that underlie these distinct scenarios of insecticide resistance, as well as the specific climatic factors involved. By examining these factors, a clearer understanding can be gained regarding the complex interactions between climate change and insecticide resistance, providing insights into the varying outcomes observed in different cases (Bass 2017). Understanding the genetic and molecular mechanisms underlying the relationship between climate change and insecticide resistance is crucial for developing effective pest management strategies. By identifying the specific genes and pathways involved in resistance and their interactions with climate variables, scientists can develop targeted approaches to mitigate resistance development and improve the sustainability of pest control efforts.

2.1. How Climate Change Can Affect Insecticide Resistance

Target site modifications, metabolic detoxification, lower penetration, higher excretion, and behavioural changes are a few of the factors that contribute to pesticide resistance. Insects can resist the harmful effects of insecticides thanks to these strategies. Target-site resistance and metabolic resistance have been the main topics of research throughout the past few decades. Target-site resistance arises from genetic mutations occurring in the specific target of the insecticide (Zafar et al. 2020). These mutations render the target less susceptible to binding with the insecticide or diminish its binding efficiency. Examples of target genes include ion channels like γ-aminobutyric acid (GABA) receptors and voltage-gated sodium channels, which are targeted by pyrethroid insecticides (Dong et al. 2014). Metabolic resistance, on the other hand, occurs when there is an increased activity of metabolic enzymes such as esterases, glutathione-S-transferases, and cytochrome P450s. This resistance mechanism is often associated with the overexpression of metabolic genes (Fig. 2) due to the evolution of cis-regulatory elements, leading to higher levels of these enzymes (Pu et al. 2016). Another mechanism contributing to metabolic resistance is gene amplification, which involves an increase in the copy number of the metabolic genes. In some cases, coding changes in these genes can also enhance their enzymatic activity, resulting in more efficient insecticide metabolism (Ibrahim et al. 2015). The alleles responsible for target-site and metabolic resistance tend to have higher frequencies in populations that experience continuous selective pressure from insecticide usage. As insects are repeatedly exposed to insecticides, these resistance alleles become favored and spread within the population (Weedall et al. 2019).

Understanding the genetic and molecular underpinnings of these different mechanisms of insecticide resistance provides insights into how resistance evolves and spreads in response to selective pressures. This knowledge is crucial for the development of effective strategies to manage insect pests while mitigating the development of resistance.

2.2. Thermotolerance and Insecticide Resistance

It has been discovered that the *Rdl* gene is duplicated in populations of *D. melanogaster*. The susceptible allele is present in one copy, whereas the resistant mutation is present in the other copy. This duplication reduces the temperature sensitivity while producing intermediate resistance to dieldrin (Kliot and Ghanim 2012). As a result, a condition of persistent heterozygosity is created at this locus, suggesting that it may have evolved as a way to balance

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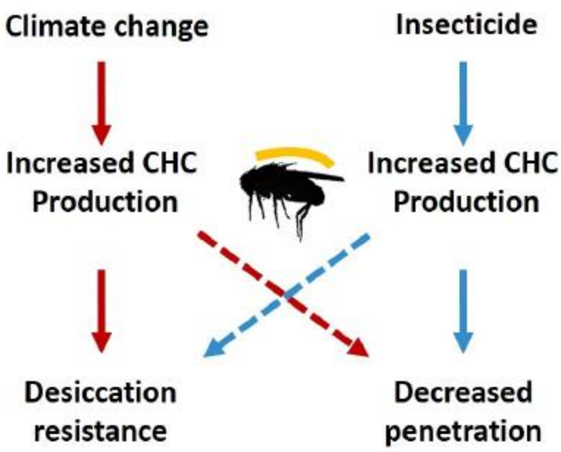

Fig. 1: Either adaptation to more arid environment or response to insecticide usage could lead to an increase in cuticular hydrocarbons (CHCs) production, leading to a thicker epicuticle and both desiccation resistance and decrease insecticide penetration. In other words, adaptation to one stress would also facilitate adaptation to the other stress (Pu et al. 2020).

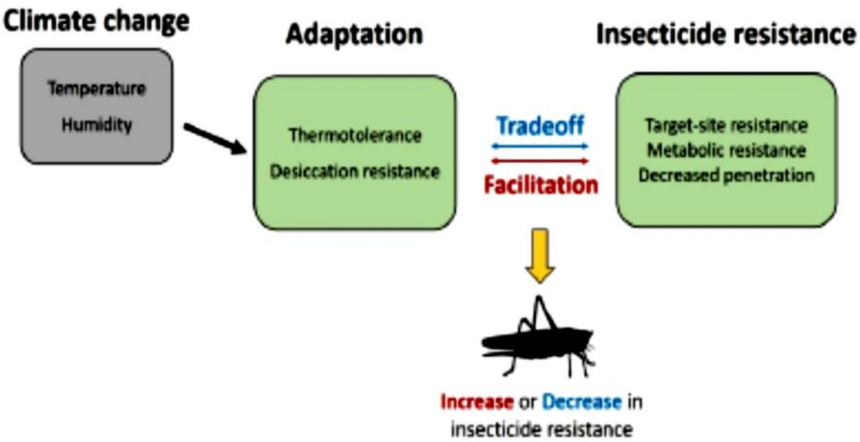

Fig. 2: Adaptation to changes in temperature and humidity as a result of climate change may lead to tradeoffs or facilitation with insecticide resistance due to pleiotropy, shared genetic mechanisms or genetic linkage (Pu et al. 2020).

the effects of heat and pesticide selection. It is worth noting that in several insect species, substitution at the same alanine residue in the *Rdl* gene confers similar resistance to cyclodienes, and duplication of the *Rdl* gene has also been observed in some of these species. This implies that parallel evolution leading to comparable systems balancing pesticide resistance and thermotolerance may be a frequent occurrence at the *Rdl* locus in other insect species. However, further experimental evidence is needed to validate these findings (Ffrenchconstant et al. 1993).

Another example that illustrates the evolutionary strategy of evolving permanent heterozygosity at insecticide resistance loci to manage fitness costs is the acetylcholinesterase (ace-1) gene. Mutations in the ace-1 gene confer resistance to organophosphate and carbamate insecticides, which are commonly used to control the malaria mosquito *Anopheles gambiae*. However, these mutations also come with a fitness cost when compared to the susceptible allele (Assogba et al. 2016). In field-collected populations of *An. gambiae* from various African countries, permanent heterozygosity has evolved at the ace-1 locus. This genetic adaptation results in mosquitoes immediately displaying an insecticide resistance phenotype. As a result, there is a significant decrease in the fitness cost associated with resistance. This allows the "permanent heterozygous" allele to spread within the population (Assogba et al. 2016).

In scenarios where there are no tradeoffs and continuous selective pressure from insecticide use, resistant alleles are advantageous and are expected to become fixed in the population. Examining selective sweeps at resistance loci will show this. The increase in resistant allele frequencies in habitats with higher temperatures, however, may be constrained when there is a trade-off between thermotolerance and pesticide resistance, as susceptible alleles continue

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to exist in the population. A notable example of this tradeoff is observed at the *Cyp6g1* locus in *D. melanogaster* (Battlay et al. 2018).

In the same study, it was found that chromosomal inversions are more prevalent in regions with higher temperatures. One specific inversion, known as In(3R)Payne, has previously been linked to adaptation to climate and occurs at increased frequencies in hot areas of Australia. Interestingly, these chromosomal inversions contain alleles linked with insecticide sensitivity. Due to the genomic structures of these inversions, which limit recombination, the introgression of insecticide resistance alleles is hindered or slowed down. As a result, the spread of resistant alleles is restricted in warmer regions where these inversions are more common. This suggests that tradeoffs between alleles conferring thermotolerance and insecticide resistance play a role in regulating the insecticide tolerance alleles in hot areas (Pu et al. 2020).

2.3. Humidity, Desiccation Resistance and Insecticide Penetration

Humidity and desiccation resistance play important roles in the effectiveness of insecticides and their ability to penetrate insect cuticles. The interaction between humidity levels and desiccation resistance can impact the efficacy of insecticides and resistance development in insect populations. Humidity is the amount of moisture present in the air, and it can affect insect behavior, physiology, and survival. Insects are highly sensitive to changes in humidity, as their small body size and relatively large surface area to volume ratio make them susceptible to desiccation. High humidity levels can create a more favorable environment for insect survival by reducing water loss through their cuticles. On the other hand, low humidity levels can lead to increased desiccation stress, which can be detrimental to insect populations (Zafar et al. 2020).

Desiccation resistance refers to an organism's ability to withstand or resist water loss. Insects have evolved various adaptations to combat desiccation, such as specialized cuticles, wax layers, and physiological mechanisms to regulate water balance. These adaptations enable insects to survive in arid environments and under conditions of low humidity. The relationship between humidity, desiccation resistance, and insecticide penetration is complex. The cuticle of an insect acts as a protective barrier against external threats, including insecticides. The efficacy of insecticides depends on their ability to penetrate the insect cuticle and reach the target site within the insect's body. However, the presence of a highly impermeable cuticle or adaptations for desiccation resistance can also limit the penetration of insecticides (Pu et al. 2020).

Insects with highly impermeable cuticles or efficient desiccation resistance mechanisms may have reduced susceptibility to insecticides. The cuticle's ability to retain moisture and prevent water loss can also hinder the entry of water-based insecticides. In such cases, alternative strategies or different types of insecticides may be required to effectively control resistant populations. Conversely, certain environmental conditions, such as high humidity, can enhance the penetration of insecticides through the insect cuticle. Increased humidity can soften the cuticle, making it more permeable to insecticide molecules. This can improve the efficacy of insecticides and increase their toxic effects on insect populations (Van den Berg et al. 2022).

The interplay between humidity, desiccation resistance, and insecticide penetration has implications for the development of insecticide resistance. Insects with enhanced desiccation resistance may possess traits that confer cross-resistance to insecticides. These traits can be selected for in environments with high insecticide usage and arid conditions, leading to the evolution of resistant populations. Understanding the intricate relationship between humidity, desiccation resistance, and insecticide penetration is crucial for developing effective pest management strategies. It requires considering environmental factors and the physiological adaptations of target insect species. By considering these factors, researchers and pest control professionals can optimize the use of insecticides and develop alternative approaches to combat insecticide resistance in diverse environmental conditions (Zafar et al. 2020).

In addition to the rising global temperatures associated with climate change, changes in rainfall patterns and increased drought conditions are also anticipated worldwide. These shifts can result in both increased aridity in certain regions and heightened humidity in others. Consequently, insects may undergo adaptive changes to cope with desiccation stress in arid areas. The primary mechanism underlying the evolution of desiccation resistance in insects involves reducing water loss through their cuticles. The cuticle of insects comprises a layer of hydrophobic cuticular hydrocarbons (CHCs) located on the outer surface of their bodies. This layer plays a vital role in regulating water loss by diminishing the rate of evaporation through the cuticle. The synthesis of CHCs occurs within specialized cells called oenocytes, involving a series of enzymes, including desaturases, elongases, and reductases, which metabolize acetyl-CoA to alcohols and aldehydes. Ultimately, a cytochrome P450 enzyme known as *CYP4G* catalyzes the final step of decarbonylation, converting these compounds into long-chained hydrocarbons (Qiu et al. 2012).

The significance of CHCs in desiccation resistance has been demonstrated in studies involving *D. melanogaster*. By using RNAi to suppress the expression of the *CYP4G* ortholog, *Cyp4g1*, researchers were able to eliminate all CHCs, leading to increased desiccation sensitivity in *D. melanogaster*. Moreover, variations in the composition and levels of CHCs have been positively correlated with differences in desiccation resistance among insect species. These findings highlight the role of CHCs in the adaptation of insects to desiccation stress. The composition and levels of CHCs can vary among species and contribute to differences in their ability to withstand desiccation. Such adaptations may enable insects to survive and thrive in environments characterized by altered humidity levels resulting from climate change. Further research is necessary to explore the specific mechanisms and genetic factors governing desiccation resistance and CHC synthesis in diverse insect species across various habitats and climatic conditions (Qiu et al. 2012). The relationship between cuticular hydrocarbons (CHCs) and desiccation resistance is distinct from their connection to insecticide resistance. However, reduced insecticide penetration has been proposed as a mode of insecticide resistance alongside target-site and metabolic resistance mechanisms. While the genetic basis for reduced insecticide penetration has not been extensively elucidated, recent research has shed light on the mechanistic link between insecticide resistance due to reduced penetration and an increase in CHC production in *An. gambiae*, the malaria mosquito. In summary, while desiccation resistance and insecticide resistance are distinct phenomena, this study revealed a specific mechanistic link between increased CHC production, reduced insecticide penetration, and insecticide resistance in An. gambiae. Further research is needed to explore the extent of this mechanism in other insect species and its relevance to insecticide resistance across diverse environments and insecticide classes (Balabanidou et al. 2016).

Furthermore, a recent study that focused on the brown planthopper *Nilaparvata lugens* found a functional connection between enhanced pesticide penetration and desiccation susceptibility. Two *CYP4G* homologs, *Cyp4g76* and *Cyp4g115*, were knocked down via RNAi in *N. lugens*. Four insecticides pymetrozine, imidacloprid, thiamethoxam, and buprofezin have greater penetration rates as a result of the knockdown because there are less CHCs on the cuticle, which lowers the barrier to desiccation. This This work revealed the modulatory role of the CHC layer in desiccation resistance and insecticide penetration but also suggested that this route of cuticular penetration may give resistance to different pesticide classes (Balabanidou et al. 2016).

Together, these findings highlight the importance of CHCs in the regulation of both desiccation resistance and insecticide penetration. They provide evidence that the overexpression or knockdown of specific *CYP4G* genes can influence CHC levels and subsequently affect the permeability of the cuticle to insecticides. This mechanism appears to be conserved across different insect species and may contribute to resistance against multiple insecticide classes. Further research is necessary to explore the extent and significance of this mechanism in various insect species and its potential implications for insecticide resistance management strategies (Chen et al. 2020).

3. Conclusion

The genetic basis of insecticide resistance is complex, involving a combination of natural genetic variation, gene amplification, gene mutations, and gene flow between populations. The article emphasizes the significance of understanding the underlying genetic mechanisms responsible for resistance, as this knowledge can inform the development of effective pest management strategies. By elucidating the specific genes involved in resistance and identifying the genetic markers associated with resistance traits, researchers can devise targeted approaches to mitigate the spread of resistance and optimize the use of insecticides. In conclusion, the article highlights the intricate interplay between climate change, insecticide resistance, and the genetic adaptations of insect populations. It emphasizes the need for ongoing research to elucidate the genetic mechanisms underlying resistance and to develop sustainable pest management strategies that consider the influence of climate change. By addressing these challenges, we can work towards safeguarding agricultural productivity, reducing reliance on chemical insecticides, and promoting environmental sustainability in the face of a changing climate.

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