

***Geographic dispersion of invasive crop pests: the role of basal, plastic climate stress tolerance and other complementary traits in the tropics***

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## **1.0. Highlights**

- High basal and plastic tolerance to stress promote pest invasion
- Polyphagy and diverse reproductive strategies aid invasiveness
- Rapid evolution to stress resistance is a common trait in prolific invasive pests
- Integrated stress resistance may form complex distribution patterns in pests
- Future models should incorporate effects of divergent interacting stressors

## **Abstract**

Global pest invasions have significantly increased in recent years. These invasions together with climate warming directly impact agriculture. Tropical climates feature extreme weather events, including high temperatures and seasonal droughts. Thus, successful invasive pests in tropics have to adapt to these extreme climate features. The intrinsic factors relevant to tropical

invasion of insects have been explored in many studies, but the knowledge is rather dispersed in contemporary literature. Here, we reviewed the potential biophysical characters of successful invasive pests' adaption to tropical environments including (1) inherent high basal stress tolerance and advanced life-history performances, (2) phenotypic plasticity, (3) rapid evolution to environmental stress, polyphagy, diverse reproductive strategies and high fecundity. We summarised how these traits and their interactive effects enhance pest invasions in the tropics. Comprehensive understanding of how these characters facilitate invasion improves models for predicting ecological consequences of climate change on invasive pest species for improved pest management.

### **Key words**

Climate change; environmental stress adaptation; invasive insect species; pest management; phenotypic plasticity

### **1.0 Introduction**

Increasing agricultural intensification, international trade of agricultural products, globalisation and anthropogenic climate change lead to the rise in invasive pest species, especially in tropical and sub-tropical environments (1, 2). Pest insects e.g. *Spodoptera frugiperda*, *Tuta absoluta*, *Bactrocera dorsalis*, *Prostephanus truncatus*, *Halyomorpha halys* and others have recently invaded new tropical and sub-tropical regions (2, 3, 4\*\*, Table 1). The invasions weaken the resilience of agricultural ecosystems and alter ecosystem integrity to disturbance (5). Coupled with frequent heat waves and droughts under climate change (6), these invasive pests limit the food and fibre productivity of agroecosystems (7), consequently threatening food security and livelihoods in the tropics (5).

Invasive species need to overcome many barriers of geographic, environmental, reproductive and dispersal factors across the invasion continuum before becoming naturalised in new habitats (8, Fig. 1). Only a few organisms survive the acute, chronic, and stochastic forces along the invasion continuum to become naturalised (9). The species with high invasiveness usually have common biological and physiological traits that make them thrive in new environments. First, they are polyphagous, metabolically flexible and have the capacity for host plant switching (10\*, 11, Table 1). Second, they have strong dispersal ability either passively as stowaways (12, 13\*) or actively through wind assisted adult flights or larval silking (9, 13\*). Third, they have higher fitness and quickly adapt to new environments (14\*\*). Fourth,

they inherently have high stress resistance e.g. to high temperatures, low humidity or desiccation and starvation (15).

Tropical climates usually feature long-term high mean temperatures, seasonal droughts and extreme weather events (16). As such, this facilitates pest invasions directly through altering habitats or indirectly by negatively affecting the survival of potential natural enemies through top-down effects (17\*\*). Furthermore, high terrestrial eutrophication will impact ecosystem integrity and services (1) and in turn facilitate pest insect outbreaks through bottom-up effects (17\*\*). For example, tropical climates feature high and extreme temperatures that facilitate rapid reproduction and higher functional responses (6, 10\*, 11). Similarly, these climate events create new environments that support new species entering ecosystems and becoming invasive (9,17\*\*). Extreme weather events also promote invasive pathways through e.g. modifying species hierarchies across tropical ecosystems, resulting in shifting species dominance and invasions and through failed natural biological control by depressing predation and/or parasitism (17\*\*). Indeed, numerical values of invasive pest propagules and the spatial-temporal patterns may be favoured under anthropogenic induced environmental changes thereby facilitating invasive pest species establishment (18).

Many abiotic factors, e.g. temperature, relative humidity (RH), precipitation, atmospheric pressure, wind (3,13\*) and biotic processes e.g. predation and/parasitism, feeding and/reproductive strategies act singly or interactively impacting on invasiveness (19\*\*). Tropical climates usually feature long-term high mean temperatures, seasonal droughts and extreme weather events (16). Thus, temperature and desiccation resistance are the most significant in shaping the fate of invasive species in tropical environments (14\*\*, 15). The actual stress tolerance comprises basal and plastic tolerance. Basal represents an inherent tolerance independent of environmental conditions (20). Whereas plasticity copes with environmental variation to enhance survival under extreme environments following exposure to sub-optimal conditions, involving hardening (exposing for a few minutes to hours) or acclimation (exposing for days or even weeks) but with no genetic changes (20, 21\*\*). Plasticity can also be developmental, transgenerational or be carried over from one developmental stage to another (carry-over effects) (21\*\*) and can manifest on different traits in morphology, physiology, behaviour and biochemical processes (21\*\*). Unravelling these factors and the links to species invasion are of paramount significance to both ecology and pest management.

Here, we review how resistance to biophysical factors either singly or interactively aid invasiveness of pest insects. Specifically, we discuss (1) short term responses to stress, (2) medium to long-term responses, (3) carry-over and transgenerational plasticity (4) rapid

evolution in basal and plastic stress tolerance and (5) emerging physiological and biological traits that are common amongst prolific pest invaders. Tolerance to climate factors, plus flexible biological traits e.g. in feeding and reproductive strategies enhance dispersal and invasion of pest insects. Explaining functional mechanisms of basal and plastic tolerances in spatial-temporal dispersal may help refine predictive models for invasive species, identify invasion risks and improve mitigation measures.

## **2.0. What is the role of basal stress tolerance in invasive insect pest dispersal?**

Environmental stress, particularly heat stress constrains phenology, abundance and invasiveness of pest populations (3). Because invasive species in the tropics experience chronic heat stress, they are likely to possess higher inherent basal stress tolerance (without prior acclimation) as an adaptive mechanism to survive heat stress associated with novel and dispersal environments (22). High basal temperature tolerance has been reported to drive invasive species dispersibility amongst pest insects (23). Given that heat stress often occurs concomitantly with desiccation or starvation stress, insects with integrated resistance of these stresses remain successful invaders (19\*\*). For example, high basal tolerance facilitated invasiveness of *Corythucha ciliata* (24) and *Bemisia tabaci* (25). Similarly, invasive *B. tabaci* MEAM 1 (Middle East-Asia Minor 1, previously known as biotype B) is known to survive very high temperature (~42°C) and low RH (~10%) in austral summer habitats (22). In addition, it tolerates heat stress better than other whitefly species (22). This inherent basal heat resistance reportedly explains geographic expansion of *B. tabaci* MEAM 1 in Colombia following prolonged heat and drought spells between 1997-2003, and resultant displacement of biotype A (22). Expression of stress-inducible heat shock proteins (Hsps) may partly account for insect heat tolerance (21\*\*). Indeed, higher basal expression of Hsps have been reported for highly invasive *Drosophila melanogaster* (26), and *B. tabaci* MED versus *B. tabaci* ZHJ1 (27). Different traits of basal heat, desiccation and starvation resistance are also key for invasive success (28). For example, invasive stemborers, *Chilo partellus* had higher upper thermal limits (UTLs) compared to indigenous African stemborers (29), likely aiding dispersal, competitiveness and overall invasiveness. Similarly, invasive *Ceratitis capitata* showed higher UTLs relative to congeneric indigenous species *Ceratitis rosa* (30). Invasive *Cydia pomonella* and *B. tabaci* MED also exhibited higher ULTs than related local *Thaumatotibia leucotreta* and *B. tabaci* ZHJ1 respectively (17\*\*,27). As such, basal heat resistance reportedly improves the dispersal ability and invasiveness of pest insects.

Many other abiotic stress resistance traits are significant for insect pest invasion propensity (reviewed in Ref. [3]). Indeed, tolerance to these other abiotic factors e.g. RH, precipitation, atmospheric pressure, altitude and wind currents may also affect invasiveness (13\*). Similarly, predation and/parasitism, feeding and/reproductive strategies can also act singly or interactively with climate stress tolerance in augmenting invasiveness (19\*\*). For example, basal starvation tolerance, and the flexibility of metabolism under resource constraints also facilitate invasion (11). Moreover, given the significance of integrated stress resistance (ISR) (19\*\*), starvation acclimation reportedly improved basal heat tolerance in invasive stemborer *C. partellus* but not in indigenous ones, *B. fusca* and *S. calamistis* (29), enabling its geographical range extension (29). This dispersal edge is likely necessitated by its inherent high basal starvation and desiccation stress (29). Moreover, ISR has also been reported in invasive stored grain pest *P. truncatus* (31). As such, it appears that common prolific pest invaders have high basal stress resistance and ISR (19\*\*) and this potentially mediates geographic dispersion.

### **3.0. The complementary role of phenotypic plasticity to basal stress tolerance in pest invasiveness**

Phenotypic plasticity is the environmentally induced, non-heritable variation in phenotypes produced by the same genotype in response to different environments (21\*\*,32). While phenotypic plasticity is near ubiquitous in insects, its role in buffering tropical organisms may be more complimentary owing to the trade-off between plasticity and basal stress resistance (20,33). Studies on the impact of warming on insects across latitude showed narrow thermal breath for tropical species (34) due to high basal heat tolerance (low safety margins) and limited plasticity (33,35,36). Therefore, high basal stress tolerance may remain more important for tropical organisms than plasticity (36), although the latter may play a complementary role for tropical pest invasiveness. Given environmental heterogeneity across the invasion continuum, plasticity may be the currency of rapid adaptation that outweighs genetic adaptation and complements basal tolerance in facilitating rapid evolutionary thermal shifts (37\*), amplifying thermal safety margins under sub-optimal novel dispersal environments (32). Invasive species are typically more phenotypically flexible than natives (14\*\*,37\*). Complete plasticity widens the breadth of species' ecological niches (32), significantly contributing to pest invasiveness. Consensus from individual studies (38) and/or meta-analyses (32, 37\*;) suggest that invasive species demonstrate higher plasticity than natives. Different types of phenotypic plasticity uniquely contribute to pest invasiveness (32) within short- (hardening), medium-

(acclimatization) to longer-timescales (e.g. epigenetic inheritance) (39). Thus, phenotypic plasticity may manifest within- (30) or across-generations (transgenerational) (40) and both significantly re-model survival and performance curves in invasive species (41). Within generations, adaptive plasticity thus creates new, ‘shifted’ phenotypic thermal optima that enables directional selection optimising key fitness traits (32,38). Similarly, reports suggest invasive species invest more in plasticity of key ecologically important traits (42\*) that potentially improve their dispersal ability (19\*\*). Across generations, epigenetics may significantly contribute to pest species survival. Through transgenerational plasticity, insects adapt extremely rapidly outside the relatively slower natural selection (43\*\*). For pest species, this is critical for surviving new stressful environments. Nevertheless, the role of plasticity for tropical species is often debatable in literature owing to the trade-off between basal heat tolerance and plasticity (20, but see Ref. [44]). As such, we argue that while basal heat tolerance may be more pertinent for tropical organisms, phenotypic plasticity may complement high basal traits thus, nuancing invasion success in tropical species.

In non-crop invertebrate species, higher plasticity has also been reported in invasive relative to native species e.g. *Prinerigone vagans* and *Myro kerguelensis* (45), *Bombus terrestris* (L.) (42\*), in springtails species (38) and other invasive species (14\*\*). Indeed, responses of species to acclimation, measured as acclimation response ratios (ARRs), is much higher in invasive than native species (14). Based on evidence from literature, ARR ranged 0.0 – 0.70 °C/°C and -0.42 – 0.19°C/°C between invasive and native species respectively (14\*\*,33). In crop pests, Ref. (29) showed similar trends for invasive versus native stemborer species. Related studies have also been in consonance, and consistently showed higher plasticity for invasive than indigenous species. For example, invasive *P. truncatus* is likely more thermally plastic than native *Sitophilus zeamais* (31) and may explain its higher dispersal competitiveness (46). In fruit flies, Ref. (30) demonstrated that invasive *C. capitata* was more thermally plastic than native congeneric *C. rosa*, and models suggested improved plasticity may contribute to higher invasiveness for the invasive *C. capitata*. Similar reports have also been documented for other fruit fly pests e.g., *Drosophila suzukii* (47), and the global pest invader, *T. absoluta* (13\*). An increasingly growing body of evidence suggests that invasive species may use different forms of plasticity adaptively to survive novel stressful environments and this may partly facilitate their invasiveness.

#### **4.0. The rapid evolution of stress tolerance**

Novel environments in the invaded regions will impose strong climatic selection on invasive insects. One of the main reasons for invasive pest insects' success is their high potential to rapidly evolve tolerance to climatic change (48\*) and this facilitates dispersal and adaptation to new environments (49). The frequent extreme high temperatures in tropics may provide thermal conditions to induce rapid evolution of thermal tolerance. The rapid thermal evolution occurs more frequently in insect species with short generation time, high fecundity and high heritability in thermal tolerances (21\*\*). Approaches for studying rapid evolution of stress resistance traits mainly include comparing thermal tolerances and/or other fitness-related metric distributions across geographical populations (50), conducting thermal selection experiments to identify the heritability of thermal tolerance traits (51\*\*) and/or modelling the response to selection of these specific traits thereof (48\*,52). However, most existing research on rapid evolution of stress tolerance traits have mainly focused on model species e.g. *Drosophila* and ants (53, reviewed by Ref. [21\*\*]), with little attention on major invasive agricultural insect pests. Related studies have only investigated introduced populations, lacking comparative studies (e.g. on indigenous vs. invasive species and native vs. introduced populations) (48\*). This has made it difficult to understand the evolutionary mechanisms of biological invasion under rapidly changing climates.

Although some previous research showed that animals, including insects, may have insufficient adaptive potential to deal with climate change (48\*), a few existing studies support that invasive insect species have strong and rapid evolutionary abilities for traits of heat and cold tolerances (50). The methods used in thermal selection experiments, e.g. static temperatures versus ramping rates can nevertheless affect the heat tolerance selection in insects (52), highlighting the complexity of insects in response to artificial or natural thermal selection. However, the invasive *B. tabaci* MEAM 1 and *B. tabaci* MED and cereal aphids show rapid evolutionary responses to thermal selection for heat tolerance e.g., UTLs, heat knockdown time and critical thermal maxima (51\*\*). This high adaptive potential increase invasiveness through facilitating dispersal and colonisation of harsh tropical climates. Thus, more studies focusing on the evolutionary potential of invasive crop pest species especially those in tropic regions and the comparative studies concerning indigenous versus invasive species and native versus introduced populations are warranted in the future.

Recent, genomic tools can provide insights in the genetic signatures of thermal selection, which may enable us to understand the mechanisms underlying the adaptive evolution of invasive insects in response to climate change via accelerated mutation rates, increased genetic diversity and enhanced plasticity (43\*\*,54). However, the major challenge of using genomics is the

difficulty in disentangling the labyrinth of genomic information to link related phenotypic traits to the exact genetic agents driving adaptive evolution of stress tolerance during natural climatic selection (55), but on the other hand, meaning a highly potential of genomic data in understanding the processes of species invasiveness in further studies.

### **5.0. Emerging patterns and complimentary mechanisms of prolific pest invaders**

There are several emerging physiological and biological traits that are common amongst prolific agricultural insect pests that partly explain their invasiveness. Whilst abiotic factors are key determinants to range expansion of invasive insects, biotic interactions e.g. mutualistic and parasitic relationships equally mediate biological invasions (3). One key trait that may enhance pest invaders' establishment in new environments is their escape from specialist natural enemies as postulated by the Enemy Release Hypothesis (56). However, invasive species establishment is mostly dependent on propagule pressure (18). Where propagule size and rate of introduction is high, invasive pest species can better withstand environmental stochasticity such as thermal variability mediated by demographic parameters such as sex ratio and fecundity (18). Thus, demographic and environmental stochasticity interact to determine pest geographic dispersion and invasion success. Indeed, the invasion success of *S. frugiperda* has been partly attributable to its high parental propagules (12).

Another key emerging feature among prolific invasive pests is their polyphagous nature and high functional responses enabling efficient exploitation of resources (10\*). For example, the top ten most destructive invasive agricultural insect pest species are highly polyphagous (3). The alternative hosts typically overlap between crops and weeds. These serve as refugia for off-season propagation and maximise spatial success following dispersal. Such feeding strategies ensure population persistence, population build up and more competitive niche exploitation. Similarly, invasive pest species have striking metabolic flexibility (11) that allows them to utilise spatially diverging resources under sub-optimal conditions while minimising energetic costs.

For many prolific invasive pests, high fecundity and short generation times coupled with multivoltinism are common traits. This ensures population persistence following introduction even in the face of stochasticity while minimising Allee effects (3,57). These Allee effects manifest in newly introduced opportunities because of limited opportunities for reproductive encounters. At low population densities, some insects struggle to locate conspecific thereby curtailing population growth. Some invasive insect pest species reportedly employ adaptive parthenogenetic reproductive strategies that allow for rapid exploitation of



resources and enable the low-density insect populations to escape local extinction due to Allee effects (57), at least perhaps in the short term. Over longer time scales, persistent overflowing of the population with a male biased sex-ratio owing to arrhenotoky may lead to population collapse due to the same Allee effects (3). Nevertheless, obligate sexually reproducing species remain more vulnerable even at higher densities as several factors may directly or indirectly introduce the Allee effects. For example, some studies have shown sex differences in tolerance to physiological stressors such as starvation and thermal stress (58). Theoretically, such sex differences can introduce Allee effects in nature where one of the sex groups is not able to mate for a sustained period. Thus, diversity in reproductive strategies of pest insects e.g. parthenogenesis may aid invasiveness through facilitating demographic and environmental stochasticity.

While acclimation manifests within a species' generation and that evolution of stress resistance traits is generally slow (14,21), most successful invaders exhibit transgenerational plasticity and/or carry over effects (40). This epigenetic stress resistance inheritance facilitates invaders to quickly adapt to new dispersal environments outside more prolonged evolution of traits. Other factors that facilitate dispersibility of invaders have been well documented by Ref. (3). For example, rapid evolution of resistance to management strategies, successful mutualisms with diverse organisms across different niches have been reported. Furthermore, prolific invaders have been reported to have high stress tolerance (e.g. heat), are adaptable to diverse niches (3) with the capacity to escape harsher conditions through diapause. Similarly, immune priming and mutualist facilitation has been recorded in pest invaders, helping organisms (1) survive stressful biotic environments and (2) develop positive interactions with surrounding biotic environment (3). Such traits are critical and may facilitate invasiveness of pest insect species.

## **6.0. Conclusions**

Given the harsh thermal conditions in tropics, inherent high basal and complementary plastic responses, as well as rapid evolution in response to heat stress are likely to favour the geographic expansion of invasive crop pests. Besides thermal resistance, many other abiotic and biotic factors can facilitate pest invasions. For instance, desiccation and starvation also have potential to influence the distribution range of invasive insects (15,59). Importantly, desiccation and/or starvation tolerance can interact with thermal tolerance affecting local adaptation (59,60), highlighting the necessity to incorporate the potential interactive effects of divergent co-occurring stressors, i.e. ISR of invasive species (19\*\*), in prediction models of

potential invasion distribution. In addition, novel biotic interactions with other species, such as weakened top-down control by escaping from their natural enemies in non-invasive regions and strengthened mutualistic interactions with the species in invasive regions, may also aid pest invasion and establishment (3,17).

Some other inherent capacities and human-mediated factors can also facilitate invasion. The inherent flexibility in resource use and reproductive strategies can help invasive species survive and complete their life cycles in new environments. For example, resource availability is also a limiting factor for the geographic dispersal of invasive species. For oligophagous insects, their potential distribution ranges are largely constrained by the availability of the host plants. However, the polyphagous invasive species such as the whitefly, *Trialeurodes vaporariorum* (61) and the spotted wing drosophila, *D. suzukii* (62\*\*) can exploit novel food sources, and retain high reproductive capacity, facilitating rapid range expansion. The flexibility in reproductive strategies such as sporadic parthenogenesis may aid invasiveness through initial population establishment and persistence. Furthermore, human-introduced agricultural practices such as irrigation and pest management can also affect the potential invasion range. Irrigated crops are likely to eliminate or reduce thermal and desiccation stress by providing more suitable microhabitats with cooler and moister microclimates within crop canopy and/or on soil surface relative to rain-fed crops (63). This increases habitat favourability and increases the potential risk of colonisation by invasive pests. The evolutionary responses to thermal stress may interact with pesticide resistance (64), leading to complicated and difficult predictions of potential invasion distribution range. As such, the future challenges are to understand the trade-offs between basal and plastic stress tolerances (20, 33,65) and between stress tolerances and key life-history traits (21) as well as the antagonistic responses to multiple concurrent stressors in invasive pests (19), and importantly, to what extent these trade-offs may contribute to their geographic dispersion. Given the complexity of interacting factors affecting biological invasions, a holistic network approach involving direct and indirect interactive abiotic and biotic factors as well as human-mediated interventions and social interactions (66) is strongly encouraged to fully understand and accurately predict the geographic dispersion of invasive crop pests.

### **Declaration of interest**

N/A

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**\* of special interest**

**\*\* of outstanding interest**

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**Table legends**

Table 1: A list of some of the recent invaders of tropical and sub-tropical agricultural landscapes and their general host plants (2,67). The list may not be exhaustive but is meant to give a snapshot of some of the most successful invaders in tropical and subtropical environments.

## **Figure Legend**

Figure 1: An illustration of some of the environmental barriers that invasive species have to overcome and factors that may aid invasive species dispersal. We emphasise on how traits of basal and phenotypic plasticity to environmental stress tolerance may facilitate dispersal of invasive species in tropical environments and how the overlapping responses to environmental stress resistance and integrated stress resistance may improve dispersibility of invasive species, The roles of other resources (habitats and plant hosts) have been deliberately omitted for brevity.

**Table 1**

<b>Scientific name</b>	<b>Common name</b>	<b>Preferred hosts</b>
<i>Spodoptera frugiperda</i>	Fall armyworm	Maize, sorghum, cotton
<i>Bemisia tabaci</i>	Tobacco whitefly	Tomato, cotton
<i>Tuta absoluta</i>	Tomato leafminer	Tomato, potato
<i>Drosophila suzukii</i>	Spotted wing drosophila	Stone fruit and berries
<i>Ceratitis capitata</i>	Mediterranean fruit fly	Citrus, stone fruit and others
<i>Bactrocera dorsalis</i>	Asian fruit fly	Citrus, apple, stone fruit and others
<i>Cydia pomonella</i>	Codling moth	Apple
<i>Thrips tabaci</i>	Onion thrips	Onion
<i>Helicoverpa armigera</i>	Cotton bollworm	Cotton, chickpea
<i>Myzus persicae</i>	Green peach aphid	Potato, pepper
<i>Plutella xylostella</i>	Diamondback moth	Cabbage, other brassicas
<i>Aphis gossypii</i>	Cotton aphid	Cotton
<i>Diaphorina citri</i>	Asian citrus psyllid	Citrus
<i>Tribolium castaneum</i>	Red flour beetle	Wheat
<i>Eriosoma lanigerum</i>	Woolly apple aphid	Apple
<i>Brontispa longissima</i>	Coconut hispine beetle	Coconut
<i>Frankliniella occidentalis</i>	Western flower thrips	Many fruits and vegetables (plums, peaches, strawberries, grapes)

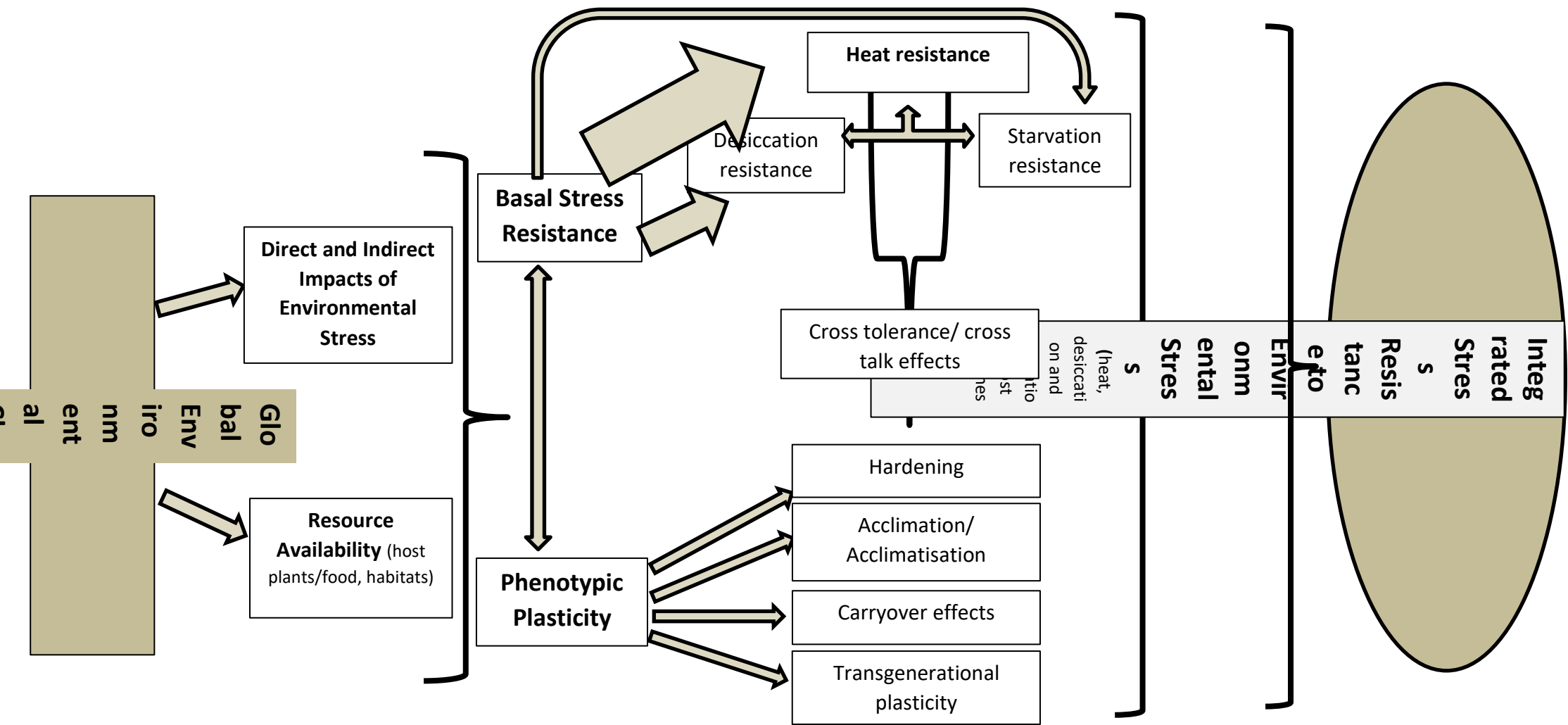


Figure 1