The life stages of the invasive ladybird, Harmonia axyridis. *The eggs (A) take 3-4 days to hatch once they are laid. Ladybirds stay in the larval stage (B) for around 3 weeks, after which they form a pupa (C). Adults emerge from their pupae 4-5 days later, and take around a week to become mature adults (D). Research on the thermal adaptation of the invasive ladybird Harmonia axyridis includes several life stages A. eggs, B. larva, C. pupa and D. adults, in order to make reliable predictions of its responses to climate change.* Image: Ingrid A Minnaar.

Ladybirds:
successful invaders in small packages

In a warming world, can an invasive ladybird take the heat? **Susana Clusella-Trullas**, **Michael Logan** and **Ingrid A Minnaar** ask the question.

Some invasive species are more successful and harmful than others. Pinpointing which species deserve the most attention remains a great challenge, especially given the complexity of biological systems. Scientists have devised several classification schemes based on the rate of spread and environmental impacts to figure out which species can be considered the worst invaders. This information can also be used to predict future impacts given scenarios of environmental change, such as global warming and habitat degradation. Among insects, the harlequin ladybird (*Harmonia axyridis*) is high on the list of successful invaders, with considerable risk to native diversity.

Invasive ladybirds

This small colourful beetle (see photo), native to Asia, triumphs as an invader by spreading fast and outcompeting indigenous ladybird species.

Its success is partly attributed to key characteristics that enable it to establish and spread rapidly in new environments. Individuals are large in body size relative to other aphid-eating ladybirds and can lay huge numbers of eggs over the course of their long lifespans. They are voracious predators with a broad diet preference, including feeding on their own eggs and siblings when food is scarce. They can also feed on the young of other ladybirds while simultaneously protecting their own progeny with chemical warfare. To make matters even worse, they may serve as vectors of disease because their immune systems appear superior to those of native ladybirds. The harlequin ladybird has become a nuisance in most places where it has been introduced by accident or intentionally as a biocontrol agent. It has negative effects on agriculture, human settlements and native ladybird diversity and abundance. It has now spread in four continents, and Africa is the most recent stop on its global conquest (see Box 1).

Spread in South Africa

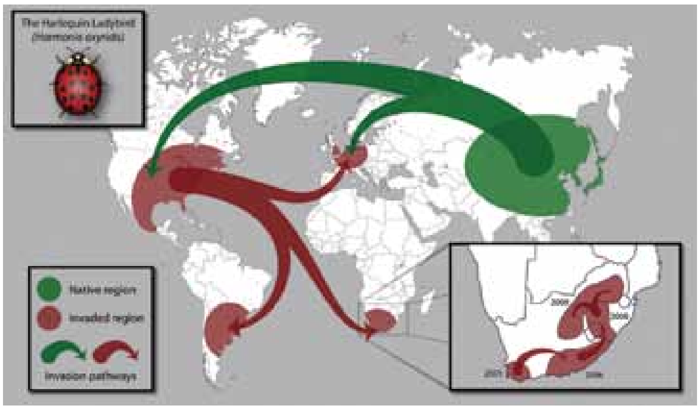
In 2004, the harlequin ladybird was recorded on a farm near Stellenbosch. Museum records later showed that specimens of these ladybirds had already been deposited as early as 2001. The species probably arrived in South Africa even earlier than this. The early discoveries of harlequin ladybirds in the Western Cape were just the beginning. Their numbers have increased and their populations have spread rapidly over the past decade. They are currently found in all provinces of South Africa, from sea level to mountain tops.

Despite their clear establishment and spread in South Africa, little is known about the ecology and evolution of the harlequin ladybird in the region. If we are to predict the future impacts and distributions of this invasive species, we must begin to examine the interactions between native and invasive ladybird populations and the ways in which these interactions change as the environment shifts around them.

The harlequin ladybird's global presence illustrates its ability to tolerate a wide range of climates: hot, cold, wet and dry. As the climate in South Africa becomes hotter and drier as a result of climate change, invasive ladybirds may gain an advantage over native species because of their adaptability. Three major mechanisms can contribute to being adaptable to climate shifts. First, ladybirds may use behaviour such as moving to more adequate climatic areas or regulate their body temperature by shuttling more efficiently or precisely among hot and cold patches. Second, they may have flexible physiological responses that compensate for extreme weather events such as heat waves or cold snaps associated with climate change. Finally, ladybirds could also adapt to a changing climate over the course of several generations through evolution. Here in the CLIME Lab at the Centre for Invasion Biology at Stellenbosch University, we are actively studying the effects of climate change on the interaction between native and invasive ladybirds by exploring these three facets.

Box 1

In a study published in 2010, Eric Lombaert and colleagues showed the spread of the harlequin ladybird across the globe. Native to Asia, it first appeared on the Eastern Seaboard of North America in 1988. From there it spread to three additional continents – to Europe, South America, and Africa in 2004 (with some evidence that a second colonisation of Europe from Asia occurred in 2001). Within South Africa (inset), ladybird records suggest that the beetle initially spread from Stellenbosch to the Eastern Cape, KwaZulu-Natal, the Free-State, and Gauteng by 2006. In 2009, it spread north into Mpumalanga and south-west into the hot and dry Northern Cape and North-West provinces.



This map shows the way in which the harlequin ladybird spread across the globe. Image: Corneile Minnaar

Behaviour and acclimation are the first lines of defence

In many parts of the globe, extreme weather events like heat waves are on the rise. These events can be extremely stressful to small 'cold-blooded' animals like insects whose body temperatures track ambient temperatures. However, insects have evolved several ways of dealing with rapid changes in temperature.

The first line of defence is usually a behavioural one. When temperatures spike, insects will move into a sheltered, shady patch of the habitat (to the underside of a leaf or underground) to prevent overheating. This kind of behaviour is known as 'behavioural thermoregulation' and is extremely common among species that do not produce their own internal heat (like mammals and birds). Behavioural thermoregulation increases insects' chances of surviving when the weather changes.

In order to assess how well the harlequin ladybird can overcome temperature variation using behaviour, we simulated their natural environment in the laboratory. This is not a simple task because the small size of insects means that they experience temperature at extremely fine spatial scales. We therefore mimicked the mosaic of the environment using small arenas with multiple 'warm' and 'hot' patches and examined their behaviour when facing good versus bad climate scenarios. These 'mini' landscapes can be altered to change the structure of the habitat or include natural complexity such as competitors, predators, and resource variation. We found that ladybirds adjust their behaviour depending on the quality of the thermal environment.

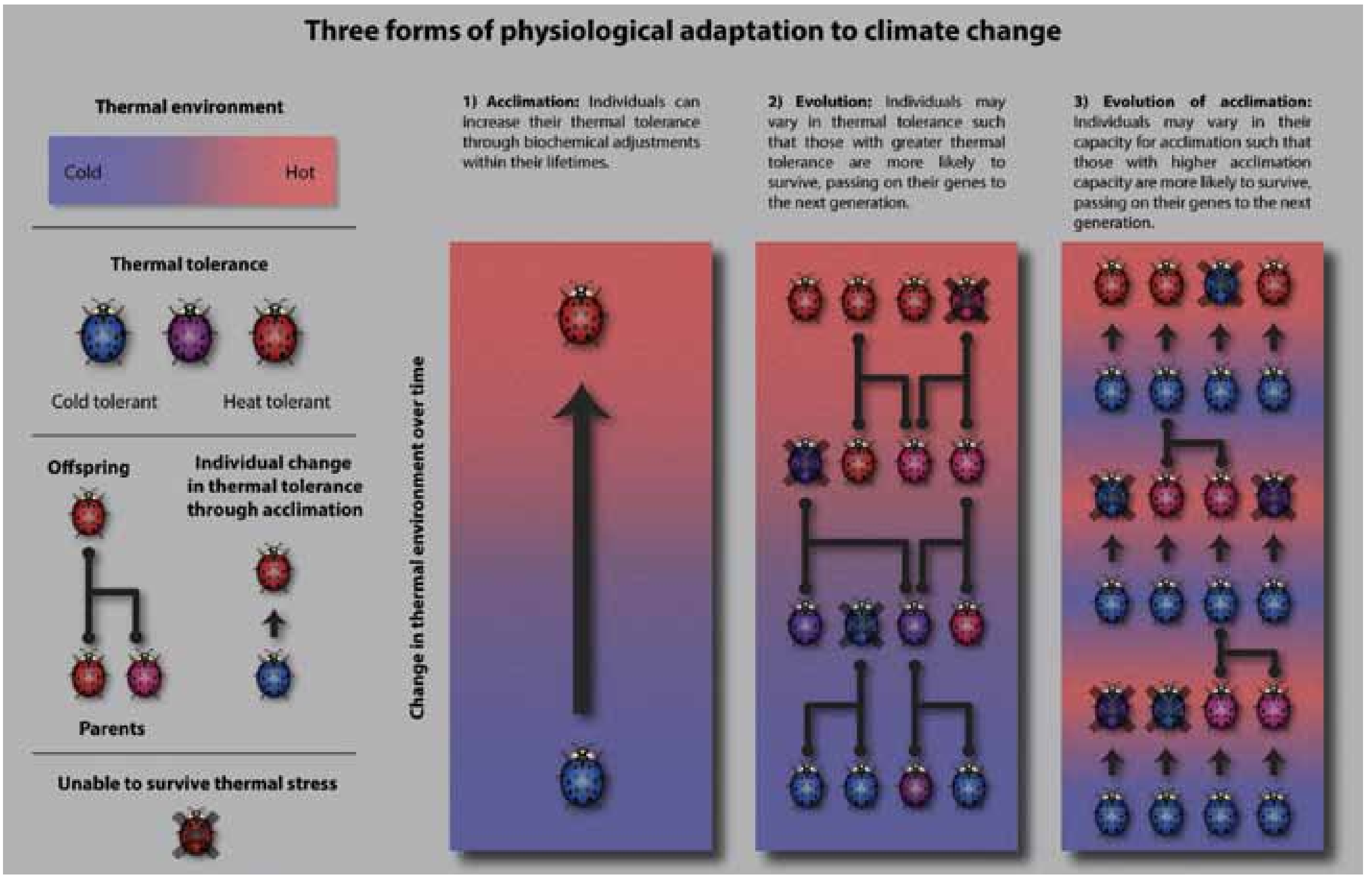
But sometimes thermoregulation is not enough. When the change in temperature is very rapid or the temperature hits extremes, insects may not have enough time to find a safe refuge. To survive these sorts of extreme events, individuals must *acclimate*. Acclimation is a direct physiological response to changing environmental conditions (see first panel in Box 2). For example, when an insect's body temperature rises sharply, certain genes are turned on that code for proteins whose specific job is to travel around the body repairing heat-induced tissue damage. These 'heat shock proteins' can persist within the animal's body for many days or even weeks, increasing its capacity to withstand additional heat waves.

Acclimatory responses to climate variation are thought to be short-term adaptive responses and are different from evolution because they occur within the lifespan of individuals. Our research examines these flexible responses across a wide range of traits, such as the highest and lowest temperature tolerated before the ladybird can no longer move away from a predator, the temperature selected by an individual when offered a broad temperature gradient, and changes in walking speed at different temperatures. We are combining these data to predict the short-term responses of harlequin ladybirds to temperature variation, and to predict their further spread into novel environments. We are also comparing native to invasive species – for example, can the harlequin ladybird acclimate to extremes faster or better than native ladybirds? Are larvae, pupae and adult ladybirds equally vulnerable to temperature variation? These questions are central to understanding the effects of climate change on biological invasions, and their answers will go a long way towards enabling us to accurately predict the future spread of the harlequin ladybird into other areas of southern Africa. However, behaviour and acclimation are only the first lines of defence against a changing climate. What about evolution?

Rapid evolution: will it tip the balance?

Since Charles Darwin first put forth his theory of evolution by natural selection in 1859, most scientists have considered evolution to be such a painfully slow process that we could only observe it indirectly (for example, by studying the fossil record). Selection experiments have now shown that,

Box 2



e.g., fruit fly body size and wing shape evolve rapidly and these changes can be observed in the lab after only a few generations (weeks to months).

In fact, many studies have successfully demonstrated evolution (even speciation) on extremely short time scales. It turns out we *can* observe evolution in real time. Remarkably, when a population contains genetic variation for some characteristic (say, the temperature at which they run fastest), and natural selection favours higher or lower values of that characteristic, observable evolution can happen after only a single generation!

The upshot of all this is that evolutionary change is likely to play a large role in determining the winners and losers in a warmer world. The species that can evolve the fastest will experience a smaller cost from changing conditions. This may give them the upper hand in competitive interactions with other species. If invasive species have particularly high evolutionary capacities, trouble is on the horizon.

Among individuals in a population, the degree to which variation in a trait is determined by genetics, independent of the environment, is referred to as the 'heritability' of the trait. All else remaining equal, the higher the heritability, the faster the trait can evolve.

Our research programme aims to generate breeding colonies of both the harlequin ladybird and the native lunate ladybird (*Cheilomenes lunata*) to study the genetics of several physiological traits in these species. The traits we are focusing on are thought to control the responses of insects to climate change, so understanding their evolutionary potential is important. In addition to measuring their heritabilities, we are also asking whether these traits are genetically correlated in ways that enhance or prevent evolutionary change. If harlequin ladybirds evolve more rapidly, it could mean that climate change will increase the extinction risk of native species by tipping the competitive balance in favour of the invasive species. In an interesting twist, it is not just the fixed thermal tolerance of a population that can evolve. Acclimation capacity itself can evolve when individuals vary in their ability to acclimate (see Box 2).

The general success of invasive species provides a hint that they may be more resilient to climate change than native species. At the CLIME lab we will continue to study the various mechanisms of adaptation to climate—behaviour, acclimation, and evolution—to better understand the impact of invasive species on South African ecosystems. **Q**

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