Ants as sentinels of the impact of global change

Auteur :
CORDONNIER Marion, Post-Doctorante, Université de Regensburg, LS Zoologie / Évolutionsbiologie, Allemagne

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Climate change and urbanization are determining factors in the distribution of species, dramatically threatening their persistence. Biological invasions modify the interactions between different species and are therefore also a major cause of concern for biodiversity conservation. What about ants in this changing world? Dominating many ecosystems, they have already colonized almost all terrestrial habitats. They are easily transported by humans because of their small size and nesting habits, and include some of the most invasive species in the world.

Ants do not produce internal heat and are dependent on the outside temperature (they are said to be ectothermic). They are therefore very vulnerable to climate change. In the past, they have answered many questions about ecology and evolution. How might ants help (and how do they already help!) to better understand global changes and their interactions?

1. Global changes: what impacts for biodiversity?

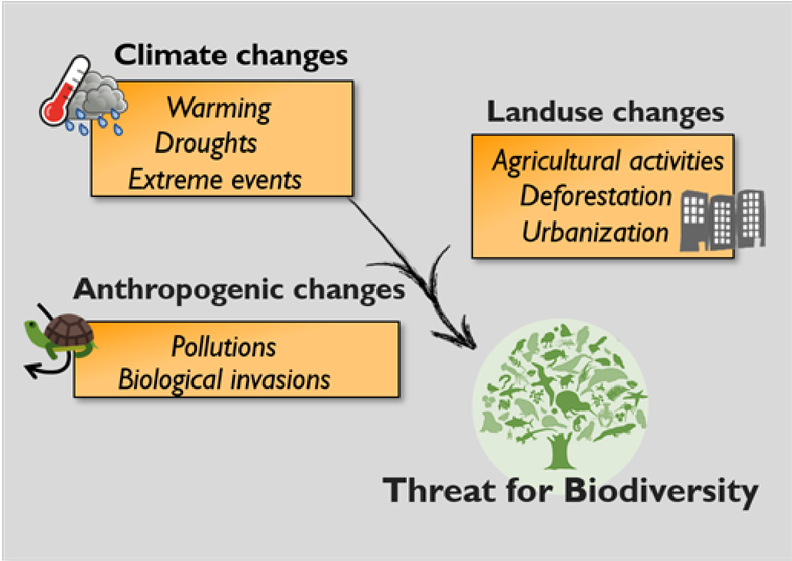

Figure 1. Major global changes. [Source: © Marion Cordonnier]

Biodiversity is facing increasing pressures from human actions, including habitat conversion and fragmentation, overexploitation of natural resources, pollution and climate change. These environmental changes are now clearly visible on a global scale, hence the name "**global changes**" (Figure 1). Of the global changes, perhaps the best known are climate change and urbanization. **Climate change** impacts the trends in climate variables (temperature, precipitation, etc.) and the frequency of climate events (floods, droughts). **Global warming** in the 21st century, for example, is of a magnitude comparable to the greatest global changes of the last 65 million years. Future climate projections predict a worsening of this global warming, but also a rise in sea level and an increase in the frequency and intensity of extreme events.

These changes have and will have considerable impacts on **biodiversity**, affecting individuals, populations, species and ecosystems. For example, changes in temperature can affect the survival, reproduction and geographical distribution of organisms, or even change their phenology, leading to the premature emergence of butterflies, the earlier return of migratory birds or the earlier flowering of plants (see Climate change and globalisation, drivers of insect invasions; How do birds adapt to a changing climate?).

Urbanization is also a rapid and large-scale global change that has a profound impact on biodiversity. Currently, more than 50% of the world's human population and about 80% of the European population live in urban areas [1]. Urbanisation has a recent but explosive growth trend in most European countries, affecting first the major cities, but also progressively smaller towns and even remote rural villages [2]. The **expansion of cities** is therefore an important cause of land conversion into urban landscapes that have been heavily modified by man. Urban areas are characterised by a high density of built-up areas, impermeable surfaces with high heat retention capacity, extensive transport infrastructure networks and a high intensification of agricultural activities on their periphery. For **biodiversity**, urban habitats are therefore profoundly modified habitats combining artificial surfaces, industrial pollution, anthropogenic disturbances and changes in energy and nutrient cycles. Urbanization thus affects all components of the environment, from soils and hydrology

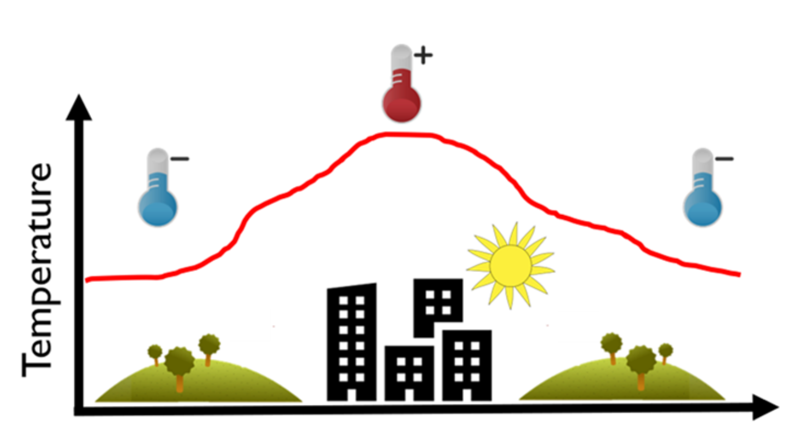

Figure 2: Urban Heat Island Effect. [Source: © Marion Cordonnier]

to vegetation and microclimates [3]. For example, cities are often warmer than nearby rural habitats (**Urban Heat Island** effect [4], Figure 2), with higher night-time temperatures or higher daytime maximum temperatures.

Consequently, from an ecological point of view, urbanization often has a negative impact on biodiversity. Cities are frequently located in naturally species-rich areas with serious conservation challenges [5]. In addition to the impacts already mentioned, urbanization can lead to a cascade of secondary effects on habitat quality, including a decrease in available habitats, high fragmentation of remaining habitats, and increased exposure to edge effects [6]. Consequences for biodiversity have been reported for many taxa (vertebrates, insects, plants, fungi and micro-organisms), for example in response to pollution, disruption of nutrient flows or landscape fragmentation (see Lichens and environmental quality).

Biological invasions [7] have also received increased scientific attention over the past two decades. Indeed, although strictly speaking they are neither new phenomena nor exclusively of human origin, the geographical scope of invasions, their recurrence rate and the number of species involved have increased sharply as a result of the development of transport and trade (see Climate change and globalisation, drivers of insect invasions; Why is the tiger mosquito so invasive?). The **role of humans** as "dispersers" of non-native species has thus probably surpassed that of natural dispersal, allowing them to overcome natural stochastic forces and biotic resistance (competition with local species) that would repel or eliminate introduced propagules [8]. Ecosystems and human society have thus been radically altered by the proliferation of invasive species, particularly in the current era of **globalization**. This current event of unprecedented mass invasion is now considered a unique form of global change [8].

As a result, biological invasions are currently one of the main concerns for **biodiversity conservation**. Non-native species negatively affect native species through a multitude of interactions, such as competition, predation, hybridization, herbivory, parasitism, but also indirectly through diseases or changes in disturbance regimes. Invasive non-native species modify the functioning of ecosystems, negatively affect populations of other species and cause local extinctions [9]. In the United Kingdom, for example, competition between the introduced grey squirrel *(Sciurus carolinensis*) and the native red squirrel *(Sciurus vulgaris*) has led to a drastic reduction in the range of the red squirrel [10].

2. Why study ants when we are interested in global change?

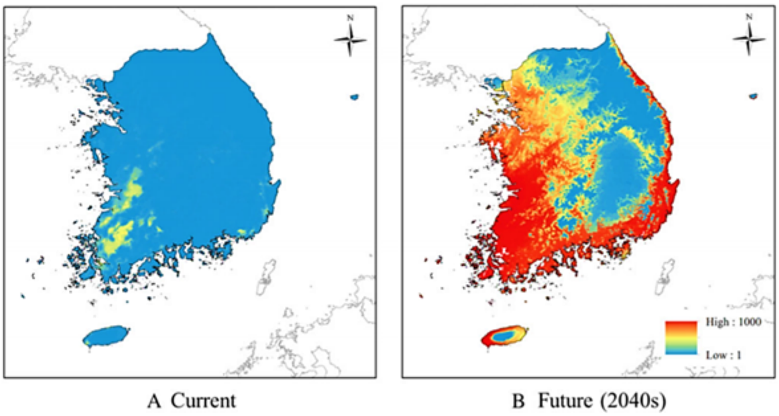

Figure 3. Potential distribution of current (A) and future (B) invasive fire ant (Solenopsis invicta) in South Korea as a result of climate change (blue: low probability of occurrence; red: high probability of occurrence). [Source from Sung et al. ref. 15]]

Social insects are characterized by a high level of sociality (called Eusociality [11], which is translated by overlapping generations, cooperative care and specialization of some individuals for reproduction (separation between sterile and fertile castes [12]. Among them, **ants** are considered ideal biological models for studying ecology and evolution [13]. Indeed, more than 15,000 species and subspecies of ants have been described in all continents, and many species are probably still unknown. They have colonized almost all terrestrial habitats, including tropical forests, deserts, savannahs, urban areas, and agricultural landscapes [12]. In some ecosystems, the **biomass** of ants reaches 15% of the total terrestrial biomass.

This high abundance and impressive diversity make ants a model of choice for biological monitoring: they are often "**keystone**" species, which have a major influence on many ecosystem functions such as seed dispersal or soil chemistry, particularly because of their incredible diversity of lifestyles. For example, there are nomadic species, species that nest in trees, in the soil or in vegetation debris, predatory species, other granivores, and some even cultivate mushrooms [13]. Ants are easily transported by humans because of their small size and nesting habits, for example through the trade in potted plants, during excavation work or through logging. In fact, more than 200 species of ants have established populations outside their native range [13] and more than 600 species have already been moved outside their native area [14]. Among them, some have become **invasive**, i.e. they have proliferated and their expansion has negatively impacted native biodiversity and/or human health.

Ants are **ectothermic insects**, their body temperature depends on that of the environment in which they live. The development of the larvae and the activities of the adults therefore depend directly on climatic conditions. Consequently, the distribution of ants is strongly affected by climate (see for example the case of the fire ant in Figure 3) [15]. Ants are therefore good models for understanding the responses of organisms to temperature variations and climate change in general.

3. Ants in the cities

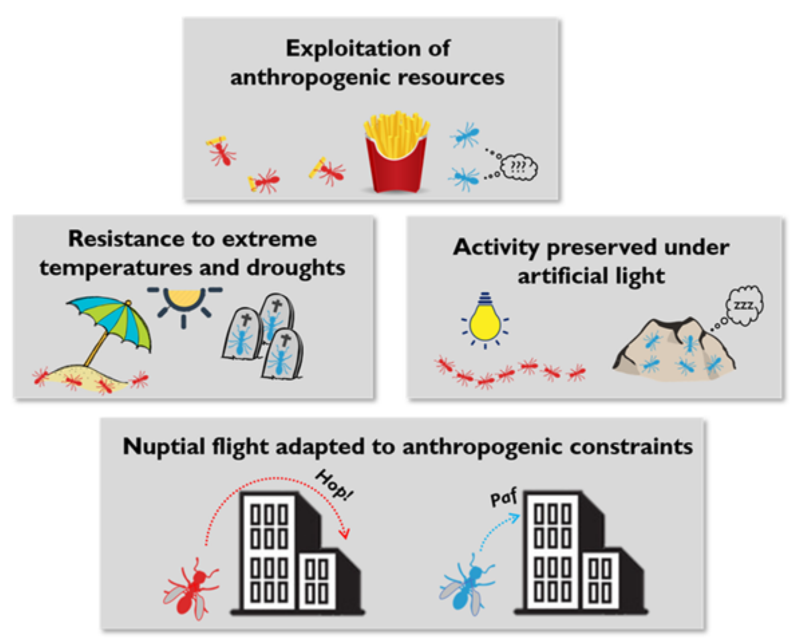

Figure 4. Some examples of characteristics that allow ant species to maintain themselves in anthropized habitats. In red, a species well adapted to urbanization, in blue, a species not adapted [Source: © Marion Cordonnier]

Among the fauna present in intensely urbanized environments, ants are good indicators of the environmental impact of **urbanization** [16]. Within ants, the magnitude and direction of the impacts of urbanization depend not only on **species characteristics** and their sensitivity to disturbance, but also on species interactions and their dispersal capacities (Figure 4).

Thus, while many species are rarely found in urban areas, several species of ants are on the contrary common in the most anthropized habitats (e.g. *Lasius niger* in France, Figure 5). Ant communities are therefore frequently studied in **urban ecology**, because of the important differences between communities in urbanized habitats and those found in adjacent rural habitats [17].

4. Invasive ants

Figure 5. Track of garden black ants (Lasius niger) in an anthropized habitat. [Source: © Benjamin Gerfand]

Ants are **social insects**, and as such they have many assets that favour **biological invasions**. Their way of life in **colonies** with many individuals increases their capacity to exploit resources and **compete** with local species and favours defence against predators. The production of winged breeding individuals ("flying ants") increases their dispersal capacity. Their flexibility in breeding patterns is also an asset. For example, the **polygyny** [12] of *Tapinoma magnum*, a new invasive species in Europe belonging to the *Tapinoma nigerrimum* group (Figure 6), allows it to disperse more rapidly and accelerates colony growth. Polygyny also increases the risk of introducing breeding females into new habitats by displacing a group of individuals, and thus initiating new colonies.

Among social insects, some species are much talked about, such as the infamous Asian Hornet *Vespa velutina*, whose impact on honey bees has been widely studied in recent years [18]. However, ants are certainly the most destructive and widespread. The Invasive Species Research Group [19] has shown that among the 100 most damaging invasive species in the world, **five are ants**: the Argentine ant *(Linepithema humile*), the fire ant (*Solenopsis invicta*), the big-headed ant (*Pheidole megacephala*), the small fire ant (*Wasmannia auropunctata*), and the yellow mad ant *(Anoplolepis gracilipes*).

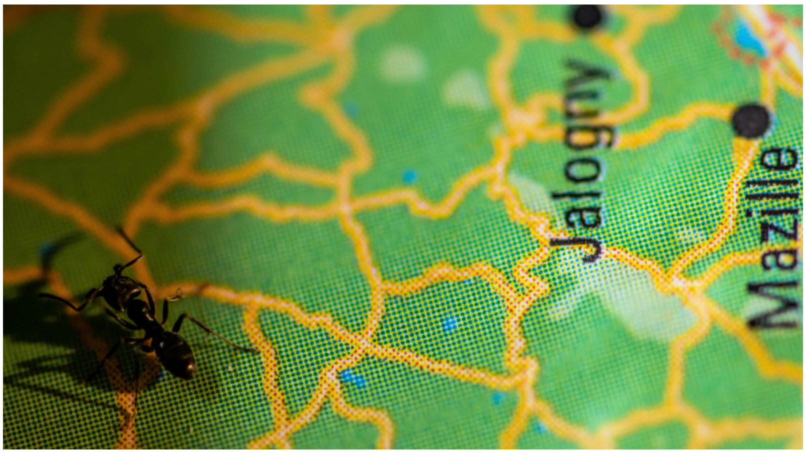

Figure 6. Tapinoma nigerrimum sp. [Source: © Benjamin Gerfand]

Heavily invasive ants are often **unicolonial** like the Argentine ant which forms supercolonies where workers and queens mix and move between physically separate nests. This has a two-fold advantage: unlike isolated colonies that are usually aggressive towards each other, the cost of territoriality is limited in supercolonies (less fighting), and this mode of operation allows very high worker densities to be reached more quickly. For example, the fire ant, a species introduced at least nine times in a row from the United States to invaded areas such as Taiwan or Australia [20], can be highly polygynous and host up to 200 queens in a single colony. This same characteristic allowed the yellow mad ant to invade Christmas Island in the middle of the Indian Ocean, where it reached a density of 70 million individuals per hectare. In fifteen years, some 15 million land crabs were killed by the ants' formic acid spray, leading to the decline of the species.

Ant invasions have very high **economic costs**, strongly alter the environment and have a strong **impact on** native **biodiversity**.

Local ant species in particular can be very negatively impacted by invasive species due to their competitive dominance, predation and nest raiding. Invasive ants also have an impact on many components of ecosystem functioning, **ecosystem services** [21] and human societies, such as changes in food web dynamics, alterations in nutrient cycling or reduced pollination [12].

5. When global changes interact

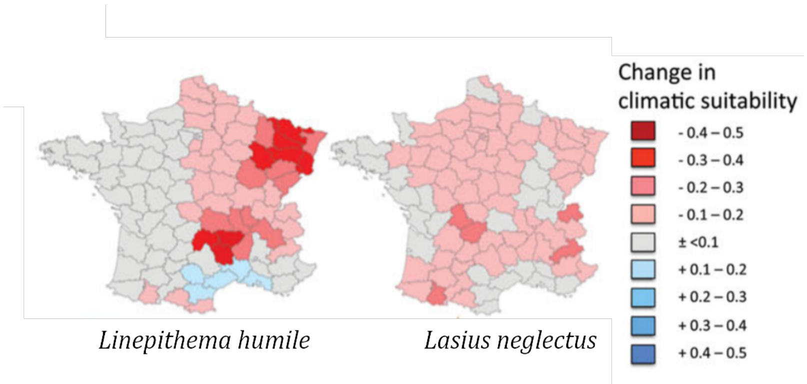

Figure 7. Change in the favourable climatic conditions in France for two invasive ant species by 2080. Source from Bertelsmeier & Courchamp, Ref. [23]

Urbanized environments are often considered degraded and hostile habitats for most species because many native species are sensitive to human disturbance. For these species, urbanization means the **destruction and fragmentation** of favourable habitat. However, these urban ecosystems can also represent an **opportunity for some species**. Numerous studies have thus highlighted a significant number of species introduced by humans into urban ecosystems [16]. The construction and expansion of cities thus encourages the loss of native species and their replacement by **non-native species** [5]. Recently, several scientific studies have highlighted high abundances and diversities of non-native species in more urbanized habitats, especially for invertebrates [22] (see also: Why is the tiger mosquito so invasive?). Three factors may explain the increase in non-native species richness [5]:

An increase in the rate of import of non-indigenous individuals due to increased accidental or intentional transport into cities as a result of constant human flows, for example through food chains (e.g. the import of fruit for the Japanese fruit fly *Drosophila suzukii*), or as a result of the import of exotic pets (the Florida turtle or the collared parakeet are good examples);

The presence of habitats favourable to the establishment of non-native species, with a favourable combination of resources and environmental conditions, and few natural enemies (predators or competitors), thus greatly improving the invader's habitability;

The fact that imported non-native species include among them species that can tolerate the unique conditions of anthropized habitats (e.g. tropical species resistant to higher temperatures), or even species that can take advantage of the opportunities offered by urban environments, as is the case for the tiger mosquito (see also Why is the tiger mosquito so invasive?).

Climate change may also exacerbate biological invasions, as the distribution of many invasive species is currently limited by thermal barriers. Climate change could thus allow them to invade higher latitudes. Extreme weather events, such as intense heat waves, hurricanes, floods and droughts, can facilitate biological invasions by increasing the movement of non-native species and decreasing the resistance of native communities to the establishment of invaders (see Climate change and globalization, drivers of insect invasions). For example, in France, most invasive ant species are likely to increase their range in response to climate change (Figure 7) [23].

6. The Case of the Pavement Ant

Figure 8. The pavement ant, Tetramorium immigrans [Source: ©Benjamin Gerfand]

Among city ants, *Tetramorium immigrans* (Figure 8) has been widely studied in recent years, particularly as it is an invasive species in North America where it was introduced into cities in the 18th or 19th century.

In France, the spatial distribution of *T. immigrans* depends both on climatic and urbanization conditions at different **spatial scales** [24]. This species, which prefers warm and relatively humid environments, is strongly represented in anthropized micro-habitats, e.g. characterized by the **presence of concrete**. In the northern part of its distribution, this species is often restricted to the most urbanized habitats. Even further north, in regions that are not climatically favourable to it beyond its referenced distribution area, it is even found exclusively in large cities such as Paris or Prague. Figure 9 illustrates the capacity of this species to exploit human resources in urbanized habitats [25]. Thus, in many large cities in northern France, the effects of **urban heat islands** allow it to survive despite the inhospitable climatic conditions in these regions.

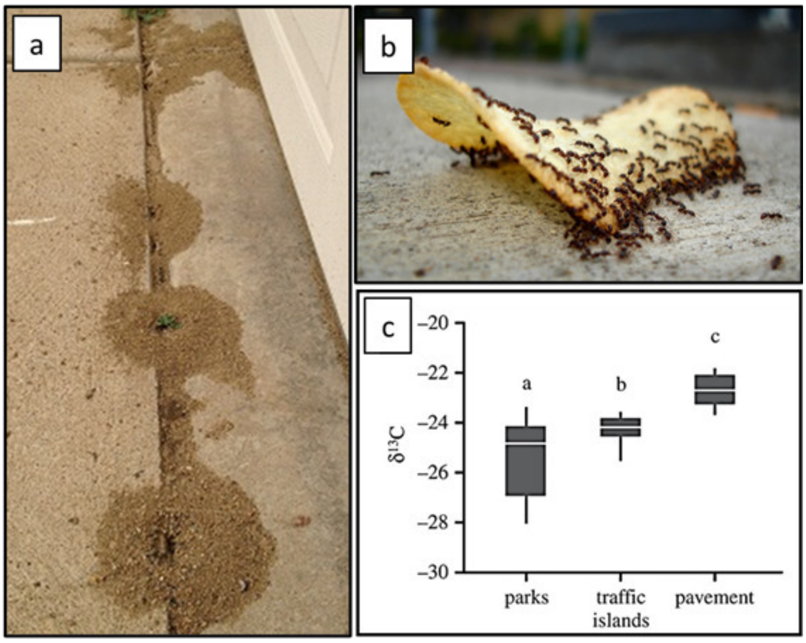

Figure 9. Exploitation of anthropogenic resources by the pavement ant Tetramorium immigrans (a) colonies established in urban ecosystems and (b) consumption of human food resources. (c) Changes in the diet of T. immigrans in urban habitats (stable isotopic values of carbon for female workers collected in parks, traffic islands and pavements). Source: (a-b) © Marion Cordonnier (from Penick et al. Ref [25])]

Tetramorium immigrans has probably only recently colonized the northernmost habitats of its distribution, benefiting from the urbanization of the 19th and 20th centuries but also from the increase in trade, travel and transport of goods. **Introduction by human activities** remains the preferred hypothesis to explain the spread of this species, due to its restricted presence in urbanized areas [26]. This northward movement has generated new contacts with locally occurring species, resulting in genetic exchanges between them [27]. This species thus perfectly illustrates the extent to which urbanization and climate change can interact and are likely to promote biological invasions (Figure 10).

7. Species distribution and multi-scale interactions

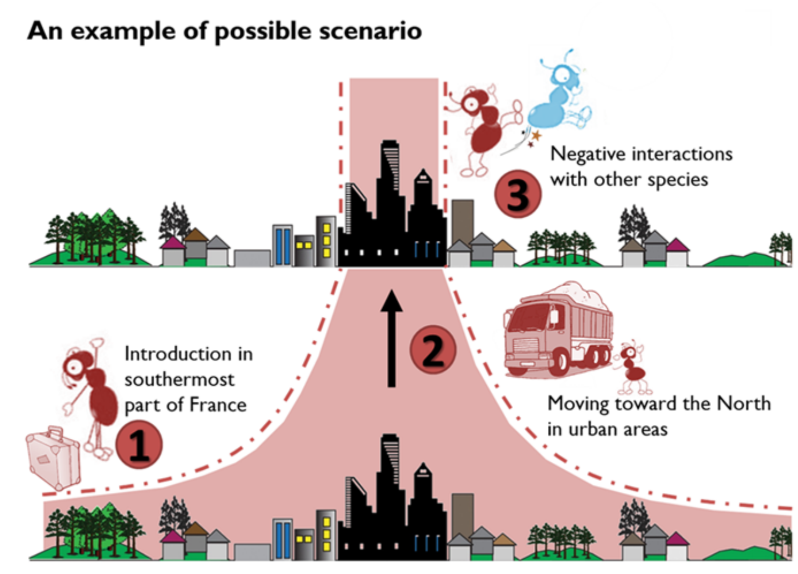

Figure 10. Example of a scenario of colonisation of the North of France by the pavement ant Tetramorium immigrans. [Source: © Marion Cordonnier]

Understanding the **impact of global changes** on the **distribution of species** is still a real challenge for scientists today. **Climate change** and **urbanization**, for example, are jointly modifying the distribution of species, and the factors associated with these global changes operate at different scales and interact with each other, making it more complex to decipher their impacts on biodiversity. Species distribution patterns are thus the result of **complex**, multi-scale **interactions**. This notion of interaction is rarely taken into account in scientific studies.

However, climate change, changes in land use or the introduction of invasive alien species are likely to occur simultaneously, and thus synergistic effects on biodiversity can be expected. For example, cities are often warmer than neighbouring rural habitats, and the impact of urbanization on climate is locally comparable to ongoing global warming, suggesting that urbanization could strongly reinforce the consequences of climate change at the local level. This complexity, involving scale effects and interaction effects, emerges even when considering only two global changes (here, climate change and urbanization). But these effects are probably catalysed by other major **anthropogenic changes**, such as pollution, agriculture, or deforestation.

Clearly, a simple causality study involving a partially described global change in the distribution of a species cannot therefore lead to a convincing understanding of the processes underlying the distribution of species. It is therefore fundamental to conduct in-depth studies on the impacts of global changes with more inclusive approaches combining several changes at several scales. To this end, ants will certainly be a model of choice, as they have already proved their ability to unravel such issues. While in the past they have made it possible to study most of these global changes individually, no doubt in the future they will make it possible to understand how they interact and to quantify their simultaneous impacts on biodiversity in greater detail...

8. Messages to remember

Climate change and urbanization are interacting and changing the distribution of species.

Ants are abundant and diverse, have colonized most terrestrial habitats and influence many ecosystem functions.

Small and nesting in soil or plants, they are easily transported by humans. As a result, they now include many invasive species.

Ants are ectothermic insects and are therefore sensitive to temperature variations. Their distribution is therefore highly dependent on climatic conditions.

Ants are frequently studied in urban ecology because they are good indicators of the environmental impact of urbanization.

Consequently, ants are very suitable models for studying the complex interactions between global changes - the study of the pavement ant *(Tetramorium immigrans*) is a good illustration of this.

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Cover image. Pavement ant *Tetramorium immigrans* in an urbanized environment. [Source: © Benjamin Gerfand]

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[6] In ecology, edge effects reflect changes in the structure of species populations and communities that occur when two very different habitats exist side by side in an ecosystem. This terminology is often used to refer to the boundaries between natural and artificial habitats.

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