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BLWK-nuusbrief CAWC newsletter

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'n Hoopvolle 2019 lê voor. Met al die nuwe uitdagings en nuwe geleenthede hoop ek julle is opgewonde oor die planttyd wat voorlê. Geniet die nuwe nuusbrief en sterkte met julle jaar.

Hopkins Uys (Voorsitter BLWK)

We look forward to a blessed 2019 full of hope. With all the new challenges and opportunities the hope is that you are all looking forward to the coming seeding time. All the best with this part of your season and enjoy the new newsletter.

Hopkins Uys (Chariman CAWC)

IMPORTANT WHEAT DISEASES IN THE WESTERN CAPE DURING 2018

Dr Gert van Coller, Professional Scientist: Plant Pathology, Western Cape Department of Agriculture, Elsenburg, 7607 E-mail: <u>gertvc@elsenburg.com</u>

> he wheat yield of the Western Cape increased significantly in 2018 compared to the previous year, partially thanks to improved rainfall. Diseases still occurred widely on the

wheat crop throughout the Province, however, and contributed greatly not only to yield losses, but also to a reduction in grain quality. The three most important wheat diseases in the Western Cape during 2018 was powdery mildew (wrongly known as white rust, or witroes in Afrikaans), black chaff / pseudo-black chaff, and Fusarium crown rot. In this review, background information will be provided for each of these diseases, and management practices discussed. The difference between white rust, powdery mildew and downy mildew, and how to distinguish between take all (*vrotpootjie* in afrikaans) and Fusarium crown rot of wheat, will also be explained.

POWDERY MILDEW (WRONGLY KNOWN AS WHITE RUST)

Powdery mildew of wheat is caused by the fungus *Blumeria graminis* f. sp. *tritici*. A close relative, namely *Blumeria graminis* f. sp. *hordei*, causes powdery mildew of barley. The term "f. sp." means *forma specialis*, which literally translates as "special form". This means that powdery mildew occurring on wheat will not infect barley, and vice versa.

Powdery mildew occurs throughout the Western Cape, and although it prefers humid regions, it is adapted to drier regions. Infection can take place throughout the growing season, as long as green tissue is available, and all above-ground parts can get infected. The fungus is a true parasite which gets its nutrition directly from the plant. It reduces the photosynthetic ability of the wheat crop and increases respiration, which reduces yields. Yield losses of up to 40% have been reported in the USA. The disease is especially damaging when the flag leaf and heads get infected. Infected kernels are sticky, with a reduced grain quality. Powdery mildew, therefore, reduces both yield and grain quality.

Disease cycle

The most favorable conditions for infection and disease development are during periods of high humidity, coupled with a temperature range of 15–22°C. Disease development decrease above 25°C. This explains the increased occurrence of the disease during 2018, which had a higher rainfall compared to previous years. However, keep in mind that infection and disease development can occur at lower humidity. Wheat is especially susceptible during the stem-elongation and flowering phase, and the disease is also most damaging during this period.

Powdery mildew is a polycyclic disease. This means that the pathogen can complete its life cycle numerous times in a single growing season, each time increasing the amount of spores that cause disease exponentially. It is important to understand the disease cycle, since it explain why the disease is so difficult to control, either with fungicides or cultivar resistance. The disease cycle is explained below.



The pathogen survives in the summer on wheat stubble from the previous season.



The pathogen survives in the summer on wheat stubble from the previous season. When the climate is favourable in the new growing season, spores of the pathogen are released from fruiting bodies on the previous season's wheat stubble. This can occur early in the growing season. These fruiting bodies (the round, circular shape in the photo above right that looks like Pacman) are known as **cleistothecia** (singular cleistothecium). The spores are carried in a sack, known as an **ascus**, while the spores inside are known as **ascospores**. The ascospores are carried by wind, or splashed by rain, onto wheat plants, which it then infects. Cleistothecia with ascospores develop as the result of mating between two individual strains of the fungus (similar to male and female). This is known as the sexual phase of the pathogen's life cycle. The sexual phase is of particular importance for disease management, and will be explained at the end of the life cycle.



Mycelia



Blumeria_Erysiphe_graminis_conidia_asexual_Oidium_anamorph.jpg? sequence=3&isAllowed=y

Ascospore typically land on the lower parts of the plants. The ascospores germinate, and hyphae (similar to roots) develop which infect and parasitizes the plant. As the fungus feeds on the plant, more hyphae develop which becomes visible as whitish fluffy patches. These patches are matrices of hyphae, called **mycelia** (photo above, left). The fungus now enters its asexual phase.

Within the mycelia, single cells in hyphae develop in chains and split off. These cells are asexual spores, known as **conidia** (photo above, right). The pathogen has now completed its first life cycle, and the second cycle begins. Many thousands of conidia develop from each "fluffy patch". **The most damaging phase of the disease now begins**. Conidia break off from the chains and are dispersed with wind for many kilometres. From a few "fluffy patches", millions of conidia are released. When these conidia land on other wheat plants, or newer leaves of the same plant, infection again takes place and the cycle repeats itself. More and more plants get infected, and the amount of conidia produced and released in the wind continue to increase exponentially. In other words, the disease start multiplying exponentially. The pathogen can complete each cycle of infection and release of new conidia within 7-10 days, and will continue as long as the climate is favourable.

Why this phase is so important: It is extremely difficult to control a disease when new spores of the pathogen (and large numbers of it) are continuously blown in with wind from all directions. A field could have been treated with a foliar fungicide, but new conidia continues to come in with wind, even from fields kilometres away, infect and cause new disease. Therefore, depending on the efficacy of the fungicide treatment, amount of coverage achieved and other factors, the disease can quickly re-establish. Also, if some disease survived the fungicide treatment, it can rapidly release new conidia and cause new infection.





GRDC, Evan Collis



http://web2.mendelu.cz/af_291_projekty2/vseo/files/93/8066.jpg

New cleistothecia

As mentioned, the disease is especially damaging when flag leaves and heads get infected, as seen in the two photos above on the left. The source of the infection observed in the photos above, could have originated from the same field, or a field kilometres away. On infected leaves and stems, the mycelia (whitish fluffy patches) matures. The pathogen again enters its sexual phase. Individual hyphae (fungal threads) within the mycelia, of opposite mating types (similar to male and female), merge and exchanges genetic material, and new cleistothecia with ascospores develop. These cleistothecia are visible as

Why this phase is so important: Each time a cleistothecium forms, it means that two individual strains of the fungus have exchanged genetic material, and the resultant ascospores contain DNA from both parents (just like a human child's DNA comes from his mother and father). If one of the parents have an increased ability to withstand a certain fungicide, or to infect a certain cultivar, the ascospores formed will also have that ability. When the ascospores infect new plants and form conidia, this ability will be present in the conidia, of which masses are formed and dispersed over many kilometres. Since the formation of cleistothecia happens so easily, and in such large numbers, this is a very real threat.

small dark spots within the mycelia, as seen in the

Disease management

photo above right.

Powdery mildew is notoriously difficult to manage, and best results are obtained when integrating agronomical practices with cultivar resistance and the use of fungicides.

Agronomical practices

1. Avoid over-fertilising with N. This results in increased vegetative growth, which will fa-

vour the disease.

- 2. **Decrease seeding density.** Since the disease is favoured by high humidity, a lessdense canopy will dry off quicker, thereby making conditions less favourable for the disease. This is especially true for fields on a southern slope, which will take longer to dry off.
- 3. Crop rotation and conventional tillage does not really help. Wheat planted after canola, for example, can easily get infected with powdery mildew originating from a wheat field kilometres away. Planting wheat after wheat is, however, not recommended, since the new plants are then easily accessible to ascospores released from wheat stubble early in the season.

Cultivar resistance

Cultivar resistance is regarded as the most durable and economic way to manage the disease, but not much is known on the level of resistance of Western Cape wheat cultivars against powdery mildew. **This is an aspect which will be addressed this year**, and we hope to be able to provide producers with results within the next year. Numerous genes conferring increased resistance against powdery mildew of wheat has been identified in Europe and the USA, and certain South African seed companies are currently working towards integrating these genes into Western Cape wheat cultivars.

Chemical control

Chemical control is an important weapon in the arsenal to defend your crop against powdery mildew. Numerous fungicides are registered against the disease. The following, however, must be remembered when applying fungicides.

- 1. New varieties of the fungus, which may be better able to withstand certain fungicides, can be present on your wheat crop (as explained at the end of the disease cycle). To help overcome this, rotate fungicides, i.e. make use of fungicides with different active ingredients for different applications.
- 2. Only make use of fungicides registered against powdery mildew of small grains.
- 3. Make sure the product(s) are used according to the manufacturer's specifications.
- 4. Do not use fungicides registered against white rust, unless it is registered against powdery mildew of small grains as well. White rust is another disease altogether, and do not even occur on small grains (will be explained in the next section).
- 5. TIMING IS CRUCIAL. As soon as the first whitish fluffy patches become visible, conidia has already started to spread with wind, which means that the disease can now begin to increase exponentially. The first fluffy patches are the match that start the veld fire. Apply fungicides a.s.a.p. to stop the spread of the disease as far as possible. If enough producers can stop the disease in its first life cycle, disease levels can be decreased significantly.

- 6. Fields on a southern slope or patches with long periods of shade are more prone for infection. Early disease detection and continuous monitoring is especially important here (see also *Agronomical* practices).
- 7. Seed treatment is important to protect wheat seedlings for the first few weeks.
- Adjuvants, and nozzles that allow for better coverage, can increase the efficacy of the fungicide treatment. Consult your relevant agent(s).

WHITE RUST, POWDERY MILDEW AND DOWNY MILDEW

White rust, powdery mildew and downy mildew are different diseases, and are caused by different pathogens.

White rust ("witroes")

White rust occur **only on** Brassicas, including canola. It does not occur on other crops. The "white rust" epidemic on wheat of the past year was in fact powdery mildew. The correct name of white rust is **white blister rust** ("witskilferroes" in Afrikaans). It is caused by the fungus *Albugo candida*.



White blister rust becomes visible as yellow necrotic spots on Brassica leaves

www.agric.wa.gov.au/broccoli/white-blister-disease-vegetable-brassica-crops

White blisters then start to form, which later coalesce (photos below).



https://www.alamy.com/white-blister-rust-albugo -candida-on-honesty-lunaria-annua-leaf-image6286447.html



www.agric.wa.gov.au/broccoli/white-blister-disease-vegetable-brassica-crops

Powdery mildew

Powdery mildew ("poeierskurf" in Afrikaans) is highly host-specific. Powdery mildew occurring on wheat for example, will not infect other crops, including barley and oats. The same principle applies to powdery mildew of other crops (and weeds). An exception is powdery mildew of Brassicas, which occur on different plants within the Brassica family, but not on any other plants. A few examples of powdery mildew on different plants are shown below.



http://canola.okstate.edu/cropproduction/diseases

Powdery mildew of Brassicas is caused by *Erysiphe cruciferarum*

Powdery mildew of wheat is caused by *Blumeria graminis f. sp. tritici*

https://ohioline.osu.edu/factsheet/plpath-fru-37

Powdery mildew of grapes is caused by *Erysiphe necator*

https://en.wikipedia.org/wiki/Erysiphe_alphitoides

Powdery mildew of oak trees is caused by *Erysiphe alphitoides*

Downy mildew

Similar to powdery mildew, downy mildew is also host specific. Downy mildew is known as "donsskimmel" or "donsige meeldou" in Afrikaans. Downy mildew occurring on one crop, will not infect another. An exception here is the fungus that causes downy mildew of wheat, which can also infect maize. It won't, however, infect Brassicas or plants from other families. A few examples of downy mildew on different plants are shown below.

Steve Marcraft

Downy mildew of Brassicas is caused by *Peronospora parasitica*

Downy mildew of grapes is caused by *Plasmopara viticola*

Downy mildew of wheat is caused by *Sclerophthora macrospora*. The disease is also known as Crazy Top and does occur on maize. It can, however, be easily confused with herbicide damage, when a hormone-based product like 2,4-D is used.

BLACK CHAFF / PSEUDO BLACK CHAFF

Black chaff is a **bacterial disease**, caused by the bacterium *Xanthomonas campestris pv. undulosa*. The term "pv." (pathovar) means that this is a variety of the bacteria that can only infect plants of a certain genus or species, in this case grasses. Black chaff occur on wheat, barley, oats, triticale and other grasses, **but not on broad-leaf crops**. It is the most destructive bacterial disease of wheat and vield

losses of close to 40% have been reported in the USA. Black chaff was already reported on wheat in the Malmesbury-region in 1931, but it is an old report, and new information on the occurrence and impact of the disease is needed. This will be addressed this year.

Pseudo black chaff is a **genetic condition** present in some wheat cultivars, and caused by certain genes conferring resistance against stem rust, like the *Sr2* gene_It is also known as **melanism**. It can be difficult

to distinguish between black chaff and pseudo black chaff. Some identifying features of black chaff is explained below.

Disease cycle of black chaff

Black chaff is a seedborne disease. This is the primary way how the pathogen survives from one season to the next, and also how it spreads to new regions.

During the growing season, the bacterium survive on plant surfaces without causing symptoms. Within a field, the pathogen can spread short distances with rain splashing from infected plants, plant-to-plant contact, and with insects.

Symptoms becomes visible on the upper leaves, and on wheat heads after head emergence. Black chaff is

especially prevalent during periods of high humidity. Leaf lesions start as small water-soaked spots, which elongate, becomes brown, and eventually extend to the whole leaf. Leaf symptoms can be confused with other leaf diseases, but can be distinguished by bacterial ooze from infected parts during high humidity. Glumes within the head becomes darker, while dark to purple streaks may become visible on the peduncle (stem below the head).

The bacterium infects seed in the heads and survives the summer in harvested wheat grain. Survival of the pathogen in stubble or soil is believed to be of lesser importance.

Wheat field severely infected with black chaff

Wheat head with black chaff

https://oropwatch.unl.edu/bacterial-streak-and-black-chaff-wheatfields-unl-oropwatch-june-14-2013

Flag leaf with black chaff

Disease management

- 1. Only make use of certified seed. If the disease is present in your fields, withholding seed to plant the next season will only increase the problem.
- 2. Unfortunately, no seed treatment are available, since it is a bacterial disease, not a fungal disease.
- **3.** Decrease seeding density. Since the disease is favoured by high humidity, a less-dense canopy will dry off quicker.
- 4. Good insect control can also reduce spread of the disease via insects.
- 5. Use of more resistant cultivars. Cultivars do differ in their level of resistance against the disease, but so far, not much is known in the Western Cape. This will be addressed this year.

FUSARIUM CROWN ROT

Fusarium crown rot (FCR) is a potentially devastating disease that occurs commonly in the Western Cape. Annual losses incurred by FCR have been estimated at \$79 million in Australia. Traditionally, FCR occurs more frequently in the Overberg and Rûens regions than the Swartland, but it can change between years, due to the climate.

The disease is caused by the fungus *Fusarium pseudograminearum* and other related species. FCR occurs on all small grains, including wheat, barley, rye, and triticale. It can also occur on grass weeds. An interesting exception is oats. **Oats is mostly a symptomless carrier of FCR, but still get infected.** FCR is frequently mistaken as take all ("vrotpootjie"). The difference between the two diseases will be explained in the final section of this article.

Disease cycle

The primary source of inoculum for FCR is mycelium present in colonised stubble on fields located close to the wheat plant. FCR is a monocyclic disease, which means that the pathogen only completes one life cycle in a growing season. Relatively moist soils are needed for infection to occur, which takes place via the lower stem region, including the crown and sub-crown internode. This results in the colonisation and rotting of the lower stem, which progresses upward. Obstructions form in the xylem and phloem tissue and disrupt water absorption from the seminal roots, which makes the plant dependent on water absorption from the crown roots. This, however, becomes difficult when dry conditions prevail later in the season. Symptoms become visible as a characteristic brown discolouration of the lower stem region and the formation of white (dead) heads containing little or no grain. The disease is, therefore, favoured by hot, dry conditions later in the season from grain fill onwards. Models predicting climate change indicate that the Western Cape, especially the western part, will become hotter and drier in future, especially in the western part. This will result in an increase in FCR. At the end of the growing season, the pathogen(s) survive in the stubble left on the field, including oats stubble.

The pathogen survives in the summer on wheat stubble from the previous season.

The crown-region of the stem (at soil surface) get infected when it comes in contact with infected stubble. Moist soils are needed.

Infection of the lower stem region cuts off the vascular tissue and disrupts water absorption from the roots. This results in characteristic wheat (dead) heads containing little or no grain.

Infection of the lower stem is visible as a characteristic brown discolouration which progresses upward.

Disease management

- 1. FCR is best managed through **crop rotation with broadleaf crops**. Although oats is a symptomless host, wheat followed by oats will increase the amount of inoculum (fungal spores and mycelia which can cause infection).
- 2. Western Cape wheat cultivars do not have high levels of resistance, some cultivars like SST087 does, however, have some level of **tolerance** against FCR.
- **3.** Strategic tillage, once in a number of years, to remove stubble, is an option, but must be weighed against gains and losses resulting from tillage.
- 4. Avoid over-fertilising with N. This results in increased vegetative growth, which will consume more groundwater, thereby helping to create dry conditions later in the season, which will favour the disease. Plants also become more susceptible at high N-levels.

- **5.** Make sure Zn-levels in the soil is sufficient, since Zn-deficiencies favour the disease.
- 6. Unfortunately, no chemical control is available. Seed treatment is still, however, important to protect seedlings from other diseases.

DIFFERENCE BETWEEN TAKE ALL AND FUSARIUM CROWN ROT

Take all and FCR look very similar in the field. Take all does, however, occur throughout the season, while FCR becomes visible toward the end of the season. Tale all also usually occur in patches in the field, while FCR tend to be distributed more evenly. Both diseases result in white stalks and heads containing little or no grain. The two photos below illustrate this.

To distinguish between take all and FCR, plants must be carefully uprooted, and soil must be shaken off, or preferably, washed off. Also strip the leaves off the lower stem. When root rotting is visible, coupled with white heads, the cause is take all (photo bottom left). When the roots appear healthy, but browning of the lower stem is visible, the cause is FCR (photo bottom right). Sometimes, however, both diseases are present on the same plant.

WHY IS THIS IMPORTANT?

FCR pathogens can infect all small grains, including oats, although it is symptomless on oats. Take all **CANNOT** infect oats. In fact, **oats is toxic to take all**. Therefore, depending on which disease is prevalent on your field, oats will be a good choice for crop rotation, or not.

Links of the month

Click on the button to visit the website. Please note you will need an Internet connection

Our food system is pushing nature to the brink. Here's what we need to do

New Market Planned to Pay Farmers for Soil Carbon, Water Quality

Regeneration Newsroom—March 2019

Ten-year cover crop study challenges negative yield perceptions

Will Brinton and Odette Menard (MAPAQ Quebec) speak at an on-farm event in Pennsylvania as part of the No-Till Alliance Field Days,

In a rare moment in an early Rover reconnaissance mission to Mars, carbon dioxide (CO_2) was released from a soil sample during a scientific test and was thought to indicate the presence of microbes. Excitement quickly faded to puzzlement, then dismay, as it was realized that a glitch in the expensive onboard lab had produced inorganic CO_2 . Chemicals used for the soil extract triggered release of inorganic CO_2 , perhaps from the ubiquitous magnesite (MgCO₃) found in Martian soil.

On Earth, the release of carbon dioxide from moist soil due to microbial activity is so pervasive that it is difficult not to observe it. We don't have the problem they do on Mars trying to distinguish biological CO_2 , in an atmosphere containing 96 percent CO_2 , from non-living sources. In science we call this dilemma "distinguishing small differences between large numbers." Here on Earth, CO_2 in the atmosphere is only 0.04 percent, and climbing just barely perceptibly, making it relatively easy to distinguish biological CO_2 . Curiously, almost nobody is doing it.

Borrowing From the Past

I learned about soil CO_2 respiration working on a graduate program in Sweden investigating fertilizer and crop effects on soil biology. Agronomists in the 1950s set up farm plots and maintained them for

Farming the CO2 Factor

October 10, 2018 in Crops, Eco-Farming, Soil Fertility, Soil Life, Soils

decades, enabling later researchers such as myself to observe the long-term effects of differing soil management.

In the process, I discovered a trove of even earlier Swedish work on soil respiration.

The legacy of this soil biology work traces to soil scientist Henrik Lundegårdh (pronounced Lun-degourd) who, in the 1920s, established an essential framework for understanding the biology of crop productivity. Lundegårdh was concerned about the early rush into inorganic chemical farming based on the new discoveries of mineral plant nutrition. In his view, soil biological functioning should be part of routine soil fertility assessment.

He selected soil CO_2 respiration since it reveals the all-inclusive metabolic activities of soil bacteria, fungi, arthropods and plant roots. He labeled this indicator "the CO_2 factor."

It's possible that Lundegårdh built the first farm CO_2 flux chambers. He set up as many as 42 in farm fields and nearby forests running year-round under differing soil and crop regimes. This kind of approach is only now coming into vogue to understand the potential of CO_2 -driven climate change. Lundegårdh already grasped the significance of the global carbon cycle at the time, but more importantly, saw an enormous upside to CO_2 in the context of quantifying "healthy soils."

Figure 2. The Soil Biological Cycle. This shows the daily carbon and nutrient release rates in relation to the mass of microbes and soil organic matter.

From this effort Lundegårdh reached several astonishing conclusions. He was a systems researcher in the best sense, and to make a point about the relevancy of soil CO_2 , he adjusted soil profiles with microberich manure until steady CO_2 rates were attained. Next, he grew wheat, oats and sugar beets and monitored their nutrient and carbohydrate assimilation.

From this he demonstrated a significant connection of soil respiration to plant photosynthesis. Considering the thoroughness of these studies and their dissemination in published literature of the time, it is hard to understand how such excellent work escaped further attention.

I have confirmed many of Lundegårdh's measurements and calculations.

The essence of the discovery is that plants obtain the CO₂ they need not from the atmosphere per se, but from soil respiration. Lundegardh showed that if soil respiration fails to furnish a sufficient quantity of CO₂, the supply from the atmosphere is furnished too slowly to prevent a CO₂ deficit in the leaves, and thus a partial starving occurs. This can be intuitively grasped as a basis of truly biological-oriented farming. Some very recent studies on forest canopies in ecological journals confirm that in highly functioning ecosystems the cycle of CO₂ (and O₂) between plants and the soil is nearly completely closed. In this regard Lundegårdh was a pioneer showing that we cannot separate living soil from high-yielding crops. This is a far cry from where we stand in the present, and this is unfortunate.

Lundegårdh outlined the biological pathways that directly contribute to crop productivity, including:

- 1. Mineralization of organic nitrogen to nitrates (due to microbial activity);
- 2. extraction and buffering of the soil solution (due to dissolved carbonic acid from microbial activity);
- 3. soil aggregate formation (due to microbial activity) and;
- 4. furnishing plants with CO₂ for photosynthetic assimilation, also due to soil respiration.

The implications of Lundegårdh's discoveries were largely ignored. Lundegårdh was aware of the conflict with prevailing mineral-theory views.

Writing a commentary in the journal Soil Science in April 1926 he voiced his concern: "The direct action of mineral fertilizers on increasing plant growth is the only one attention is being paid to in agriculture."

Domination of the Mineral View

Lundegårdh's remark in which he regrets the narrow focus on mineral nutrition of plants is certainly as true today as it was then — or even more so. Europeans in Lundegårdh's time witnessed the explosive growth of the inorganic fertilizer industry and its integration into farming, sweeping away centuries of old customs. The founding of our Land Grant University system grew out of this turbulent era, a result of political fears that Europeans would gain an advantage over the United States with the new mineral theories applied in agriculture to attain stupendous crop yields.

Today, if you operate a soil lab as I do, virtually all the equipment and technology is tasked for testing inorganic minerals. The basics were laid down a century ago. Advances in technology have largely focused on making it easier to measure more minerals faster. Harsh soil extracts are designed to pull the nutrients from soil as rapidly as possible. We combine this with mathematical equations formulated in the late 19th century by German chemists Liebig and Mitscherlich to "calibrate" extracted minerals to crop response.

This chemistry-mathematical approach is also very convenient: it is directly tied to applying inorganic fertilizers keyed to soil analysis, a business model that catapulted the mineral industry into becoming the cornerstone of modern farming. As the damage from a century of one-sided practices comes more into focus, some are asking: was the compelling post-war business opportunity of industrialization, more than the science itself, the real impetus for these agricultural changes? Some caution that we are being too critical of these early advancements or not appreciating the extraordinary amount of early scientific work that went into the new protocols. The problem is, all that work was done before the field of soil biology was even recognized.

Lundegårdh could well have been an organic science pioneer, but the movement was yet to be born. He did something that was highly significant by drawing attention to the shortsightedness of the new chemistry discoveries, and he tied the best science to measurements in soil biology.

Lundegårdh was not opposed to inorganic nutrients. He pointed out that in some circumstances increasing inorganic fertilizers also increased soil biology and CO_2 respiration due to greater root mass and more crop residues.

His approach clearly fits current concepts of soil health (the connection of soil-respiration to carbohydrate assimilation certainly belongs in the soil health arena). The point is that we have been trained for over a century to overlook soil biology with the best excuse being that it takes care of itself (which is partly true), and the somber threat that without inorganic fertilizers the world's populations will starve.

A scientific survey from Richard Mulvaney (Univ. Illinois/Urbana) examining soil tests nationwide found that in spite of increased soil mineral applications, soils are steadily declining in organic nitrogen, the key indicator of soil vitality. I believe this proves that there is no connection between mineral fertilizers and soil improvement.

The inescapable conclusion is that soil degradation — despite our best efforts — is likely to continue unabated. Aside from erosion and salinization, the central crisis is depletion of soil biological capital, or Lundegårdh's "CO factor." In fact, it is possible that we are approaching, for the first time, a new lowwater mark in soil fertility, for which Lundegårdh's studies are a harbinger and warning.

But without new testing tools, no one will notice it.

Crisis to New Action

There is nothing like impending crisis to trigger new experimentation. Part of the exciting turning point is seen in efforts by progressive farmers who appear to be training the government and the Land Grant researchers.

Private soil labs have jumped into the fray to evolve new indexes for biological fertility. Underlying this is the age-old axiom that you can't manage what you cannot measure. It explains our laboratory's introduction of a new type of soil test called "Solvita," making measuring soil CO_2 factor respiration practical and cost-effective within the infrastructure of soil labs and crop consultants, who are starting to see the connections.

A transition era is upon us and is captured in Figure 1, showing the prevailing and new views.

Putting Numbers to CO₂

The basis for biological functioning related to soil CO_2 starts with calculations anyone can perform. Take your entire dry matter crop yield and multiply by 50 percent to get your approximate carbon yield per acre.

Figure 3. Fertility Comparison of two soils. Left: Truck farm continuously tilled soil,

Right: Virgin prairie soil.

Divide this into 60 (the most active carbon assimilation days) and you have the carbon factor per day, which multiplied by 3.7 gets you to the CO_2 factor. This was Lundegårdh's basis in comparing soil respiration to crop carbohydrate assimilation. These two sets of numbers — the plant uptake and the soil respiration of CO_2 — can be found to be roughly comparable, in a healthy system.

Crop CO_2 needs such as in corn can be as high as 450 pounds per day per acre during the active period (as pure carbon this is 125 pounds per day). It turns out that nature has designed redundant biological systems in soil to furnish adequate amounts of CO_2 to keep plants in top shape, while the biology itself regulates the commensurate supply of nutrients and maintains soil structural integrity.

The cycle can be quantified, using an example of a soil moderate organic content as follows (Figure 2). By more accurately quantifying the CO_2 respiration rate we get closer to the mass of microbes and the potential nutrient supply to plants. Over time these measurements will be interpreted with greater precision. In the following example we show relative CO_2 rates with the Solvita 24hr CO_2 -Burst test, used by Soil Health Tool labs (see note at end for a soil map showing labs offering this soil biology test).

In the example, given the "dead soil" on the left, a continuously cropped (truck farm) soil from North Carolina, had very low (12 ppm) daily CO_2 rates. This is depletion farming (mineral test levels in the same soil were adequate and did not reveal the extent of the problem). For comparison we tested a virgin prairie soil from Nebraska, which showed almost seven times more biological activity. That system has accumulated biological capital. Associated with such a rich soil is a potentially high organic nutrient cycle. Modern mineral soil tests just do not show this. Getting to the CO_2 Factor

We need to alter the way we measure yield response in soil testing by paying attention to the capability of soil to produce the CO_2 , an integrated measure of all soil biota. In time, we will learn more about relationships of the biota to each other (fungi, bacteria, mycorrhizae) and to organic nitrogen fertility. It is well known that these have been factored out of calibration studies used in soil interpretation.

Correcting this omission is a challenge and is critical to assuring soil health and high-yielding crops and to fixing soil testing from being all about minerals to including biology.

Incidentally, we may rediscover mineral nutrition of soil from a new perspective: creating the optimal balance to foster microbial activity and diversity according to the edict: feed the soil. This work is only beginning today.

It is noteworthy that soil mineral theory is a selffulfilling prophecy — not focusing on biology leads to emphasis on minerals, this in turn fosters management practices that ignore biology; this leads to increased dependency on inorganic fertilizers: the cycle repeats.

Including Soil Labs in the Biology Transition

We need to foster the independent relationship of grower to soil lab, with the new biology standing in for mineral theory. Growers interested in soil biology should contact their soil labs. A new open-source methodology integrating soil biology with common nutrient tests, called the Soil Health Tool, originated with support from USDA-ARS and is available to any lab. More than 30 labs around the world now offer the Solvita biology test.

The success of the transition depends not on a new era of "expertism" of the sort that brought us the chemical mineral revolution, but by on-farm efforts comparing yield stability and quality with soil biology. Therein may lie the key to breaking the 150-year-old N-P-K spell.

The author dedicates this article to the memory of Jerry Brunetti, a pioneer in soil, livestock and human health.

By Will Brinton, Ph.D. This article appeared in the April 2015 issue of Acres U.S.A.

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Meta-analysis on carbon sequestration through Conservation Agriculture in Africa

Check for updates

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ABSTRACT

Africa is the smallest contributor to global greenhouse gas emissions among the continents, but the most vulnerable to the impacts of climate change. The effects will not be limited to a rising average temperature and changing rainfall patterns, but also to increasing severity and frequency in droughts, heat stress and floods.

Agriculture is not only impacted upon by climate change but also contributes to global warming. However, not all agricultural systems affect negatively climate change. Conservation Agriculture (CA) is a farming system that promotes continuous no or minimum soil disturbance (i.e. no tillage), maintenance of a permanent soil mulch cover, and diversification of plant species. Through these principles it enhances biodiversity and natural biological processes above and below the ground surface, so contributing to increased water and nutrient use efficiency and productivity, to more resilient cropping systems, and to improved and sustained crop production. Conservation Agriculture is based on the practical application of three interlinked principles along with complementary good agricultural practice. The characteristics of CA make it one of the systems best able to contribute to climate change mitigation by reducing atmospheric greenhouse gas concentration.

In this article, the carbon sequestration potential of CA is assessed, both in annual and perennial crops, in the different agro-climatic regions of Africa. In total, the potential estimate of annual carbon sequestration in African agricultural soils through CA amounts to 143 Tg of C per year, that is 524 Tg of CO_2 per year. This figure represents about 93 times the current sequestration figure.

1. Introduction

Africa is the smallest contributor to global greenhouse gas emissions (GHGs) among the continents, but the most vulnerable to the impacts of climate change (UNFCCC, 2016). According to the Intergovernmental Panel on Climate Change (IPCC), temperatures across Africa are expected to increase by 2–6 °C within the next 100 years (IPCC, 2014). The effects will not be limited to a rising average temperature and changing rainfall patterns, but also to increasing severity and frequency in droughts, heat stress and floods (Niang et al., 2014; Hummel, 2015; Rose, 2015). These climatic risks have a direct negative impact on the natural resources supporting agricultural production processes with a

detrimental impact on food security and livelihoods (Awojobi and Tetteh, 2017; Abebe, 2014; Science for Environmental Policy, 2015). The agricultural sector in Africa has been impacted by flooding, droughts, soil erosion, land degradation and deforestation, leading to human migration within Africa and to out migration from Africa.

Agriculture is not only impacted upon by climate change but also contributes to global warming. Even if agriculture would not be the only productive sector affected by global warming, the impacts on it would definitely have negative effects on food security and social welfare. Crops need adequate land, water, sunlight and temperature to grow and complete their production cycles. Global warming has already altered the duration of the growing season in some areas. The periods of

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Fig. 1. Climatic zones of Africa. Source: Authors' diagram based on Ngaira (2007) and www.gifex.com.

Fig. 2. Geographical distribution of studies addressing carbon sequestration per climatic zone.

flowering and harvest of cereals are already several days ahead. It is foreseeable that these changes may continue to occur in many regions (EEA, 2016). The sector needs to adapt to the changes in climatic conditions and also help in mitigation. Agriculture, which is part of the AFOLU sector (Agriculture, Forestry, and Other Land Use) is unique, since its climate change mitigation potential is derived from both an enhancement of removals of GHGs from the atmosphere, and a reduction of emissions through management of land, crops and livestock

(Smith et al., 2014).

Africa remains a food deficit region, yet it has potential to become a future 'bread basket', and the sustainable intensification of agricultural output, with a focus on soil and water conservation and optimum use of production inputs with minimum negative impact on the environment is part of the solution (Conway, 2012). Lal (2008) alerts of the effects of projected climate change on yield of food crops in Africa that may reach significant declines of 17.2% in wheat, 14.6% in sorghum and 13.1% in

Table 1

Carbon sequestration rates in Conservation Agriculture (CA) for each climatic zone.

Source: Carbon sequestration rates based on the papers reviewed and listed in the references.

	Carbon sequestration rate for CA in annual crops (Mg ha^{-1} yr ⁻¹)	Carbon sequestration rate for CA in woody crops (Mg ha^{-1} yr ⁻¹)
Mediterranean	0.44	1.29
Sahel	0.50	0.12
Tropical	1.02	0.79
Equatorial	1.56	0.26

Table 2

Current soil organic carbon (SOC) fixed annually by CA cropland systems compared to systems based on tillage agriculture in Africa. *Source: Kassam et al., 2018.

Country	No-tillage adoption* (ha)	Carbon sequestration rate in no-tillage (Mg ha ⁻¹ yr ⁻¹)	Current annual carbon sequestration (Mg yr ⁻¹)	Climatic zone
Algeria	5,600	0.44	2,464	Mediterranean
Ghana	30,000	1.56	46,800	Equatorial
Kenya	33,100	1.02	33,762	Tropical
Lesotho	2,000	1.02	2,040	Tropical
Madagascar	9,000	1.56	14,040	Equatorial
Malawi	211,000	1.02	215,220	Tropical
Morocco	10,500	0.44	4,620	Mediterranean
Mozambique	289,000	1.02	294,780	Tropical
Namibia	340	0.50	170	Sahel
South Africa	439,000	1.02	447,780	Tropical
Sudan	10,000	0.50	5,000	Sahel
Swaziland	1,300	1.02	1,326	Tropical
Tanzania	32,600	1.02	33,252	Tropical
Tunisia	12,000	0.44	5,280	Mediterranean
Uganda	7,800	1.56	12,168	Equatorial
Zambia	316,000	1.02	322,320	Tropical
Zimbabwe	100,000	1.02	102,000	Tropical
TOTAL	1,509,240		1,543,022	

maize. For many developing countries, the main concern regarding agriculture relates to food security, poverty alleviation, economic development and adaptation to the potential impacts of climate change.

A well designed and executed soil management system has the potential to increase yields (e.g., in sub-Saharan Africa) while also providing a range of co-benefits such as increased soil organic matter (Keating et al., 2013; Kassam et al., 2017a). Two-thirds of developing countries have implemented strategic plans to mitigate greenhouse gas (GHG) emissions from agriculture (Wilkes et al., 2013).

In this context, Conservation Agriculture (CA) is a sustainable agriculture system, able to produce food and other agricultural products in all land-based agroecologies (Kassam et al., 2018). According to the Food and Agriculture Organization of the United Nations (FAO, 2018a), CA is a farming system that promotes continuous no or minimum soil disturbance (i.e. no tillage), maintenance of a permanent soil mulch cover, and diversification of plant species. It enhances biodiversity and natural biological processes above and below the ground surface, so contributing to increased water and nutrient use efficiency and productivity, to more resilient cropping systems, and to improved and sustained crop production. CA is based on the practical application of three interlinked principles along with complementary good agricultural practice, namely:

(1) Avoiding or minimizing mechanical soil disturbance involving seeding or planting directly into untilled soil, eliminating tillage altogether once the soil has been brought to good condition, and keeping soil disturbance from cultural operations to the minimum possible.

- (2) Maintaining year-round biomass mulch cover over the soil, including specially introduced cover crops and intercrops and/or the mulch provided by retained biomass and stubble from the previous crop.
- (3) Diversifying crop rotations, sequences and associations, adapted to local environmental and socio-economic conditions, and including appropriate nitrogen fixing legumes; such rotations and associations contribute to maintaining biodiversity above and, in the soil, add biologically fixed nitrogen to the soil-plant system, and help avoid build-up of pest populations. In CA, the sequences and rotations of crops encourage agrobiodiversity as each crop will attract different overlapping spectra of microorganisms and natural enemies of pests.

No-tillage is clearly identified as a CA technique, whereas the application of Conservation Agriculture in perennial crops has been less studied. The agronomical practise of CA in woody crops are the groundcovers, whereby the soil surface between rows of trees remains protected against erosion by a cover. With this technique, at least 30% of the soil is protected either by sown cover crops, spontaneous vegetation or inert covers, such as pruning residues or tree leaves. For the establishment of sown cover crops and the spread of inert covers, farmers must use methods in coherence with CA principle of minimum soil disturbance (Gonzalez-Sanchez et al., 2015).

In both type of crops, annual or perennial, the characteristics of CA make it one of the systems best able to contribute to climate change mitigation by reducing atmospheric GHGs concentration. On the one hand, the changes introduced by CA in the carbon dynamics in the soil lead directly to an increase in soil C (Reicosky, 1995; Lal, 2008). This effect is known as 'soil's carbon sink'. At the same time, the drastic reduction in the amount of tillage and the mechanical non-alteration of the soil reduce CO_2 emissions arising from energy saving and the reduction in the rates of the mineralization of soil organic matter (Carbonell-Bojollo et al., 2011; Kassam et al., 2017a). CA adoption requires a much lower level of capital investment and production inputs and is thus more readily applicable to smallholder farmers in low income countries (Kassam et al., 2017b).

Soil carbon sequestration is a process in which CO₂ is removed from the atmosphere and stored in the soil carbon pool. This process is primarily mediated by plants through photosynthesis, with carbon stored in the form of soil organic carbon (SOC) (Lal, 2008). In terms of climate change mitigation, CA contributes the increase of SOC, whilst reducing the emissions of carbon dioxide. On the one hand, the decomposition of the crop biomass on the soil surface increase soil organic matter and soil organic carbon. On the other hand, emissions are reduced as a result of less soil carbon combustion due to no-tillage, and less fuel burning because of fewer field operations and lower energy use for seeding and crop establishment. The net sum effect of these processes results in an increase in the carbon sink effect in the soil, leading to a net increase of soil organic carbon; measured in Mg of carbon in soil per hectare per year (Mg ha⁻¹ yr⁻¹). Numerous scientific studies confirm that soils are an important pool of active carbon (González-Sánchez et al., 2012), and play a major role in the global carbon cycle.

Several international initiatives have identified CA as a major contributor to the mitigation and adaptability of agricultural land use to climate change. The initiative "4 per 1000" (4p1000, 2015), launched by France on 1 December 2015 at the COP 21 in Paris, aims to demonstrate that agriculture, and in particular agricultural soils, can play a crucial role where food security and climate change are concerned. The following year, the Adaptation of African Agriculture (AAA, 2016) was identified as one of the priorities of the Moroccan presidency for COP22 in Marrakesh. The Triple A aims to reduce the vulnerability of Africa and its agriculture to climate change. Both 4p1000 and AAA are governmentally supported, and show that agriculture can provide some practical solutions to the challenge and threats posed by climate

Fig. 3. Potential area for the application of CA in annual crops in Africa in 2016. Source: Authors diagram based on FAOSTAT, 2018.

Fig. 4. Potential area for the application of CA in woody crops in Africa in 2016. Source: Authors diagram based on FAOSTAT (2018).

change. The promotion of CA is among the key solutions and recommendations identified in both initiatives. The "4 per 1000" initiative intends to increase soil organic matter and carbon sequestration through the implementation of agricultural systems and practices adapted to local environmental, social and economic conditions, whereas the AAA promotes and supports three over-arching solution clusters to enhance soil management through soil fertility and crop fertilisation; arboriculture and agroforestry; and agroecological innovations and carbon sequestration. CA has also been incorporated into the regional agricultural policies, and increasingly, has been 'officially' recognized as a core element of climate-smart agriculture (FAO, 2016, 2017; Kassam et al., 2017b).

At present some 11 percent (1.5 Gha) of the globe's land surface (13.4 Gha) is used in crop production (arable land and land under

Table 3

Potential annual carbon sequestration in annual crops due to no-tillage. Potential adoption of no-tillage elaborated on country statistics of eligible crops based on FAOSTAT (FAO, 2018b).

Country	Potential adoption of no-tillage (ha)	Carbon sequestration rate in no- tillage (Mg $ha^{-1} yr^{-1}$)	Potential annual carbon sequestration in no-tillage (Mg yr ⁻¹)	Climatic zone
Algeria Angola	2,298,018 1,294,527	0.44 1.56	1,011,128 2,019,462	Mediterranean Equatorial
Angola	1,294,527	1.02	1,320,418	Tropical
Benin	1,763,758	1.56	2,751,462	Equatorial
Burkina Faso	120,400 6 200 742	0.50	6416557	Tropical
Burundi	446.863	1.02	455.800	Tropical
Cabo Verde	63,396	1.02	64,664	Tropical
Cameroon	1,630,294	1.56	2,543,258	Equatorial
Cameroon	1,630,294	1.02	1,662,899	Tropical
Central African	330,367	1.56	515,373	Equatorial
Ched	2 052 614	0.50	1 026 207	Sabal
Chad	2,052,614	0.50	1,020,307	Tropical
Comoros	2,032,014	1.02	2,093,000	Tropical
Congo	49,484	1.56	77,195	Equatorial
Côte d'Ivoire	1,046,568	1.56	1,632,646	Equatorial
Democratic Republic	2,435,696	1.56	3,799,686	Equatorial
of the Congo				
Eritrea	598,467	0.50	299,234	Sahel
Ethiopia	3,032,626	0.50	1,516,313	Sahel
Ethiopia	9,097,877	1.02	9,279,835	Tropical
Gabon	40,598	1.50	03,333	Equatorial
Ghana	1 879 696	1.02	217,379	Fauatorial
Guinea	676.016	1.56	1.054.585	Equatorial
Guinea	676,016	1.02	689,536	Tropical
Guinea-Bissau	57,660	1.02	58,813	Tropical
Kenya	2,300,622	0.50	1,150,311	Sahel
Kenya	2,300,622	1.02	2,346,634	Tropical
Lesotho	89,068	1.02	90,849	Tropical
Liberia	8,532	1.56	13,310	Equatorial
Madagascar	361 970	1.56	143,338 564 673	Fauatorial
Malawi	2.864.440	1.02	2.921.729	Tropical
Mali	2,876,307	0.50	1,438,154	Sahel
Mali	2,876,307	1.02	2,933,833	Tropical
Mauritania	342,236	0.50	171,118	Sahel
Mauritius	395	1.56	616	Equatorial
Morocco	4,164,886	0.44	1,832,550	Mediterranean
Mozambique	3,004,979	1.02	3,065,079	Tropical
Niger	303,033 16 362 647	0.50	8 181 324	Sahel
Nigeria	10,557,289	1.56	16,469,370	Equatorial
Nigeria	10,557,289	1.02	10,768,434	Tropical
Reunion	5,066	1.56	7,903	Equatorial
Rwanda	519,023	1.56	809,676	Equatorial
Rwanda	519,023	1.02	529,403	Tropical
Sao Tome and Principe	949	1.56	1,480	Equatorial
Senegal	/24,221	0.50	362,111	Sahel Tropicol
Senegal Sierra Leone	724,221	1.02	738,705	I ropical
Somalia	435.096	0.50	217.548	Sahel
South Africa	587,257	0.44	258,393	Mediterranean
South Africa	587,257	0.50	293,629	Sahel
South Africa	1,761,771	1.02	1,797,006	Tropical
South Sudan	1,230,241	1.02	1,254,846	Tropical
Sudan	15,262,789	0.50	7,631,395	Sahel
Swaziland	86,070	1.02	87,791	Tropical
Tanzania	9,693,740	1.02	9,887,615	i ropical
Tunisia	1,524,877	0.44	2,370,000 438 862	Mediterranean
Uganda	1.523.709	1.56	2.376.985	Equatorial
Uganda	1,523,709	1.02	1,554,183	Tropical

Table 3 (continued)

Country	Potential adoption of no-tillage (ha)	Carbon sequestration rate in no- tillage (Mg ha^{-1} yr ⁻¹)	Potential annual carbon sequestration in no-tillage (Mg yr ⁻¹)	Climatic zone
Zambia Zimbabwe TOTAL	1,648,278 2,171,103 142,172,059	1.02 1.02	1,681,244 2,214,525 130,746,653	Tropical Tropical

permanent crops) (FAO, 2003), therefore a major shift from tillagebased agriculture to climate smart systems, such as CA, would have a significant impact on global climate, food security and society. The aim of this study is to provide knowledge with a solid scientific base on the carbon sequestration potential of CA, both in annual and perennial crops, in the different agro-climatic regions of Africa.

2. Material and methods

The results presented in this paper are based on a literature review of scientific articles published in peer reviewed journals. The terms "Conservation Agriculture; carbon sequestration; Africa; climate change mitigation; no-tillage; groundcovers" have been consulted at the scientific databases *sciencedirect.com* and *webofknowledge.com*.

This review has been carried out for the different climatic zones of Africa (Fig. 1) using as baseline reported carbon sequestration rates under CA and the current area of CA adoption in annual and perennial cropping systems. It then estimated the potential of carbon sequestration based on both the potential sequestration rates in annual and perennial cropping systems and different climatic zones, and the potential area that could be converted from conventional tillage agriculture to CA across Africa. Fig. 2 shows the geographical distribution of the studies. No data for carbon sequestration in desert areas is presented, as no articles with a carbon sequestration rate of CA have been found, and there is little expectation of a significant carbon increase in those environments as a result of farming activities.

The methodology for obtaining the carbon sequestration rates is described in González-Sánchez et al. (2012). To estimate the potential of CA for C sequestration, in each study, the increase of observed organic matter in the conservation system was evaluated in relation to conventional tillage. C increases are proposed in terms of quantities of C from the organic carbon (OC) in the soil. To estimate the potential area suitable for the adoption of CA the areas of different crops in the different climatic zones as provided by FAOSTAT (FAO, 2018b) was used. Among the annual crops, those best adapted to no-tillage CA systems were selected as eligible crops: cereals, pulses, oilseeds, cotton, among other crops that do not need soil disturbance for harvesting, whereas most of the woody perennial crop areas were found suitable for CA. It could not be identified if root crops are in rotation with eligible crops.

In climate change international agreements, emissions are referred to carbon dioxide; however, soil carbon studies refer to carbon. For transforming carbon into carbon dioxide, the coefficient of 3.67 was used. The atomic weight of carbon is 12 atomic mass units, while the weight of carbon dioxide is 44, because it also includes two oxygen atoms that each weigh 16. So, to switch from one to the other, one Mg of carbon equals 44/12 = 3.67 Mg of carbon dioxide.

3. Results and discussion

According to the latest statistics available, farmers in almost 20 African countries are practising CA, including Algeria, Ghana, Kenya, Lesotho, Madagascar, Malawi, Morocco, Mozambique, Namibia, South Africa, Sudan, Swaziland, Tanzania, Tunisia, Uganda, Zambia and Zimbabwe (Kassam et al., 2018).

The most recent figures of adoption of CA for annual crops in Africa

LSD = 555,0

Table 4

Potential annual carbon sequestration in woody crops due to groundcovers. Potential adoption of groundcovers elaborated on country statistics of eligible crops based on FAOSTAT (FAO, 2018b).

Country	Potential adoption of groundcovers (ha)	Carbon sequestration rate in groundcovers (Mg ha ^{-1} yr ^{-1})	Potential annual carbon sequestration in groundcovers (Mg yr ⁻¹)	Climatic zone
Algeria	813,371	1.29	1,049,249	Mediterranean
Angola	39,795	0.26	10,347	Equatorial
Angola	39,795	0.79	31,438	Tropical
Benin	785,872	0.26	204,327	Equatorial
Botswana	32	0.12	4	Sahel
Burkina Faso	167,148	0.79	132,047	Tropical
Cabo Verde	443	0.79	350	Tropical
Cameroon	60.607	0.26	15.758	Equatorial
Cameroon	60,607	0.79	47,879	Tropical
Central	55,932	0.26	14,542	Equatorial
African				
Republic				
Chad	4,316	0.12	518	Sahel
Chad	4,316	0.79	3,409	Tropical
Congo	969 18 790	0.79	4 885	Fouatorial
Côte d'Ivoire	4.312.885	0.26	1.121.350	Equatorial
Democratic	113,234	0.26	29,441	Equatorial
Republic of the Congo				•
Equatorial Guinea	11,587	0.26	3,013	Equatorial
Ethiopia	201,770	0.12	24,212	Sahel
Ethiopia	605,309	0.79	478,194	Tropical
Gabon	520	0.26	135	Equatorial
Gambia	3,841	0.79	3,034	Tropical
Ghana	329,980	0.26	85,795	Equatorial
Guinea	94,616	0.26	24,600	Equatorial
Guinea-	558 346	0.79	441 093	Tropical
Bissau	330,340	0.75	441,055	Hopical
Kenya	133,040	0.12	15,965	Sahel
Kenya	133,040	0.79	105,102	Tropical
Liberia	7,294	0.26	1,896	Equatorial
Libya	509,133	1.29	656,782	Mediterranean
Madagascar	227,889	0.26	59,251	Equatorial
Malawi	16,138	0.79	12,749	Iropical
Mali	96,010 96,010	0.12	75 848	Tropical
Mauritius	203	0.26	53	Equatorial
Morocco	1,686,040	1.29	2,174,992	Mediterranean
Mozambique	260,859	0.79	206,079	Tropical
Namibia	7,061	0.12	847	Sahel
Niger	40,600	0.12	4,872	Sahel
Nigeria	888,532	0.26	231,018	Equatorial
Reunion	888,532 690	0.79	701,940	Fountorial
Rwanda	24.318	0.26	6.323	Equatorial
Rwanda	24,318	0.79	19,211	Tropical
Sao Tome	429	0.26	112	Equatorial
and Principe				
Senegal	32,019	0.12	3,842	Sahel
Senegal	32,019	0.79	25,295	Tropical
Seychelles	81	0.79	64	Tropical
Sierra Leone	36,034	0.26	9,369	Equatorial
Somalia	4,299	0.12	516	Sahel
South Africa	46,198	1.29	59,595	Mediterranean
South Africa	40,198	0.12	5,544 109 488	Tropical
South Sudan	1,943	0.79	1.535	Tropical
Sudan	117,096	0.12	14,052	Sahel
Swaziland	13,746	0.79	10,859	Tropical
Tanzania	1,263,844	0.79	998,437	Tropical
Togo	48,816	0.26	12,692	Equatorial

Table 4 (continued)

ential Ca ption of sec undcovers rat) gro (M yr	arbonPoquestrationante insecoundcoversin Mg ha ⁻¹ gro $(M)^{-1}$ (M)	otential Cli nnual carbon equestration n roundcovers Mg yr ⁻¹)	matic zone
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(season 2015/16) totaled 1.5 Mha. This corresponds to some 211% increase from 0.48 Mha in 2008/09 (Kassam et al., 2018). This significant increase is because of the many years of research showing positive results for CA systems, plus increasing attention being paid to CA systems by governments, NEPAD (New Partnership for Africa's Development), and NGOs such as ACT (African Conservation Tillage), and the private sector, international organizations and donors.

Reported average of values of carbon sequestration by CA in agricultural soils found in literature for each climatic zone in Africa are presented in Table 1. The total carbon sequestration estimated for the whole of Africa, of 1,543,022 Mg C yr⁻¹ is shown in Table 2. On average, the carbon sequestered for Africa due to CA is thus around 1 Mg C ha⁻¹ yr⁻¹, corresponding to a total amount of 5,657,747 Mg CO₂ yr⁻¹. This relatively high figure is because degraded soils are 'hungry' for carbon, as the degradation caused by years of tillage, soil mining and crop biomass removal has resulted in a drastic reduction of soil's organic matter (Reicosky, 1995; Jat et al., 2014; Kassam et al., 2017b).

Results presented in this paper are in agreement with previous meta-analyses and studies, where CA in annual and perennial crops have been found to have incremented soil organic carbon (González-Sánchez et al., 2012, 2017; and the studies referenced for obtaining the C sequestration rates for Africa).

In CA systems major inputs in carbon can be expected through the retention of crop biomass, crop rotation and the reduction in soil disturbance (Cheesman et al., 2016). Conversely to the results presented for Africa in this article, González-Sánchez et al. (2012) in a study for European agriculture found that C sequestration rates for perennials were higher than for annual crops. This might be because African perennial crops are not as intensive as yet as European ones, and therefore their soils are closer to the carbon sequestration plateau or the equilibrium.

Sometimes, controversial results can be found in literature attributed to CA when in fact some of the key CA principles were not applied, thus not dealing with real CA systems. Indeed, according to Derpsch et al. (2014), broad understanding is lacking of what CA systems research means. This has led to a situation of conflicting research results because different technologies, methodologies, and erroneous definitions of CA systems have been applied. A practice such as no-tillage can only be considered to be a CA practice if it is part of a CA system as per the definition provided earlier, otherwise it is just a no-tillage practice. Similarly, for soil mulch practice and crop diversification practice both of which can only be considered to be CA practices if they are part of a CA system based on the application of the three interlinked principles. Only when the three principles of CA are applied in field, the best results are achieved, including for carbon sequestration, as confirmed in a recent study for Africa by Corbeels et al. (2018).

These positive results from CA systems are compared with the "business as usual" tillage agriculture cases. Conventional farming globally is based on soil tillage which promotes the mineralization of soil organic matter whilst increasing the release of CO_2 into the atmosphere due to C oxidation. Also, tillage operations can incorporate crop

Fig. 5. Potential soil organic carbon (SOC) fixed annually by CA cropland systems compared to tillage-based agricultural production systems in Africa. Authors diagram.

biomass into soil layers where microorganisms and moisture conditions favour their decomposition and thus resulting in more carbon oxidation. Moreover, soil tillage physically breaks down soil aggregates and leaves carbon in them exposed to the action of soil microorganisms which were encapsulated and thus protected within the soil aggregates that existed prior to the performance of tillage (Reicosky and Archer, 2007).

One of the consequences of management systems based on tillage is the reduction of the soil carbon sink effect, which has as a consequence the decrease in the content of organic carbon. This decrease is the result of (1) the lower contribution of organic matter in the form of crop stubble and biomass from previous crops; and (2) the higher rate of mineralization of soil humus caused by tillage. Tillage facilitates the penetration of air into the soil and therefore the decomposition and mineralization of humus, a process that includes a series of oxidation reactions, generating CO_2 as the main byproduct. One part of CO_2 becomes trapped in the porous space of the soil, while the other part is released into the atmosphere through diffusion across the zones of the soil with different concentration: and (3) the higher rate of soil erosion and degradation which causes significant losses of organic matter and minerals as well as soil health. In conventional tillage agriculture, the preparation of soil for sowing and crop establishment leaves the soil exposed to erosive agents for longer periods of time. For all of the above reasons, many researchers agree that mechanical soil disturbance by tillage is one of the main causes of organic carbon reduction in the soil (Balesdent et al., 1990; Six et al., 2004; Olson et al., 2005). Reicosky (2011) argues that intensive tillage agriculture has contributed to the loss of between 30% and 50% of soil organic C in the last two decades of the 20th century. Kinsella (1995) estimates that, in only 10 years of tillage, some 30% of the original soil organic matter was lost.

Even though CA has positive effects, the increase of soil C is not permanent in time, and after a number of years, the rate of accumulation slows down towards a plateau level depending on the soil type, length of growing period and climatic conditions, and the rate of turnover of C. The time to reach the plateau level varies but is considerable, and may take over 10–15 years before a deceleration in the rate of C increase is observed (González-Sánchez et al., 2012). Therefore, even if after 10–15 years C sequestration rates are lower, carbon is still being captured in the soil which supports the value of a long-term and continuing engagement with CA land management. Also, even when top soil layers may be reaching plateau levels, deeper soil layers continue to sequester C through the action of earthworms and biomass and carbon exudates provided by deeper root systems. As CA adoption rates in Africa are improving more significantly over the last decade, the sequestration coefficients presented in this paper can be considered as those applicable to the initial period of transformation from conventional agriculture.

In Figs. 3 and 4, the potential area that could be shifted from conventional tillage agriculture to CA is presented, for both annual and permanent cropping systems. Multiplying the rates of C sequestration presented in Table 1 by the potential areas per country and per type of crop (Tables 3 and 4) permits estimates of the potential carbon sequestration following the application of CA in the agricultural lands of Africa. Where more than one climate affects a single country, the climate of the major cropping area has been selected, i.e. Algeria's rate of C sequestration has been that of the Mediterranean climate, as most of its cropland is affected by that climate. In cases where there were two co-dominant climates, two rates of C sequestration have been applied.

Finally, Fig. 5 shows the total amount of potential carbon sequestration for Africa, for each climatic region, with respect to current carbon sequestration status. Table 5 offers the same result as Fig 5, but split by country. In total, the potential estimate of annual carbon sequestration in African agricultural soils through CA amounts to 143 Tg of C per year, that is 524 Tg of CO_2 per year. This figure represents about 93 times the current sequestration figure. To put this figure into context, according to the United Nations Framework Convention on Climate Change, South Africa, the world's 13th largest CO_2 emitter, total national emissions by 2025 and 2030 will be in a range between 398 and 614 Tg CO_2 -eq per year (UNFCCC, 2018). Thus, the carbon dioxide sequestration potential of CA for Africa is almost 3 time higher than that document for Europe by González-Sánchez et al. (2017), i.e. 189 Tg CO_2 per year.

Table 5

Potential annual carbon sequestration in Conservation Agriculture over conventional tillage-based agriculture (annual plus woody crops).

Country	Potential annual carbon	Climatic zone	
	sequestration in Conservation		
	Agriculture (Mg yr^{-1})		
Algeria	2.060.377	Mediterranean	
Angola	2,029,809	Equatorial	
	1,351,855	Tropical	
Benin	2,955,789	Equatorial	
Botswana	60,234	Sahel	
Burkina Faso	6,548,604	Tropical	
Burundi Galar Marila	468,425	Tropical	
Cabo Verde	05,014	I ropical	
Califertoon	1 710 779	Tropical	
Central African	529 915	Equatorial	
Republic	023,310	Equatorial	
Chad	1,026,825	Sahel	
	2,097,075	Tropical	
Comoros	23,591	Tropical	
Congo	82,080	Equatorial	
Côte d'Ivoire	2,753,996	Equatorial	
Democratic Republic of	3,829,127	Equatorial	
the Congo	2.012	Equatorial	
Equatorial Guinea	3,013	Equatorial	
Effica	1 540 525	Sahel	
Епторіа	9 758 029	Tropical	
Gabon	63.468	Equatorial	
Gambia	220,614	Tropical	
Ghana	3,018,121	Equatorial	
Guinea	1,079,185	Equatorial	
	764,283	Tropical	
Guinea-Bissau	499,907	Tropical	
Kenya	1,166,276	Sahel	
· .1	2,451,736	Tropical	
Lesotho	90,849	Tropical	
Liberia	15,200	Equatorial	
Madagascar	623 924	Fauatorial	
Malawi	2.934.478	Tropical	
Mali	1,449,675	Sahel	
	3,009,681	Tropical	
Mauritania	171,118	Sahel	
Mauritius	669	Equatorial	
Morocco	4,007,541	Mediterranean	
Mozambique	3,271,157	Tropical	
Namibia	152,674	Sahel	
Niger	8,186,196	Sahel	
Nigeria	10,700,388	Tropical	
Reunion	8 082	Fauatorial	
Rwanda	815.998	Equatorial	
	548,614	Tropical	
Sao Tome and Principe	1,592	Equatorial	
Senegal	365,953	Sahel	
	764,000	Tropical	
Seychelles	64	Tropical	
Sierra Leone	405,433	Equatorial	
Somalia Couth Africa	218,064	Sahel	
South Africa	317,988	Sebel	
	1 906 494	Tropical	
South Sudan	1,256,381	Tropical	
Sudan	7,645,446	Sahel	
Swaziland	98,651	Tropical	
Tanzania	10,886,052	Tropical	
Togo	2,391,500	Equatorial	
Tunisia	3,272,747	Mediterranean	
Uganda	2,426,840	Equatorial	
	1,705,664	Tropical	
Zambia	1,687,985	Tropical	
Zimbabwe	2,236,555	Tropical	
IUIAL	143,100,442		

4. Conclusions

Conservation Agriculture is a promising sustainable agricultural system, as it can effectively contribute to mitigating global warming, being able to sequester carbon in the soil, thus offsetting agricultural and non-agricultural CO_2 emissions. CA is a proven and effective agricultural system that African countries need to promote to fulfill the international agreements and initiatives related to climate change mitigation and adaptation, such as the Paris agreement on climate change, the 4p1000 initiative and the Adaptation of African Agriculture (AAA).

Carbon sequestration rates in Africa are in agreement with those found in other meta-analyses performed in other agroclimatic regions. As performed in this review, the accounting methodology for carbon sequestration in agricultural soils should be based on the relative gains when compared to conventional tillage-based agriculture. In addition, and with regard to African carbon sinks, areas of annual and perennial cropping systems when converted to CA should be accounted for as new net carbon gains, both in the carbon markets and the international climate change agreements.

According to the estimation of the climate change mitigation capacity through CA in Africa there exists an enormous C sink potential which is around 93 times greater than under the current situation, i.e. at present only around 1.1% of the overall C sequestration potential through CA is used.

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Worldwide decline of the entomofauna: A review of its drivers

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ABSTRACT

Biodiversity of insects is threatened worldwide. Here, we present a comprehensive review of 73 historical reports of insect declines from across the globe, and systematically assess the underlying drivers. Our work reveals dramatic rates of decline that may lead to the extinction of 40% of the world's insect species over the next few decades. In terrestrial ecosystems, Lepidoptera, Hymenoptera and dung beetles (Coleoptera) appear to be the taxa most affected, whereas four major aquatic taxa (Odonata, Plecoptera, Trichoptera and Ephemeroptera) have already lost a considerable proportion of species. Affected insect groups not only include specialists that occupy particular ecological niches, but also many common and generalist species. Concurrently, the abundance of a small number of species is increasing; these are all adaptable, generalist species that are occupying the vacant niches left by the ones declining. Among aquatic insects, habitat and dietary generalists, and pollutant-tolerant species are replacing the large biodiversity losses experienced in waters within agricultural and urban settings. The main drivers of species declines appear to be in order of importance: i) habitat loss and conversion to intensive agriculture and urbanisation; ii) pollution, mainly that by synthetic pesticides and fertilisers; iii) biological factors, including pathogens and introduced species; and iv) climate change. The latter factor is particularly important in tropical regions, but only affects a minority of species in colder climes and mountain settings of temperate zones. A rethinking of current agricultural practices, in particular a serious reduction in pesticide usage and its substitution with more sustainable, ecologically-based practices, is urgently needed to slow or reverse current trends, allow the recovery of declining insect populations and safeguard the vital ecosystem services they provide. In addition, effective remediation technologies should be applied to clean polluted waters in both agricultural and urban environments.

1. Introduction

For years, biologists and ecologists have been concerned about the worldwide reduction in biodiversity undergone by many terrestrial and aquatic vertebrates (Ceballos and Ehrlich, 2002; Pimm and Raven, 2000; Wilson, 2002), yet scientists have only recently voiced similar concerns about invertebrate taxa, particularly insects. Population declines imply not only less abundance but also a more restricted geographical distribution of species, and represent the first step towards extinction (Diamond, 1989). Much of the blame for biodiversity loss falls on human activities such as hunting and habitat loss through deforestation, agricultural expansion and intensification, industrialisation and urbanisation (Ceballos et al., 2017; Maxwell et al., 2016), which jointly claimed a 30-50% encroachment on natural ecosystems at the end of the 20th century (Vitousek et al., 1997).

There is compelling evidence that agricultural intensification is the main driver of population declines in unrelated taxa such as birds, insectivorous mammals and insects. In rural landscapes across the globe, the steady removal of natural habitat elements (e.g. hedgerows), elimination of natural drainage systems and other landscape features together with the recurrent use of chemical fertilisers and pesticides negatively affect overall biodiversity (Fuller et al., 1995; Newton, 2004; Tilman et al., 2001). Recent analyses point to the extensive usage of pesticides as primary factor responsible for the decline of birds in grasslands (Mineau and Whiteside, 2013) and aquatic organisms in streams (Beketov et al., 2013), with other factors contributing to or amplifying their effects to varying extent. Yet, we don't know whether the same factors explain the parallel entomological demise that we are witnessing.

In 2017, a 27-year long population monitoring study revealed a

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Review

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Fig. 1. Geographic location of the 73 reports studied on the world map. Columns show the relative proportion of surveys for each taxa as indicated by different colours in the legend. Data for China and Queensland (Australia) refer to managed honey bees only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shocking 76% decline in flying insect biomass at several of Germany's protected areas (Hallmann et al., 2017). This represents an average 2.8% loss in insect biomass per year in habitats subject to rather low levels of human disturbance, which could either be undetectable or regarded statistically non-significant if measurements were carried out over shorter time frames. Worryingly, the study shows a steady declining trend over nearly three decades. A more recent study in rainforests of Puerto Rico has reported biomass losses between 98% and 78% for ground-foraging and canopy-dwelling arthropods over a 36year period, with respective annual losses between 2.7% and 2.2% (Lister and Garcia, 2018). The latter authors showed parallel declines in birds, frogs and lizards at the same areas as a result of invertebrate food shortages. Both studies agree with the declining trend in flying insects (mainly Diptera) observed a decade earlier in parts of Southern Britain (Shortall et al., 2009). As insects comprise about two thirds of all terrestrial species on Earth, the above trends confirm that the sixth major extinction event is profoundly impacting life forms on our planet (Thomas et al., 2004).

While the arthropod declines in tropical rainforests correlate well with climatic changes, the 12 different factors (e.g. increases in arable land, deforestation, global warming) that were thought to be responsible for year-to-year drops in insect biomass in Germany barely accounted for $\sim 20\%$ of observed declines. Rather surprisingly, 80% of observed inter-annual variability in insect numbers was left unexplained (Hallmann et al., 2017). Although the authors did not assess the effect of synthetic pesticides, they did point to them as a likely driver of the pervasive losses in insect biomass.

The above studies, however, are in line with previous reports on population declines among numerous insect taxa (i.e. butterflies, ground beetles, ladybirds, dragonflies, stoneflies and wild bees) in Europe and North America over the past decades. It appears that insect declines are substantially greater than those observed in birds or plants over the same time periods (Thomas et al., 2004), and this could trigger wide-ranging cascading effects within several of the world's ecosystems.

This review summarises our current state of knowledge about insect declines, i.e., the changes in species richness (biodiversity) and population abundance through time, and points to the likely drivers of the losses so that conservation strategies to mitigate or even reverse them may be implemented. Previous reviews are partial in scope, restricted to individual groups of insects (e.g. butterflies, carabids) in specific regions, but no study has put together a comprehensive review of all insect taxa nor compared the local findings among different parts of the world.

2. Methodology

We aimed at compiling all long-term insect surveys conducted over the past 40 years that are available through global peer-reviewed literature databases. To that effect we performed a search on the online Web of Science database using the keywords [insect*] AND [declin*] AND [survey], which resulted in a total of 653 publications. The majority of these referred to Hymenoptera (55), Diptera (45), Coleoptera (44) and Lepidoptera (37) taxa, among which only a few dealt with long-term surveys. Reports that focused on individual species, pest outbreaks or invasive species were excluded. We selected surveys that considered all species in a taxon (e.g. family or order) within large areas (i.e. a region, a country) or smaller areas surveyed intensively over periods longer than 10years. Additional papers were obtained from the literature references. Finally, only surveys that reported changes in quantitative data over time, either species richness or abundance, were considered. Thus, this review covers 73 reports on entomofauna declines in various parts of the world (Fig. 1) and examines their likely causes (Table S1). Because the overwhelming majority of long-term surveys have been conducted in developed countries, particularly in the northern hemisphere, this review is geographically biased and does not adequately cover trends in tropical regions, where information on insect biodiversity is either incomplete or lacking (Collen et al., 2008).

The above literature records use accurate scientific data on species distribution from museum specimens (56%), which are compared with long-term survey data obtained decades later (72%), and sometimes rely upon citizen science data (8%). Because the latter data tend to overestimate the diversity of insects due to over-reporting of rare species (Gardiner et al., 2012), the overall assessment of biodiversity can be considered conservative.

Conservation status of individual species follows the IUCN classification criteria (IUCN 2009): threatened species include vulnerable (> 30% decline), endangered (> 50%) and critically endangered (> 75% decline) species. Data on population abundance are more difficult to obtain than geographical distribution records, but a few reports quantified the extent of such declines for Lepidoptera, Hymenoptera and dung beetles (Coleoptera). An annual rate of decline (percentage of species declining per year) was estimated for each taxon and region.

A meta-analysis of the declines among the various taxa and regions was performed, with groups compared using analysis of variance (ANOVA). Enumerated drivers of the declines -as indicated by the reports' authors- are tabulated and analysed, and further discussed with reference to experimental and other empirical data available in the literature.

3. Taxa declines

3.1. Lepidoptera

Butterflies and moths are valuable indicators of environmental quality, considering their high degree of host-plant specialisation and vulnerability to habitat deterioration (Erhardt and Thomas, 1991). Given their presence in a broad range of habitats, the loss of Lepidoptera may directly impact the delivery of key ecosystem services such as pollination and natural pest control (Fox, 2013). Moths, which are about 10 times more diverse than butterflies, constitute important prey items of bats and help sustain population levels of myriad other insectivorous animals (Hahn et al., 2015; Vaughan, 2008; Wilson et al., 1999).

Maes and van Dyck (2001) were the first to report drastic changes in butterfly biodiversity in Flanders (Belgium) during the 20th century, including the extinction of 19 (out of 64) native species since 1834. Habitat loss resulted in a steady decline of 69% of the 45 extant species, while the extinction rate increased from 0.2 to 1.7 species/5-year since 1950 as urbanisation and agricultural intensification expanded eightfold (Maes and Van Dyck, 2001). A follow-up study in the Netherlands found that 11 of the 20 most common and widespread butterfly species declined both in distribution and abundance between 1992 and 2007, whereas populations of species associated with natural habitats in nature reserves remained stable. Local populations of Lasiommata megera and Gonepteryx rhamni are now endangered and two other species (Aglais io and Thymelicus lineola) are vulnerable (van Dyck et al., 2009). In parallel, the range of distribution of 733 species of day-flying moths was recorded between 1980 and 2000: overall declines were observed in 85% of species, 38% of them experiencing > 75% reduction in their area (i.e. critically endangered), 34% being considered threatened and 15% vulnerable (Groenendijk and van der Meulen, 2004). In particular, 47 of the 55 species monitored in peat-bog marshes declined, six remained stable and only two (Plusia putnami and Deltote bankiana) increased in range (Groenendijk and Ellis, 2011). The most affected species are those with lower dispersal abilities and preference for oligotrophic habitats.

Among the 269 species of macro-lepidopterans monitored for 50 years at the Kullaberg Nature Reserve (Sweden), 45% were declining, 22 were coloniser species and 159 were no longer found in 2004 (Franzén and Johannesson, 2007). Monophagous and oligophagous species using grass or herbs in wetlands were declining more than those feeding on deciduous trees or shrubs, confirming that dietary specialists bear the brunt of the declines. Species with a short flightperiod or those restricted to non-forest habitats were all associated with a high extinction risk. A comparison of historical records of 74 butterflies in Finland showed how 60% of grassland species declined over the past 50 years, whereas 86% of generalist species and 56% of those living at forest edge ecotones increased in abundance (Kuussaari et al., 2007). Common traits of the 23 declining species are a reduced mobility, oligotrophic habitat preference and seasonal migration behaviour. Another study on the populations of 306 species of noctuid moths in Finland over 1988–1997 reported the greatest declines for species with comparatively small geographic range, whereas polyphagous moths with longer flight periods and those that overwintered as adults had the widest distributions (Mattila et al., 2006). By contrast, species that overwintered as either larval or pupal stages suffered the largest declines over that period.

Similar findings were reported for north-eastern Spain, where yearly monitoring of 183 butterfly species over 1994–2014 permitted an indepth analysis of population trends and associated factors for 66 species. While 15 species had increased in abundance, five remain stable and 46 are declining (Melero et al., 2016). Although the extent of species decline did not differ among seven habitat types selected, forest butterflies appeared to be declining faster than those from other habitats due mainly to specialisation of the larval trophic stage and multi-

voltinism.

A comprehensive report on the status of 576 species of butterflies in Europe found that 71 were threatened and declined over a 25-year period (van Swaay et al., 2006). The largest declines occurred among specialist butterflies of grassland biotopes (19% species), wetlands and bogs (15%) and woodlands/forests (14%), due to habitat conversion into crops and the adoption of intensive agricultural practices, e.g. fertilisers and pesticides negatively affected 80% species. Some species (Lopinga achine and Parnassius apollo) had declined due to afforestation, i.e. conversion of open woodland habitats to dense forests. Climate change only affected a few endemic species adapted to mountainous biotopes. A more recent assessment of 435 butterflies native to Europe (van Swaay et al., 2010) found that populations of 19% of species are declining, particularly in Mediterranean and eastern countries, 8.5% species are threatened, and three are critically-endangered, i.e. Pieris brassicae wollastoni, Triphysa phryne and Pseudochazara cingovskii. Belgium and the Netherlands are the European countries with the highest losses of butterfly biodiversity (19 and 17 country-level extinctions, respectively), whereas Denmark and the U.K. have the least (4 species extinct each) (Maes and Van Dyck, 2001). One species (Aricia hyacinthus) is considered extinct over the European continent.

Butterflies appear to be declining faster in the United Kingdom, as 74% of 46 non-migratory butterflies restricted their distribution over 1970-1999 (Warren et al., 2001). Using a comprehensive database compiled by amateur collectors and scientists over a 29-year period in the entire British Isles, the authors showed that habitat specialists experienced the largest reductions in distributional area. Specialist and sedentary species not showing changes in abundance over 25 years had reduced their distribution on average by 15%. Other studies indicate that 41 out of 54 common butterflies had been declining since the 1970s, with 26% of species showing decreases over 40% of their range (Fox et al., 2006), while 13% of 10-km squares in the monitoring grid reported disappearance of butterfly species (Thomas et al., 2004). Although authors did not attempt to correlate the declines with specific drivers, the following combination of factors was suggested: habitat fragmentation and/or destruction, intensification of agriculture, including the increased usage of chemical fertiliser and pesticides, and perhaps over-collecting - although such practice has been greatly reduced by more environmental awareness. To minimise biodiversity losses among butterflies and moths, the UK Butterfly Monitoring Scheme (UKBMS) was created, which compiles data on the abundance and distribution of all species across the country since 1976. An initial analysis of 50 species showed a large fluctuation in butterflies among years, with specialist species having declined by 34% nationally since the scheme was established; generalist species had declined in England (12%) but little (6%) or not at all in Scotland. Major declines occurred in forests and farmland regardless of the efforts to restore biodiversity from 2000 onwards (Brereton et al., 2011). A further analysis of 17 widespread and resident species of butterflies between 1984 and 2012 showed that abundance of all species decreased by 58% since the year 2000, while 15 species exhibited population declines at average annual rates between -0.8% and -6.7% (Gilburn et al., 2015). Thus, 41% of the species studied are threatened. Increasing summer temperatures had a marked positive effect on butterfly abundance, whereas none of the other climatic factors could explain the decrease in their populations. By contrast, the steepest declines occurred in areas with high proportions of farmland treated with neonicotinoid insecticides; indices for the 15 declining species showed negative associations with neonicotinoid usage.

Similar rates of decline were reported among 337 moth species throughout England between 1968 and 2003: 222 showed declining populations over the 35-year study period, with a median 10-yr population decrease of 12%, although decreases were larger in the south of the country (17%) compared to the north (5%) (Conrad et al., 2006). The larger declining trends in the south were associated with the degree of agricultural intensification, as also recorded at Rothamstead between

the 1940s and 1960s (Woiwod & Gould, 2008 cited in Fox, 2013). At that time, 71 species of moths were considered threatened, 58 were vulnerable and 13 endangered. Subsequent surveys of about 900 species of moths by experts and amateurs over 25 years corroborated the previous findings, with decreases in range size for moths mirroring those of butterflies (Fox et al., 2011). Notable declines were recorded for Macaria wauaria (77% decrease) Graphiphora augur and Dasypolia *templi* (> 45% each), which are now included in the country's Red List, while decreases of M. wauaria and Eulithis mellinata were likely due to insecticide use on their host plants (i.e., currants). A northward shift of 12 common moth species showed that these insects were moving at 7.8 km/year since 1985. Species such as Katha depressa, Idaea rusticata and Collita griseola have each doubled their distribution and spread northwards by approximately 100 km. Some moths extended their range as a result of the widespread cultivation of their host plants in gardens or commercial conifer plantations.

For the United States, long-term monitoring data of butterflies are limited. Surveys in prairie habitats and bogs of Wisconsin and Iowa over 2002-2013 indicate fluctuating populations of certain species, but lack of consistency prevents drawing temporal trends. Main drivers appear to be habitat modification and moisture levels dependent on climate change (Swengel et al., 2011; Swengel and Swengel, 2015). In Massachusetts, the distributional ranges of 116 species shifted northwards between 1992 and 2010. Two southern species adapted to warmer conditions expanded in range (Papilio cresphontes and Poanes zabulon), while populations of 80% of butterflies declined in southern parts of that State; the only trait that correlated significantly with the declines was the overwintering stage of each species (Breed et al., 2012). In California, surveys on presence/absence of 67 butterfly species at four sites between 1972 and 2012 revealed that the average number of species at any site (30) remained stable until 1997, but dropped steeply to 23 in the last year of the study. The overall trend implies that 23% of species are disappearing. Data on species richness were correlated to annual variables such as summer temperatures, percentage of land converted to agriculture and usage rates of different insecticide classes. Only the latter two variables showed a significant correlation with the observed declines, and within the pesticides only neonicotinoid usage showed a positive correlation; incidentally, the start of the declining trend in 1997 followed the introduction of these systemic insecticides in that State in 1995 (Forister et al., 2016).

Although survey records are limited, Lepidoptera declines appear to be less dramatic in certain parts of the Asian region. In Japan, 15% of the 240 species of butterflies are threatened, but among those 80% of the grassland species are endangered, with two species close to extinction in the national territory: Melitaea scotosia (98% decline) and Argynnis nerippe (95% decline) (Nakamura, 2011). At the individual island level, seven species are now extinct. Species of the woodlands (40) are the most stable, while the steady intensification of Japan's traditional "satoyama" landscape (i.e., a mosaic of rice paddy fields, grassland and coppice forests) has negatively affected most species. Collecting of specimens was also as a minor driver after 1990. In Malaysia, some 19% of moths at Mount Kinabalu (Borneo) had their abundance reduced between 1965 and 2007 (Chen et al., 2011). Species typical of high altitudes (28) have shrunk their range as they shifted some 300 m uphill, whereas a third of the moths expanded their upper boundary upward by 152 m and retreated their lower boundary by 77 m as a result of global warming during the 40-year period.

3.2. Hymenoptera

Bees are essential pollinators of flowering plants, accounting for a third of all pollinators (Ollerton et al., 2011) and honey bees have been managed for millennia as a source of honey and beeswax. Knowledge about their population status, therefore, is important for the ecosystem services they provide as well as their economic value (Gallai et al., 2009). However, the status of most other hymenopterans – i.e., ants,

wasps and parasitoids; several of which provide equally important ecosystem services – remains practically unknown to this date.

3.2.1. Bumblebees (Bombus spp., Apidae)

The first report on the status of 18 bumblebees in Britain, using a numerical approach on a national map grid, showed declining trends for seven species since the 1960s, with large reductions in the range of four species (i.e., Bombus humillis, B. ruderatus, B. subterraneus and B. sylvarum) in the southern and central parts of England (Williams, 1982). An analysis of the causal factors responsible for such declines, using foraging data on eight native bumblebees and information on their distribution, found that the species subject to the greatest reduction in distribution were host-plant specialists. Thus, bumblebees that forage on grasslands and farmland flowers underwent the largest reductions. Particularly, three species of long-tongued bumblebees (B. humillis, B. ruderatus and B. subterraneus) that forage on clover and other legumes, traditionally used in rotations as a source of nitrogen, had their populations curtailed after the foraging plants were steadily replaced by chemical fertilisers in southern England (Goulson et al., 2005). By contrast, short-tongued bumblebees remain common in gardens and urban areas where they have access to a large array of native and introduced flowers.

In Denmark, long-tongued bumblebee species have declined in richness and abundance since the 1930s, particularly during the redclover flowering season, while short-tongued species were unaffected. Five out of the original 12 species present eight decades earlier were absent, all long-tongued species, and the once common *B. distinguendus* is now endangered. Only B. pascuorum seemed to be increasing in abundance, possibly by occupying some of the niches left vacant by declining species (Dupont et al., 2011). A larger study of 60 species and subspecies of bumblebees in central Europe found that 48 have declined in abundance over the past 136 years, with 30% of them being considered threatened and four having become extinct (Kosior et al., 2007). Most of the country extinctions occurred in the second half of the 20th century, coinciding with the expansion of agricultural intensification brought about by the Green Revolution. The abundance of pollinators in Swedish red clover fields also declined dramatically since 1940, with only two rare species remaining stable while two short-tongued generalist species now dominate the landscape: B. terrestris and B. lapidarius (Bommarco et al., 2012). Such a dramatic change in relative abundance has negatively affected the yields of that crop, which depends entirely on pollination services of long-tongued species. As in Denmark, B. distinguendus has completely disappeared from the southern part of Sweden. Large-scale conversion of landscapes to intensive agriculture together with unrelenting pesticide use are blamed for the changes in bumblebee biodiversity observed over the past 75 years (Bommarco et al., 2013). Major declining trends were identified among 46% of all Bombus species in Europe, of which 24% are threatened and one (B. *callumanns*) shows > 80% decline due mainly to habitat fragmentation and the replacement of clover with chemical fertilisers in agricultural areas (Rasmont 2005 cited by Nieto et al., 2014).

Several large studies have been conducted in North America to assess the status of bumblebee populations and their temporal and spatial changes in that continent since the middle of the 19th century. Half of the 14 species of bumblebees surveyed in southern Ontario (Canada) between 1971 and 2006 were declining, three were increasing (*B. bimaculatus, B. impatients and B. rufocintus*) while another three could not be found in that period: *B. affinis, B. pensylvanicus and B. terricola* (Colla and Packer, 2008). Higher tolerance to pesticides could explain the expansion of the three most abundant species at the expense of the more sensitive species, which had practically disappeared from the region. The Xerces Society reported losses of bumblebees in northern California and southern Oregon in 2005 and blamed the pathogen microsporidian *Nosema bombi* for most of the declines (Thorp and Shepherd, 2005). Using museum records from the Illinois Natural History Survey for the period 1900 to 2007, the distributional range of 16

species of bumblebees were analysed. Half of them have declined in numbers, whereas four species have become extinct in midwestern regions: B. borealis, B. ternarius, B. terricola and B. variabilis. The main reductions occurred during 1940-1960, coinciding with the expansion of intensive agriculture and increases in pesticide use (Grixti et al., 2009). At a national scale, changes in the distribution of eight bumblebee species could be determined by comparing historical records with intensive surveys across 382 locations in the USA. Half of the species declined in abundance by as much as 96% of their initial populations only in the last 30 years, and their geographical range was reduced between 23 and 87%. Declines were blamed on reduced floral and nesting resources, but declining populations also had greater infection rates by N. bombi and lower genetic diversity than the non-declining bee populations; some of the sharpest declines were recorded in regions dominated by intensive agriculture (Cameron et al., 2011). In Oklahoma, only five of the 10 species of bumblebees that were present in 1949 were found in 2013 after extensive surveys in 21 counties. Contrasting with other States, B. pensylvanicus was the most common species, whereas B. variabilis is presumed extinct (Figueroa and Bergey, 2015). In the latest study to date, historical records of 16 species of bumblebees in the eastern USA (New Hampshire) over 1866-2015 were analysed. Nine species have been declining, including five that are presently threatened: B. ashtoni, B. fernaldae, B. rufocintus, B. pensylvanicus and B. sandersoni. One species, B. terricola, was found only at high elevations, suggesting that the current warming trend is restricting its original distribution (Jacobson et al., 2018). Given their preference for cold habitats, the range and population densities of many bumblebees in Europe and North America appear to be restricted by global warming.

3.2.2. Other wild bees

Wild bees are estimated to provide at least 20% of pollination services in agricultural production (Losey and Vaughan, 2006). Their populations are largely dependent on food specialisation within a limited foraging range and habitat resources for nesting (Roulston and Goodell, 2011). Thus, 34% of the 105 bee species near Krakow (Poland) are rare and prefer wet meadows to other grasslands (Moron et al., 2008).

Using historical records on a grid of 10 km squares, declines in 52% of wild bee species in Britain and 67% in the Netherlands were observed after 1980, whereas increases in species richness were only observed in 10% of British cells and 4% of the Netherlands cells. Declining species were habitat and dietary specialists, univoltine and sedentary species in all cases, among which solitary bees were the most affected; moreover, plant species reliant on bee pollination alone were declining in both countries (Biesmeijer et al., 2006).

In Europe, an assessment of 1965 species of wild and naturalised bees found that 77 species are threatened and seven are critically endangered, including three endemic species: Ammobates dusmeti, Andrena labiatula and Nomada sicilensis. However, since population trends for 57% of species are unknown, 9.2% species of European bees were estimated to be declining (Nieto et al., 2014). An exhaustive analysis of almost half a million historical records of flower-visiting Hymenoptera in Britain since the mid-1800s, led to distinguish 4 main phases of extinction in that country: i) the second half of the 19th century, with the introduction of guano fertilisers and conversion of arable crops to permanent grasslands, which reduced floral resources; ii) after the First World War, when florally-diverse crop rotations were replaced with chemical fertilisers; iii) between 1930 and 1960, when most species went extinct probably due to changes in agricultural policy (i.e. Green Revolution) that fostered agricultural intensification; and iv) from 1987 to 1994, when rates of decline slowed down perhaps because the most sensitive species were already lost or reduced substantially (Ollerton et al., 2014). As agriculture occupies 70% of land-use in Britain, a causal relationship between species decline and farm management may involve multiple factors, including habitat changes and the use of chemical fertilisers and pesticides. The net result is the country-wide

extinction of 23 species of flower-visiting Hymenoptera, including once common species.

The first long-term study on the distribution of wild bees in North America was done at Carlinville, Illinois (USA). A 1970-1972 survey found 140 bee species, implying a 32% reduction in biodiversity compared to historical records from the same location 75 years earlier: only 59 of the 73 prairie-inhabiting bees and 15 of the 27 forest-dwelling ones were recovered (Marlin and LaBerge, 2001). In addition to obvious changes in land use over the period, the authors blamed herbicide sprays that killed trees and vegetation that support specialist bees. Another comprehensive long-term study focused on stingless bees (Megachilidae) at Itasca State Park (Minnesota), where 293 species were found in eight habitats over 2010-2012. A comparison of the abundance of a subset of 30 species with historical records from 1937 showed that 11 species had declined in numbers, another 11 were missing while 4four new species had been found (Gardner and Spivak, 2014). In particular, Megachile latimanus had disappeared and no causal factors could be identified for its demise or for the sharp reductions in abundance of other species. A model that includes nesting resources and foraging landscapes as predictors of local bee densities suggests that wild bee abundance is high in resource-rich areas of the USA such as chaparral and desert shrublands, whereas intermediate densities are typical in temperate forests and grasslands, and low densities in agricultural crops (Koh et al., 2016). Wild bees were declining in 23% of the country between 2008 and 2013, mainly in the Midwest, Great Plains and the Mississippi valley, where grain production - particularly corn for biofuel production (Bennett and Isaacs, 2014) - had almost doubled during that period. Increased abundances were reported on a mere 10% of the land, specifically where crop fields had been abandoned or converted to shrublands. A detailed analysis of the interactions between 109 pollinating bees and their host plants was studied in 26 forests of Illinois (USA), and compared to historical records for the same site from the late 1800s and early 1970s. This floral network revealed many changes over the years, with only 24% of the original pollinator-plant interactions remaining. Shifts in network structure were due to losses of individual bee species in 45% of cases (Burkle et al., 2013). Overall, the network became less nested, more vulnerable, had lower redundancy and, while species richness per plant did not change much, experienced marked drops in abundance of pollinators over the past 40 years. Losses were more prevalent among specialist species, parasitic and cavitynesters (e.g. Megachilidae), as predicted by other authors (Williams et al., 2010).

Losses of biodiversity among wild bees are also documented for tropical regions. A 12-year comparison of 24 orchid bees (Apidae: Euglossina) in two Atlantic forest reserves of Brazil showed declines in abundance of 63% species, mostly forest-dependent bees, while those of open and disturbed habitats increased in numbers (Nemesio, 2013). Similarly, regular surveys of wild bees visiting dry forest trees along a highway in Costa Rica over 1972–2004 showed a 60% decline in species up to 1996, coinciding with the urban sprawl in the region during that period (Frankie et al., 2009). Concurrently, populations of three species increased, probably due to more diversity of garden flowers in new dwellings. Bees belonging to the Halictidae and Megachilidae families suffered the greatest losses.

3.2.3. Honey bees (Apis mellifera L.)

In the USA, a peak of six million honey bee colonies was recorded in 1947 but this number has been declining ever since, with losses of 3.5 million over the past six decades at 0.9% annual rate of decline (Ellis, 2012). The demise started immediately after the introduction of the organochloride insecticide DDT in agriculture and has since continued unabated (Ellis et al., 2010). The main factors responsible for this steady decline include: widespread parasite and pathogen infections that are becoming more virulent in recent years (Anderson et al., 2011; Yang and Cox-Foster, 2007); lack of genetic variability; stress due to seasonal movement of hives for pollinating fruit and vegetable crops (Smart et al., 2016); toxic pesticide residues found in the pollen and nectar or applied to hives for controlling *Varroa* mites (Johnson et al., 2013); poor nutritional value of agro-landscapes dominated by monocultures (e.g. corn, oilseed rape, cotton (Huang, 2012)); and finally the harsher climatic conditions of recent decades. The most likely explanation for the declines, however, is a combined effect derived from synergistic interactions between parasites, pathogens, toxins and other stressors (Alburaki et al., 2018; Goulson et al., 2015; Sánchez-Bayo et al., 2016b), which has resulted in the colony collapse disorder (CCD) (Underwood and vanEngelsdorp, 2007). Two thirds of American beekeepers presently lose about 40% of their colonies every year (Kulhanek et al., 2017), whereas 30% annual losses are reported for Europe, 29% in South Africa (Pirk et al., 2014) and 3–13% in China for both *A. mellifera* and *A. cerana* (Chen et al., 2017).

Managed colonies of honey bees worldwide are suffering from the same maladies and declining at similar rates (about 1% per year) in North America, Europe (Potts et al., 2010) and Australia (Gibbs, 2013). While parasites and diseases appear to be the proximate driver of the losses, synthetic pesticides have been involved in the losses from the very beginning (Ellis, 2012). The new generation of systemic insecticides, particularly neonicotinoids and fipronil, impair the immune system of bees (Di Prisco et al., 2013; Vidau et al., 2011) so that colonies become more susceptible to Varroa infections (Alburaki et al., 2015) and more prone to die when infected with viral or other pathogens (Brandt et al., 2017). Apart from bringing about multiple sub-lethal effects that reduce the foraging ability of worker bees (Desneux et al., 2007; Tison et al., 2016), neonicotinoid and fipronil insecticides equally impair the reproductive performance of queens and drones (Kairo et al., 2017; Williams et al., 2015), thus compromising the longterm viability of entire colonies (Pettis et al., 2016; Wu-Smart and Spivak, 2016).

3.2.4. Cuckoo wasps (Chrysididae)

This rare group of parasitic wasps has recently been studied in Finland, and surveys reveal that 23% of the 48 local species are declining, together with one of the host species (Paukkunen et al., 2018). Unlike with other taxa, none of the cuckoo wasps seem to be increasing in numbers or distribution. Declining species are typically small, rare and tend to nest above ground, whereas populations of the larger and/ or ground-nesting species appear to be stable. Authors attribute the declines to habitat loss (i.e. deforestation) for agricultural purposes, which restrict the availability of logs for nesting.

3.2.5. Formicidae

Studies on ant (Formicidae) populations and trends are lacking except for a few invasive species (Cooling and Hoffmann, 2015; Vogel et al., 2010). Tropical deforestation has been invoked as a major cause for biodiversity losses of ants and other insects at the global scale – specifically for forest-inhabiting species (Wilson, 2002). Equally, logging of Nordic forests using established management practices was harmful to populations of the polydomous wood ant *Formica aquilonia*, because ants had their feeding and nesting resources restricted while abiotic conditions necessary for the development of the colonies had changed (Sorvari and Hakkarainen, 2007). Nothing is known about the fate of the multiple ant species that inhabit other types of habitats in both temperate and tropical settings.

3.3. Diptera

Hoverflies (Syrphidae) are important pollinators and key natural enemies of agricultural pests such as aphids, with a preference for damp habitats. Several surveys in Mediterranean countries have shown large local variations in biodiversity within this taxon, with 249 species alone in Greece (Petanidou et al., 2011) and 429 in Spain (Stefanescu et al., 2018). However, the only long-term study to date found parallel reductions in species richness among hoverflies in the Netherlands and the U.K. (Biesmeijer et al., 2006). That migratory hoverflies fared better than their sedentary counterparts in the latter two countries suggests that mobility is an important trait for survival. While plant species reliant on bee pollination alone were declining in both countries, plants pollinated by both bees and hoverflies were increasing only in the Netherlands.

3.4. Coleoptera

The largest order of insects includes important groups of predatory and saprophytic species that provide essential ecosystem services in pest control and recycling of organic matter among others.

3.4.1. Carabidae

Ground beetles are a ubiquitous taxa and tiger beetles (Cicindelidae) are regularly used as indicators of biodiversity; this group occurs within habitats that harbour a diverse array of native butterflies and birds (Pearson and Cassola, 1992). Most of the changes among European carabids can be explained by habitat destruction, increased eutrophication due to agricultural intensification and expanding urbanisation. A study on 419 species within 10-km grid cells throughout the Netherlands, Belgium, Luxemburg and Denmark found that 34% of carabids declined between 1950 and 1980, with over 50% of xerophilic species of the genera *Amara*, *Harpalus* and *Cymindis* as well as *Carabus* decreasing in numbers (Desender and Turin, 1989). In the Netherlands, carabids with limited degrees of dispersal were the most affected, whereas those with large mobility or associated with manmade habitats had stable populations (Turin and den Boer, 1988).

In the U.K., dramatic declines of 49 out of the 68 carabids studied at 11 sites over 15 years, led to consider 26 species as vulnerable and eight endangered, whereas 19 species appear to be either stable or even increasing. Overall, a 16% loss of carabid beetle biomass was recorded during the 15-year period (Brooks et al., 2012). Changes in biodiversity were not linear and correlated with habitat and geographical variation, being most pronounced in mountainous regions of the west and north (64% of declining species), followed by moorlands (31%) and pastures (28%), whereas increases occurred in the southern downlands. Carabids in upland pastures, woodlands and hedgerows remained stable during the study period. Small species or those with spring breeding, dispersive or diurnal habits tend to be negatively affected. Microclimatic changes that alter soil moisture also affected some upland species (Brooks et al., 2012).

In New Zealand, 12 species of large carabid beetles are endangered and another 36 declining, together comprising about 8% of all known species in that country. Affected species belong mostly to two genera of giant carabids, *Mecodema* and *Megadromus* (McGuinness, 2007). The proportion of endangered carabids (about 4%) is twice as much as that of other local beetles, perhaps because they are large terrestrial species vulnerable to predation by introduced rats, hedgehogs, ferrets, weasels and possums. Habitat change due to forest clearance and conversion to pastures for sheep grazing have exacerbated the plight of these giant beetles, 92% of which are endemic and evolved in isolation during the past 80 million years.

3.4.2. Coccinellidae

Harmon et al. (2007) reviewed 62 historical datasets of aphidophagous coccinellids in the USA and Canada, spanning 1914–2004. Although biased towards predatory species within agricultural landscapes, the surveys showed that ladybird species richness and population sizes did not change much until 1986, when a major decline in native species began to be noticed and affected 68% of species over the following 20 years (Harmon et al., 2007). At least two previously common species (i.e. *Adalia bipunctata* and *Coccinella novemnotata*) have since become very rare or entirely disappeared from the north-eastern USA (Wheeler, 1995). At the same time, 22 introduced species have been recorded, though only six of those have established in North America. Two likely causes of the declines include: i) habitat change, either towards intensive agriculture in the Midwest States or through afforestation (i.e., New York State); and ii) competitive displacement by foreign generalist species such as *C. septempunctata* and *Harmonia axyridis* (Brown and Miller, 1998), possibly fuelled by a steep population build-up of invasive aphid pests in agricultural crops. *H. axyridis* is outcompeting native ladybirds in Great Britain (Roy and Brown, 2015), other European countries (Camacho-Cervantes et al., 2017) and Japan (Sato and Dixon, 2004), and gaining a competitive edge through its predation of aphids in agricultural crops (Rutledge et al., 2004).

Systematic records of abundance and distribution of ladybirds since 1976 in cereal crops, herbaceous plants and trees are available for the Czech Republic. Of the 13 species studied, six had declined in abundance while seven had increased, including *H. axyridis* (Honek et al., 2014). Agricultural intensification is the main driver of population changes in cereal crops and herbaceous stands, whereas coccinellid diversity and abundance in tree habitats remained stable over the 35-year period. Specifically, the extensive use of insecticides impacts both aphid pests and associated ladybird predators, and the recent conversion of crops to oilseed rape monocultures had an overall negative effect on *C. septempunctata* populations. Warming climate, by contrast, favoured the expansion of *Hippodamia variegata* (Brown and Roy, 2015).

In Britain, records of nine ladybird species collected by citizen scientists, along with systematic surveying between 1990 and 2013 were analysed by Brown and Roy, 2015). Five species were declining, two remained stable and two were expanding – *H. variegata* and *H. axyridis*. Changes in certain agricultural practices that led to lower aphid numbers in crops (i.e., reduced fertiliser use) may have resulted in the decline of three common native species (*A. bipunctata, C. undecimpunctata* and *Propylea quattuordecimpunctata*) and the concurrent increase of *H. variegata* and *H. axyridis*, indicating parallel coccinellid population trends for both the U.K. and continental Europe (Honek et al., 2014).

3.4.3. Dung beetles

Dung beetles comprise three main groups: rollers (Scarabaeinae), tunnellers (Geotrupidae and most Scarabaeidae) and dwellers (Aphodiidae). Their unique ecological function is of vital importance to the livestock sector and for the soil fertility of grasslands. Studies on the decline of these specialized beetles are available only for the Mediterranean region, which has the largest diversity of dung beetles in Europe.

Roller dung beetles comprise a fifth of the 55 local species in Spain. An analysis of their abundance and distribution during the 20th century showed that while most species increased in numbers up to 1950, the relative abundance of nine of them dropped since then from 28% to 7%, while their distributional range contracted from 48% to 29% of the 10-km grid cells (Lobo, 2001). The most threatened species were *Scarabaeus pius* and *Gymnopleurus mopsus*, whereas populations of *S. cicatricosus* increased in its restricted southern area of distribution and those of *S. typhon* remained unchanged. Multivariate analyses reveal that large-scale urbanisation of the coasts for tourism and post-1950s agricultural intensification are primary causal factors.

In Italy, analysis of the abundance and distribution of 6870 records of 11 species of roller dung beetles for the entire 20th century showed a 31% reduction in both abundance and distribution affecting nine species (Carpaneto et al., 2007). Major declines started in the 1960s (2 species), increased in the 1970s (3 species) and became widespread in the 1980s (6 species). Their distribution, however, increased during the first half of the century and then decreased by 23% on a national level. The declines correlate with the local reduction of rangelands: 43% conversion of pastures to either forests or intensive agriculture since 1960. In addition, a shift from free-ranging livestock to stalled animals meant that dung was no longer available to foraging beetles. Two *Scarabaeus* and four *Gymnopleurus* species are considered threatened, and *G. mopsus* is probably extinct. The largest beetles are most at risk, suggesting that lower fecundity and enhanced predation by crows may be factors at play. The use of helminthicides (i.e. avermectins) and other anti-parasitic insecticides was considered of minor importance, though other authors have documented their negative impacts on dung beetles (Lumaret et al., 1993; Strong, 1992).

In France, a 1996 survey in the coastal region of the Camargue collected 337 individuals of 11 species only (nine Scarabaeidae and two Aphodiidae; none Geotrupidae), though the entire dung beetle fauna of the region is known to comprise 72 species (Lumaret, 1990). Such a significant drop in biodiversity affects more generalist species with greater dispersal abilities than the dwellers and rollers. Among the latter group, abundance of *Scarabaeus semipunctatus* has lowered 45-fold over 24 years, while populations of *S. sacer* are restricted to two sites between France and Spain (Lobo et al., 2001). The use of insecticides for mosquito control and livestock treatment as well as urbanisation are the main factors explaining the declines, since no agricultural changes have taken place in the area for decades.

3.4.4. Saproxylic beetles

Saprophytic beetles play a major role in decomposition of wood in ecosystems, thus recycling nutrients that would otherwise be locked in decay logs and branches. Some species are also involved in pollination (Stefanescu et al., 2018).

In Europe, logging, wood harvesting and agricultural expansion have caused losses of old native forests, thus threatening the survival of 56 species of saproxylic beetles (a third of them endemic). While populations of at least 61 species are declining or have experienced a more confined distribution, nine others are increasing in numbers. Most threatened species are in Central and Eastern Mediterranean regions. and two endemic species, Glaphyra bassetti (Cerambycinae) and Propomacrus cypriacus (Euchiridae), are now regarded as critically endangered. However, since population trends for 57% of the 436 known species are unknown, the number of declining species could be even higher (Nieto and Alexander, 2010). The only long-term study available is for long-horn beetles (Cerambycidae) in Sweden, where 118 species are known from historical records. About half of the beetles had maintained the same distribution and relative abundance since the early 1900s (Lindhe et al., 2011). The status of the remaining 50% is affected by a local shift from agriculture to industrial, large-scale forestry: 26 species experienced significant declines, 32 increased in abundance, and 5-10 species are presumed extinct.

3.5. Hemiptera

One study of planthoppers and leafhoppers (Auchenorrhyncha) in protected grasslands of Germany was found (Schuch et al., 2012). These are typical phytophagous insects of open areas, accounting for a large proportion of the biomass of flying insects in natural and anthropogenic grasslands of Europe (Biedermann et al., 2005). Historical sweep-net samples (1963-1967) were compared to recent samples (2008-2010) at the same sites with respect to species diversity, species composition, and abundance. Regardless of the strong inter-annual variability in abundance and weather conditions, overall species richness did not change. However, species composition changed considerably, with 14 species declining (mostly specialists) and nine others increasing (mostly generalists), while one species (Zyginidia scutellaris) characteristic of acidic grasslands became very dominant. Moreover, median abundance decreased by 66% (from 679 to 231 individuals per site) over the 47year period (Schuch et al., 2012). Airborne and soil acidification, partly due to agricultural intensification, is the main factor affecting local grassland composition and the associated herbivore fauna.

3.6. Orthoptera

A single long-term study on grasshoppers and crickets is available, conducted at the same German sites as above (Schuch et al., 2011). Their biodiversity in protected grasslands did not change over four

decades (median 9 species per site), and changes in species assemblages were small. The only significant change included a sharp decline in a grasshopper of bare soils (Myrmeleotettix maculatus) and increases in two generalist species of bush-crickets typical of open woodland and scrub (Tettigonia viridissima, Phaneroptera falcata). Contrasting with other taxa, few Orthoptera species showed detectable temporal trends, perhaps because most species are highly-adaptable polyphagous grazers. Nevertheless, about half of the species are considered threatened in Germany.

3.7. Odonata

Dragonflies (Anisoptera) and damselflies (Zygoptera) comprise a relatively small order of insects that depend on water bodies for their larval development. Both nymphs and imagos are predators of aquatic organisms and flying insects respectively, and they play an important role in controlling nuisance mosquitoes and agricultural pests, e.g. of rice (Painter et al., 1996; Relyea and Hoverman, 2008). Of the 118 aquatic species of endangered insects listed by the IUCN, 106 are Odonata (Kalkman et al., 2010), although it is clear that other aquatic taxa are underrepresented due to insufficient knowledge (DeWalt et al., 2005). A recent IUCN assessment indicates that 10% of the world's Odonata are threatened with extinction, although that study only covered a quarter of all species known and acknowledged data gaps for 35% of species, particularly those from tropical and Australasian regions (Clausnitzer et al., 2009). Given the above, 15% of all species may be threatened.

In the USA, recent surveys at 45 sites across California and Nevada were compared to historical records from 1914 to 1915. Occurrence rates of 52 species of dragonflies and damselflies (65% of all recorded) have declined over the 98-year period while those of 29 species have increased. Two generalist and pollution-tolerant species that were not recorded in 1914-1915 greatly expanded their range into California and became common, particularly in urban areas. At least nine species declined significantly, including four species (Sympetrum danae, S. costiferum, Ophiogomphus occidentis and Libellula nodisticta) that were also rare in early surveys. Declines occurred mostly among habitat specialists, whereas increases were recorded for generalist and migratory species that replaced the losses at the same sites. Specialist species included those with overwintering diapause, which appear to have declined due to an increase of minimum temperature over the period (Ball-Damerow et al., 2014). While species richness has not declined, Odonata assemblages have become more homogeneous in species composition, which is typically an effect of urbanisation (McKinney, 2006).

In Europe, 15% of the 138 Odonata species are currently threatened, with two damselflies (Ceriagrion georgifreyi and Pyrrhosoma elisabethae) and one dragonfly (Cordulegaster helladica sp. kastalia) critically endangered in the Balkan Peninsula. A quarter of all species (33) are declining in population numbers and distribution, whereas 10% of them are increasing and about half remain stable. Major declines took place during post-1960 agricultural intensification, with canalisation of rivers for irrigation and water pollution by urban runoff, pesticides and fertilisers (i.e. eutrophication) being the main drivers of population extinctions over large areas (Kalkman et al., 2010). Ubiquitous species such as Coenagrion puella and Sympetrum striolatum, however, increased and shifted their range some 300 km northwards in Britain between 1960 and 1970 and 1985-1995 (Hickling et al., 2005). In central Finland, populations of 20 common species of Zygoptera and Anisoptera were surveyed at 34 small creeks over 1995-1996, and their distribution patterns were compared with historic records from 1930 to 1975. Two specialist and lentic dragonflies, Coenagrion johanssoni and Aeshna caerulea have disappeared from streams, and 45% of the 219 surveyed populations vanished. Local extinctions occurred in peat bogs and dynamic waters upstream, which are habitats for lentic-specialist species, whereas downstream water bodies had lower losses. Generalist species

(i.e., those that breed in both lentic and lotic waters) were less likely to become locally extinct. The construction of agricultural ditches and habitat fragmentation from forestry further impacted on populations of rare species (Korkeamäki and Suhonen, 2002).

In Japan, 57 out of 200 Odonata species are declining, with 23 being vulnerable and 19 endangered (Kadoya et al., 2009). The largest drops in abundance and distribution are among lentic species once common in rice paddy fields (e.g., Lestes japonicus, Libellula angelina, Sympetrum maculatum and S. uniforme). Island endemics are next in the extinction list, whereas those of lotic habitats of mountain streams are the least affected. The sharp decline in populations of red dragonflies (Sympetrum spp.) since the mid-1990s (Fukui, 2012; Futahashi, 2012) has been linked to the use of fipronil and neonicotinoid insecticides (Nakanishi et al., 2018), which affect the aquatic nymphal stages by curtailing the emergence of adults (Jinguji et al., 2013).

Of the 155 Odonata species recorded in South Africa, 13 are declining and four are extinct (Samways, 1999). The protection of rare species in nature reserves of that country does not necessarily guarantee their survival, as current livestock management and other human activities negatively impact on these aquatic insects.

3.8. Other freshwater taxa

Freshwater insect taxa tend to have rather inflexible life cycles, with many species being univoltine, thus making them particularly sensitive to habitat change. Flow alterations, habitat fragmentation, pollution and invasive species are the main threats to all aquatic organisms, including insects (Allan and Flecker, 1993; Zwick, 1992). Data pertaining to three main orders of freshwater insects, Plecoptera, Ephemeroptera and Trichoptera, are reported here but no surveys were found for Coleoptera (e.g. Dytiscidae, Hydrophilidae), Hemiptera (e.g. Notonectidae, Gerridae) or Diptera (e.g. Chironomidae, Tipulidae).

3.8.1. Plecoptera

Stoneflies (Plecoptera) are numerically and ecologically a significant component of the entomofauna of running waters, typified by high degrees of endemism and narrow ecological requirements (Zwick, 2000). More than half of the species are univoltine and their nymphs require mainly cold and well-oxygenated waters of temperate and cold regions. In Europe, once common species of lowland rivers such as Taeniopteryx araneoides and Oemopteryx loewi are now extinct over the entire continent, while Isogenus nubecula has locally disappeared (Fochetti and de Figueroa, 2006). The percentage of species threatened with extinction ranges from 50% in Switzerland (Aubert, 1984) to 13-16% in Mediterranean countries like Spain and Italy, where many species are endemic. Up to 63% of the 516 European species of stoneflies are susceptible to climate change, particularly species endemic to the high mountains of the Alps, Pyrenees and Mediterranean peninsulas, which experience altitudinal shifts in habitat (Tierno de Figueroa et al., 2010). Although stoneflies are relatively tolerant of acidification as compared to other macro-invertebrates, they are highly sensitive to changes in water flows and eutrophication by organic pollution (Tixier and Guérold, 2005).

In the Czech Republic, species diversity and abundance of 78 stoneflies in rivers, streams and lakes were compared at 170 sites between 1955 and 1960 and 2006-2010 (Bojková et al., 2012). Three quarters of the changes in species diversity occurred at low- and midaltitude streams, with pollution, impoundment and channelization affecting those sites. Lowland river habitats had five threatened species of the original 14 species recorded at the turn of the 19th century, while four are now extinct. Over a 50-year time frame, 12% of the species were no longer found, whereas two new species have appeared (Brachyptera monilicornis and Leuctra geniculata). Moreover, 22% species had declined by > 50%, including once common species such as Perla abdominalis, Amphinemura standfussi and Nemurella pictetii, and a further 10% have become vulnerable. Contrary to terrestrial taxa, most

declines were observed among habitat generalists and less specialized species (60–70%), which are tolerant to organic pollution. These species survived a first wave of extinctions during the 1920s–1930s and the industrialisation of the 1960s–1980s. Sites affected by organic pollution showed, however, the greatest change in community assemblage, particularly in agricultural and urbanised settings, whereas communities in montane and sub-montane areas have remained almost intact: only 17–33% of sensitive and eurytopic species declined since the mid-1990s (Bojková et al., 2014); some degree of species recovery has been observed following pollution mitigation in acidified habitats (Nedbalová et al., 2006). In Switzerland, half of the species of stoneflies and mayflies in water courses of industrial and agricultural areas were lost between 1940s and 1980s (Küry, 1997), and the same occurred in other European countries and the USA, where the entire Plecoptera fauna of lowland rives can now be considered threatened.

In Illinois (USA), 29% of the 77 local stonefly species were lost and 62% of the remainder became threatened over the past century (DeWalt et al., 2005). Main losses occurred in the large rivers and agricultural areas of the Grand Prairie during the 1940s and 1950s, when both agricultural and urban expansion took place. Structural modification of river flows due to dams, channels and tile drainage networks have all impacted negatively on these insects, as they increased siltation and organic waste. The large, long-lived species of Perlidae (summer stones) and Perlodidae (spring stones) were impacted the most, and 36% of summer stones have gone extinct since 1860. For sensitive genera such as *Acroneuria*, 88% of the entire contingent was lost over the past century, whereas genera tolerant to organic pollution such as *Perlesta* have increased 4-fold. Species losses were largest within semi-voltine and univoltine stoneflies adapted to permanent waters.

3.8.2. Ephemeroptera

The most comprehensive checklist of mayflies (Ephemeroptera) of the Czech Republic recognised 107 species of which four had become extinct, seven are critically endangered, seven endangered, 16 vulnerable and 14 near threatened - a 43% overall decline of local species of mayflies (Zahrádková et al., 2009). A comparison of local mayfly communities in 60 streams between 1955 and 2011 showed clear changes in species composition but no losses in biodiversity except for the large lowland rivers, which lost five specialist species but gained several silt-tolerant species (Zedková et al., 2015). Biodiversity, however, increased slightly in mid- and upper streams and rivers, indicating perhaps some recovery given the substantial reduction in water pollution post-1989 (Bojková et al., 2014). Two species became extinct (Isonychia ignota and Ephemerella mesoleuca), three became very rare, 11 were declining and nine were expanding their range, including the dominant Centroptilum luteolum and Baetis niger. Main changes were due to losses or turnover of previously common and widespread species such as *B. alpinus* and *Epeorus assimilis*, so the overall dissimilarity among sites (15-30%) was mainly driven by species replacement. The current communities have shifted towards more simplified and less specialized assemblages in large rivers, whereas mayflies in small creeks have been replaced with species tolerant to pollution and siltation.

In North America, a total of 672 species of mayflies are listed though no details are available regarding distribution or status (McCafferty et al., 2010; McCafferty, 1996). A similar compilation for North and South Carolina (USA) reported 204 species (Pescador et al., 1999), but again no status was indicated. A later study in relation to 10 rare species revealed, however, that four of the species collected in the early 20th century should be considered extinct (McCafferty, 2001).

3.8.3. Trichoptera

Another taxon of inconspicuous insects, the caddisflies (Trichoptera) has been poorly studied. Of the 278 species recorded in relatively undisturbed regions of Minnesota (USA) since the 1890s, 6–37% of species losses have occurred in different areas, especially

within the Limnephilidae (44% of species), Phryganeidae (21%) and Leptoceridae (12%) families (Houghton and Holzenthal, 2010). Agrypnia glacialis and Anabolia sordida are currently extinct, and 17 rare species have not been found since the 1950s, while only one record is known of Limnephilus secludens since 1985 (Houghton and Holzenthal, 2010). All species in the affected families are either univoltine or semivoltine and, because of their long lifespan and feeding habits, are particularly vulnerable to anthropogenic disturbances in water courses. The majority of losses are found among shredder (72%) and predatory species (11%), in agreement with loses of aquatic taxa in other countries (Jenderedjian et al., 2012; Karatayev et al., 2009). The regional caddisfly community is now dominated by filtering collectors (65% of species), with tolerant species such as Potamyia flava (Hydropsychidae) having increased in abundance several-fold since the 1950s, particularly in large rivers and agricultural regions that now account for over 95% of the original prairie habitats.

4. Discussion

Biodiversity loss has become a major global issue, and the current rates of species decline – which could progress into extinction – are unprecedented (Barnosky et al., 2011; Pimm and Raven, 2000). Yet, until recently, most scientific and public attention has focused on charismatic vertebrates, particularly on mammals and birds (Ceballos and Ehrlich, 2002; Manne et al., 1999), whereas insects were routinely underrepresented in biodiversity and conservation studies in spite of their paramount importance to the overall functioning and stability of ecosystems worldwide (Fox, 2013; McKinney, 1999; Thomas et al., 2004).

This review brings to the fore the demise of major insect taxa (albeit no studies are available for most Diptera, Orthoptera and Hemiptera), which started at the dawn of the 20th century, accelerated during the 1950s–1960s, and attained alarming proportions globally over the last two decades. Our aim is to draw attention to the extent of the problem and point out its drivers, so that adequate conservation measures may be implemented and prioritised.

From our compilation of published scientific reports, we estimate the current proportion of insect species in decline (41%) to be twice as high as that of vertebrates, and the pace of local species extinction (10%) eight times higher, confirming previous findings (Dirzo et al., 2014). At present, about a third of all insect species are threatened with extinction in the countries studied (Table 1). Moreover, every year about 1% of all insect species are added to the list, with such biodiversity declines resulting in an annual 2.5% loss of biomass worldwide (Fig. 2).

Among terrestrial taxa, the largest losses of biodiversity are among dung beetles in Mediterranean countries, with > 60% of species in decline and a large proportion considered threatened (Fig. 3a). About half of Coleoptera and Lepidoptera species (both moths and butterflies) are declining at a faster rate than the annual average (2.1% and 1.8% respectively, Fig. 2). A similar trend is observed among bees, where one in six species have gone regionally extinct. The fate of other pollinators such as hoverflies is, however, largely unknown. In agreement with biodiversity losses reported in other animal taxa (Ricciardi and Rasmussen, 1999), declines are even higher among aquatic insects, despite the scarce knowledge available for most countries: 33% of aquatic insects are threatened compared to 28% among terrestrial taxa (Fig. 3b).

Insect declines appear to be similar in tropical and temperate regions of the world (mean 45.3% vs 45.4% of species, p = 0.93), though the low number of studies in the tropics (n = 3) does permit statistical comparison. Within temperate regions, the U.K. seems to have the largest documented declines across taxa (60% of species), followed by North America (51%) and Europe (44%), but with no significant differences among them (p = 0.21, F = 3.15, df = 59, ANOVA); within Europe, insect declines are also similar between Mediterranean and

Table 1

Proportion of declining and threatened species per taxa according to IUCN criteria (> 30% decline), the annual rate of decline in	species (i.e. additional declines per
year) and the local or regional extinction rate (i.e. percent of species not observed in > 50 years).	

Taxon	Declining (%)	Threatened (%)	Annual species declines (%)	Extinction rate (%)	No. Reports
A) Insects	41	31	1.0	10	73 ^a
Coleoptera	49	34	2.1	6.6	12
Diptera (Syrphidae)	25	0.7 ^g	n.a.	n.a.	4
Ephemeroptera	37	27	0.6	2.7	3
Hemiptera (Auchenorrhyncha)	8 ^g	n.a.	$0.2^{ m g}$	n.a.	1
Hymenoptera	46	44	1.0	15	21
Lepidoptera	53	34	1.8	11	17
Odonata	37	13	1.0	6	6
Orthoptera	49	n.a.	1.0	n.a.	1
Plecoptera	35	29	0.6	19	7
Trichoptera	68	63	0.6	6.8	1
Terrestrial	38	28	1.2	11	56
Aquatic	44	33	0.7	9	17
B) Vertebrates	22	18	2.5	1.3	11
Amphibians	23	23	n.a	n.a.	1 ^b
Birds	26	13	2.3	0.8	3 ^c
Mammals (land)	15	15	0.1	1.8	3 ^d
Mammals (Chiroptera)	27	n.a.	5.2	1.2	3 ^e
Reptiles	19	19	n.a.	n.a.	1^{f}

^a This paper; see Table S1.

^b Temple and Cox, 2009.

^c Thomas et al., 2004; Birdlife_International, 2015.

^d Ceballos and Ehrlich, 2002; Temple and Cuttelod, 2008; Temple and Terry, 2009.

^e Mickleburgh et al., 2002; Mitchell-Jones, 1990; Van der Meij et al., 2015.

f Cox and Temple, 2009.

g Insufficient data.

-Box — Mean line * Extreme outliers

Fig. 2. Annual rate of decline of the three major taxa studied (percentage of species declining per year) and of insect biomass.

central or northern countries (p = 0.27, F = 4.15, df = 33, ANOVA). Studies from all other regions have a significantly lower proportion of insect declines (23%, p = 0.01, F = 2.51, df = 68, ANOVA), except for a single study that showed a 62.5% decline of orchid bees (Euglossina) in Brazil, which can be regarded as an outlier (Fig. 4).

The pace of modern insect extinctions surpasses that of vertebrates by a large margin, although the extent of losses cannot be accurately quantified. This is largely due to a dearth of historical knowledge in many regions (e.g. China, sub-tropical and tropical countries and Australia), an absence of comparative surveys for multiple insect orders and an underestimation of the host-associated species (e.g., specialist herbivores, pollinators, obligate parasitoids and parasites) that are lost through co-extinction of their host plant or animal (Dunn, 2005; Koh et al., 2004). Since the declines affect the majority of species in all taxa, it is evident that we are witnessing the largest extinction event on Earth since the late Permian and Cretaceous periods (Ceballos et al., 2017; Raup and Sepkoski Jr, 1986). Because insects constitute the world's most abundant and speciose animal group and provide critical services within ecosystems, such event cannot be ignored and should prompt decisive action to avert a catastrophic collapse of nature's ecosystems (May, 2010).

Most worrying is the fact that the declining terrestrial insect fauna comprise not only specialists with narrow ecological requirements, such as dependence on particular host plants (e.g., Coenonympha oedippus in bogs), ecological niches (e.g., roller dung-beetles) or restricted habitats (e.g., Bombus terricola in the USA), but also generalist species that were once common in many countries (e.g., Aglais io in the Netherlands or Macaria wauaria in the U.K.). This suggests that the causes of insect declines are not tied to particular habitats, but instead affect common traits shared among all insects (Gaston and Fuller, 2007). The disappearance of habitat generalists is particularly notorious among aquatic insects, for which major losses have been recorded among stoneflies, mayflies, caddisflies and dragonflies that once inhabited the large rivers of Europe and North America (Bojková et al., 2014). Thus, the biodiversity of the Rhine river plummeted during the industrial expansion of the 1930s, and subsequent efforts aimed at its recovery have failed to bring back many of the native species (Marten, 2001). Interestingly, aquatic insect communities remain stable or show lesser declines in pristine mountain streams and lakes. In aquatic environments, the evidence points to pollution as the main driver of the declines and extinctions recorded so far.

Anthropogenic pressure is shifting multiple insect communities towards species-poor assemblages dominated by generalists (White and Kerr, 2007), with current biodiversity losses and shifts in community composition being the forerunners of extinction (Chapin-III et al., 2000). In aquatic settings, the disappearance of susceptible species and their steady replacement with (often non-native) tolerant ones poses a major threat to freshwater biodiversity (Karatayev et al., 2009). Species losses are expected to lead to a steady decay of insect-mediated ecosystem services, which are likely to be provided by fewer and less specialized species (Bartomeus et al., 2014; Pimentel, 1961). As insect biodiversity is essential for the proper functioning of all ecosystems, the current trends are disrupting – to varying degree – the invaluable pollination, natural pest control, food resources, nutrient recycling and decomposition services that many insects provide (Aizen et al., 2009;

Fig. 3. Proportion of insect species in decline or locally extinct according to the IUCN criteria: vulnerable species (> 30% decline), endangered species (> 50% decline) and extinct (not recorded for > 50 years). A) terrestrial taxa; B) aquatic taxa.

Davis et al., 2004; Kreutzweiser et al., 2007).

While countless insect species are disappearing, few others are occupying vacant niches and expanding their distribution. In terrestrial ecosystems, most of the occupying species are generalists with diverse ecological preferences (e.g., *Bombus impatients, Plusia putnami, Laemostenus terricola* and *Hippodamia variegata*). In aquatic environments, species replacement is also mediated by ecological traits such as degree of tolerance to pollutants (e.g. *Sympetrum striolatum, Brachyptera risi* and *Potamyia flava*), with communities thus becoming more uniform and less diverse in composition (Houghton and Holzenthal, 2010). Species replacement may help retain the delivery of certain ecosystem services, but it's unclear to what extent natural ecosystems can sustain their overall ecological resilience (Memmott et al., 2004).

Species extinctions equally impact the overall biomass of entire ecosystems, as insects form the base that supports intricate food webs. Indeed, the essential role that insects play as food items of many vertebrates is often forgotten. Shrews, moles, hedgehogs, anteaters, lizards, amphibians, most bats, many birds and fish feed on insects or depend on them for rearing their offspring. Even if some declining insects might be replaced with others, it is difficult to envision how a net drop in overall insect biomass could be countered. The large declines in insect biomass observed in Europe (Hallmann et al., 2017) and Puerto Rico

Fig. 4. Proportion of declining insect species in different regions of the world.

(Lister and Garcia, 2018) inevitably lead to a starvation of dependent vertebrates (Hallmann et al., 2014; Lister and Garcia, 2018; Poulin et al., 2010; Wickramasinghe et al., 2003). This kind of cascading effect was first observed with grey partridge (*Perdix perdix*) populations in England since 1952, and was ascribed to reproductive failure. The ultimate cause of the partridge collapse was a combined use of insecticides and herbicides in agricultural land, leading to insufficient insect numbers to feed the chicks (Potts, 1986). Equally, in the U.K. the diversity and abundance of bats in intensive agricultural landscapes is considerably lower than on organic farms because of a reduction in insect biomass caused by pesticide use in the former settings (Wickramasinghe et al., 2004), and direct insecticide exposure through the bats' prey items (Mispagel et al., 2004; Stahlschmidt and Bruhl, 2012).

4.1. Drivers of the declines

A large proportion of studies (49.7%) point to habitat change as the main driver of insect declines, a factor equally implicated in global bird and mammal declines (Chamberlain and Fuller, 2000; Diamond, 1989). Next on the list is pollution (25.8%) followed by a variety of biological factors (17.6%), whereas few studies (6.9%) indicate climate change as triggering the losses (Fig. 5; Table S2).

4.1.1. Habitat change

Habitat change is an immediate consequence of human activities. Its global pace and scope has been expanding over the past centuries, with increasing amounts of land being transformed to provide dwellings, facilitate transportation and enable tourism (urbanisation), grow food

Fig. 5. The four major drivers of decline for each of the studied taxa according to reports in the literature.

(agriculture) and manufacture goods (industrialisation) at the expense of various natural habitats. Among Coleoptera, Lepidoptera and Hymenoptera, land-use change and landscape fragmentation is surely the main cause of species declines (Fig. 5), with agricultural conversion and intensification for food production listed in 24% of the reports (Fig. 6). Urbanisation, by contrast, is reported in 11% of cases, while deforestation appears in 9% of reports.

As agricultural crops comprise about 12% of the total land surface on the planet (FAO, 2015), farming directly affects a considerable proportion of insect species (Dudley and Alexander, 2017). In Europe and North America, the expansion of the agricultural frontier took place mostly in the first half of the 20th century, whereas in South America, Africa and Asia occurred mainly in the second half of the century (Foley et al., 2005; Gibbs et al., 2010). In its wake, rare species associated with pristine ecosystems and natural habitats either retreated or were entirely lost (Grixti et al., 2009; Ollerton et al., 2014). Major insect declines occurred, however, when agricultural practices shifted from traditional, low-input farming style to the intensive, industrial scale production brought about by the Green Revolution (Bambaradeniya and Amerasinghe, 2003; Ollerton et al., 2014). The latter practices did not necessarily involve deforestation or habitat modification (e.g., grassland conversion, drainage of wetlands) but rather entailed the planting of genetically-uniform monocultures, the recurrent use of synthetic fertilisers and pesticides, the removal of hedgerows and trees in order to facilitate mechanization, and the modification of surface waterways to improve irrigation and drainage. Monocultures led to a great simplification of insect biodiversity among pollinators, insect natural enemies and nutrient recyclers, and created the suitable conditions for agricultural pests to flourish. A quarter of the reports indicate these agriculture-related practices as the main driver of insect declines in both terrestrial and aquatic ecosystems (Wilcove et al., 1998).

The susceptibility of specialist pollinators to land-use changes (involving loss of floral resources, nesting and hibernation sites), appears to be a determining factor in the decline of many bumblebees and wild bees (Williams and Osborne, 2009). For specialist ground beetles, the loss of hedgerows and trees likely triggered their decline (Brooks et al., 2012). Declines in moths are tied to the fate of their overwintering larval host plants: forbs for species overwintering as larvae, and trees for those overwintering as egg, pupa, or adult. The combined removal of weeds and trees in intensive agricultural settings may thus explain the decline of moth species overwintering as larvae (Fox, 2013; Mattila et al., 2006; Merckx et al., 2009; Pocock and Jennings, 2008). Conversely, the change from intensive farming to organic farming has led to increases in abundance and diversity of moths (Taylor and Morecroft, 2009), while the abandonment of grazing land has allowed the recovery of some common butterflies (Kuussaari et al., 2007).

Agricultural intensification also entails stream channelization, draining of wetlands, modification of floodplains, and removal of riparian canopy cover with subsequent loss of soil and nutrients - all resulting in homogenization of stream microhabitats and alteration of aquatic insect communities (Houghton and Holzenthal, 2010). These activities increase eutrophication, siltation and sedimentation in water bodies, thus reducing the richness of shredders and predators while favouring filterer species (Burdon et al., 2013; Niyogi et al., 2007; Olson et al., 2016). Diverse communities of aquatic plants are an important habitat component in lentic systems such as paddy fields, allowing herbivory, oviposition and emergence of many insects and providing refugia for Odonata nymphs (Nakanishi et al., 2014). In general, loss of permanent flows in streams and rivers leads to a decrease of biodiversity (King et al., 2016), whereas irrigation and man-made water bodies in urbanised areas may have favoured certain species (Kalkman et al., 2010).

In recent decades, urbanisation has taken over agricultural land across the globe, causing the disappearance of many habitat specialists and their replacement with a few generalists adapted to the artificial

Fig. 6. Main factors associated with insect declines - see also Fig. 5.

human environment. However, such losses can be partially counterbalanced by the creation of urban parklands and gardens, which offer refuge to native and newly-colonising species, including pollinators like *Bombus* spp. (Botías et al., 2017) and butterflies like *Lycaena phlaeas* and *Aphantopus hyperantus* (van Dyck et al., 2009).

In tropical countries of South America, Africa and Asia, deforestation has been and still is a main driver of biodiversity loss and insect declines (Carrasco et al., 2017; Wilson, 2002), including dragonflies (Samways, 1999). Recent research on herbariums of Pacific islands suggests that deforestation and other human impacts on those ecosystems are not confined to the extinction of birds, mammals and snails (Kingsford et al., 2009) but also of insects such as leafminers (Lepidoptera: Gracillariidae) (Hembry, 2013). In Europe, deforestation is the main driver of saproxylic beetles' decline (Nieto and Alexander, 2010). Conversely, afforestation may increase the number of generalist butterflies by increasing habitat diversity at the forest edge (Kuussaari et al., 2007), but woodland diversity, structural and micro-climatic heterogeneity are far more important than forested area per se for maintaining the diversity of moths, butterflies as well as birds (Fuller et al., 2005; van Swaay et al., 2006). Very few generalist species benefit and expand under afforestation, and some European butterfly species even exhibited notable declines (van Swaay et al., 2006). In Britain, a 20-fold increase in conifer plantations since the 19th century did not increase biodiversity nor abundance of Lepidoptera species (Brereton et al., 2011; Fox, 2013).

4.1.2. Pollution

Pollution is the second major driver of insect declines (Fig. 5). Sources of environmental pollution include fertilisers and synthetic pesticides used in agricultural production, sewage and landfill leachates from urbanised areas and industrial chemicals from factories and mining sites. Among these, pesticide pollution is reported in 13% of cases (Fig. 6), followed by fertiliser inputs (10%) and to a lesser extent urban and industrial pollutants (3%).

Intensive agriculture implies the systematic and widespread use of pesticides for controlling crop pests (insecticides), competing weeds (herbicides) and fungal infections (fungicides) among others (Dudley and Alexander, 2017). In terms of toxicity, insecticides are by far the most toxic to all insects and other arthropods, followed by fungicides but not herbicides (Mulé et al., 2017; Sánchez-Bayo and Goka, 2014).

Herbicides, however, reduce the biodiversity of vegetation within the crops and in surrounding areas through drift (Egan et al., 2014) and runoff, thus impacting indirectly on the arthropod species that depend upon wild plants, which either disappear completely or decline significantly in numbers (Goulet and Masner, 2017; Marshall et al., 2003). Thus, the application of herbicides to cropland has had more negative impacts on both terrestrial and aquatic plants and insect biodiversity than any other agronomic practice (Hyvonen and Salonen, 2002; Lundgren et al., 2013). Pesticides have caused the decline of moths in rural areas of the U.K. (Hahn et al., 2015; Wickramasinghe et al., 2004) and pollinators in Italy (Brittain et al., 2010); broad-spectrum insecticides reduce the abundance and diversity of beneficial grounddwelling and foliage-foraging insects (Lundgren et al., 2013); systemic insecticides reduce populations of ladybirds and butterflies in gardens and nurseries (Krischik et al., 2015), and inflict multiple lethal and sublethal effects on bees (see 3.2.3) and other arthropods. Fungicides are not less damaging to insects, and synergism of a particular group of compounds (i.e., azoles) with insecticide toxicity (Biddinger et al., 2013; Pilling and Jepson, 1993) is certainly involved in honey bee collapses (Simon-Delso et al., 2014).

Pyrethroid, neonicotinoid and fipronil insecticides have a devastating impact on aquatic insects and crustaceans due to their high acute and chronic toxicity (Beketov and Liess, 2008; Kasai et al., 2016; Mian and Mulla, 1992; Roessink et al., 2013), thus reducing significantly their abundance in water bodies (van Dijk et al., 2013). Persistent residues of fipronil in sediments inhibit the emergence of dragonflies (Jinguji et al., 2013; Ueda and Jinguji, 2013) and the development of chironomids and other insect larvae, with negative cascading effects on fish survival (Weston et al., 2015). Systemic insecticides impair the long-term viability of shredder larvae that decompose leaf litter and other organic material (Kreutzweiser et al., 2008), undermine the basis of the insect food web (Sánchez-Bayo et al., 2016a) and thus derail natural biological control mechanisms e.g., in rice paddy ecosystems (Settle et al., 1996). Also, these products readily translocate to pollen, nectar, guttation drops, and all tissues of the treated crops and adjacent plants, impacting on nectar-feeding biota such as bees, butterflies, hoverflies and parasitic wasps (van der Sluijs et al., 2015). Unlike the short-term effects of other pesticides on aquatic organisms (Schäfer et al., 2011; van den Brink et al., 1996), neonicotinoids do not allow the recovery of univoltine and semivoltine aquatic insects (Beketov et al.,

2008), and appear to be the main driver of dragonfly declines in Japan (Nakanishi et al., 2018).

Also, the treatment of livestock with persistent avermectins and insect growth regulators has inadvertently contributed to a reduction of dung beetles in many countries, as residues of these pesticides in dung pats eliminate the developing larvae (Lumaret et al., 1993; Strong, 1992; Wardhaugh and Mahon, 1991). Unfortunately, more tolerant species of Ceratopogonidae and Psychodidae flies that breed in the same pats had their numbers boosted in Japan (Iwasa et al., 2005).

Overall, the systematic, widespread and often superfluous use of pesticides in agricultural and pasture land over the past 60 years has negatively impacted most organisms, from insects to birds and bats (Mineau and Callaghan, 2018; Sánchez-Bayo, 2011). Several multivariate and correlative statistical analyses confirm that the impact of pesticides on biodiversity is larger than that of other intensive agriculture practices (Fuentes-Montemayor et al., 2011; Gibbs et al., 2009; Mineau and Whiteside, 2013), though some authors continue to emphasize habitat and climate changes (Fox, 2013). Hallmann et al. (2017) demonstrated that 80% of the flying insect biomass losses in Germany was not caused by increases in agricultural land, deforestation, urbanisation or climate change but instead by an unknown factor, which the authors believe is pesticide use. This is even more evident for aquatic environments, where pesticide residues from agricultural and urban runoff are the major cause of biodiversity declines at all taxa levels (Beketov et al., 2013; Weston et al., 2014).

Apart from pesticides, the introduction of synthetic fertilisers early in the 20th century is recognised as a key driver of pollinator losses in the U.K. and Europe (Ollerton et al., 2014), particularly among specialist bumblebees. In terrestrial ecosystems, the diversity of plants and associated insect populations correlates negatively with nitrogen input (Öckinger et al., 2006; Pollard et al., 1998; van Swaay et al., 2006). Aquatic species such as dragonflies have also been affected by the eutrophication of surface waters, caused by excessive fertiliser use in rural areas (Kalkman et al., 2010). Equally, anoxia due to eutrophication by fertiliser and sewage has been linked to the depletion of Chironomidae, Trichoptera and Ephemeroptera in lakes (Jenderedjian et al., 2012).

The acidification of waters in Sudbury (Ontario, Canada), as a consequence of reckless mining and smelting activities since the 1850s, has inflicted direct and indirect impacts on aquatic insect communities: mayflies were eliminated in streams with pH below 5.5, but some Odonata and Diptera species increased in numbers due to lack of fish predation (Carbone et al., 1998). Acidic waters, nevertheless, reduce the abundance of Diptera (Ceratopogonidae, Chironomidae), although aquatic insect communities can recover slowly after neutralization and recolonization.

The impact of industrial chemicals (e.g., heavy metals, persistent halogenated hydrocarbons) on insect populations has not been adequately studied. Sub-lethal effects of metal pollution on moth larvae have been reported in Europe (van Ooik et al., 2007), but its link to population-level impacts is not well established. There is consensus, however, that global declines of stoneflies, mayflies and caddisflies can be ascribed to man-made pollutants discharged into streams and rivers (Aubert, 1984; Boiková et al., 2012). Occasionally, industrial spills have wiped out entire communities of aquatic organisms, not just insects, and their recovery has taken years of cleaning efforts (Capel et al., 1988; Giger, 2009). Nevertheless, since aquatic organisms are exposed simultaneously to mixtures of several pollutants, it is difficult to assign causality to individual toxic compounds. A weight-of-evidence approach concluded that insecticides were the most toxic to chironomids, snails and fish, whereas metals and other organic pollutants had a minor effect on those organisms (Kellar et al., 2014). Similar findings have been reported by other authors working with combinations of chromium and pesticides on honeybees: neonicotinoid insecticides were the most toxic to bees, whereas the metal had an antagonistic effect upon fungicide toxicity (Sgolastra et al., 2018).

4.1.3. Biological factors

Parasites and pathogens are definitively involved in the collapse of honeybee colonies in various countries (Goulson et al., 2015) and also appear associated with the declining wild bees in North America (Thorp and Shepherd, 2005). The global spread of *Varroa destructor* mite and the small hive beetle (*Aethina tumida*) pose a real concern for the apicultural industry because they transmit viral infections (vanEngelsdorp et al., 2012). However, pathogens have historically co-existed with managed bee colonies: their recent virulence is more likely to have been fostered by the exposure of bees to pesticide-contaminated pollen and nectar (Long and Krupke, 2016) that weakens their immune system (Sánchez-Bayo et al., 2016b; Tesovnik et al., 2017).

Insect biological control has helped mitigate hundreds of harmful invasive pests worldwide, though unintended ecological impacts have been recorded for at least 10 ill-fated historical efforts (Heimpel and Cock, 2018; Hajek et al., 2016; Hoddle, 2004). The human-assisted introduction of exotic species for biological control can contribute to a decline of endemic insects through processes such as competitive displacement (Roy and Brown, 2015), or direct predation and parasitism (Boettner et al., 2008; Henneman and Memmott, 2001). Yet, few documented species extinctions can be directly ascribed to insect biological control, with such cases largely confined to vulnerable island ecosystems in the Pacific (Hoddle, 2004; King et al., 2010). In the meantime, the practice of biological control has matured over the past decades, and the necessary safeguards have now been put in place to avert the introduction of species that pose tangible ecological risk - e.g., generalist feeders or vertebrate predators (Heimpel and Cock, 2018). Although carefully selected host-specific agents might still cause minor, transient impacts, they regularly reach background population levels as their (invasive) pest targets are being suppressed. Moreover, scientifically-guided biological control can help to permanently resolve invasive species problems and protect biodiversity over extensive geographical areas (Wyckhuys et al., 2019). Hence, this practice need not be viewed as a prime threat to insect biodiversity, but should instead be embraced as a tailor-made alternative to pesticide measures for invasive species control, crop protection or habitat restoration. Biological control, as a core component of ecological intensification (Bommarco et al., 2013; Wyckhuys et al., 2013), can help cut insecticide pollution in agricultural environments, revert insect biodiversity declines and help conserve insect-feeding vertebrates.

Invasive species, on the other hand, can have major impacts on the make-up and functioning of ecosystems in both mainland and island settings (Kenis et al., 2009; Reaser et al., 2007). Ecological impacts are relatively well documented for invasive ants, forest herbivores and bumblebees, with effects on locally-occurring insect communities through trophic interactions such as predation or parasitism (Kenta et al., 2007). For some invasive species, impacts can be temporary as introduced species succumb due to poor adaptation to the novel environment (Cooling and Hoffmann, 2015), while others inflict longlasting effects, i.e. mammals that prey on giant carabids of New Zealand (McGuinness, 2007). For multiple invasive plant and animal species, ecosystem-wide cascading effects have been reported with pervasive impacts on native insect communities (Bezemer et al., 2014). For example, a global meta-analysis revealed how in 56% cases, invasive plants had negative effects leading to a reduction in the overall abundance, diversity and fitness of different organisms, including insects (Schirmel et al., 2015). The introduction of fish predators such as the rainbow trout (Oncorhynchus mykiss) for economic and recreational activities in South Africa has reduced the distribution of the rare dragonfly Ecchlorolestes peringueyi, which is currently a threatened species (Samways, 1999). Cattle grazing and the planting of exotic trees along the rivers' edge of that country have also impacted negatively on the diversity of lotic dragonflies, which are at greater risk of extinction than their lentic relatives (Clausnitzer et al., 2009).

Many reports (13%) associate the insect declines with several ecological or life-history traits (Fig. 6). The responsible traits vary among

taxa, but some general trends appear consistently. For example, specialist species are declining at higher rates than non-specialists, because they are either most susceptible to habitat changes and losses of host plants or have lower fecundity rates – usually both traits are combined in *K*-selected species. Generalist species are by nature more adaptable to environmental change due to their broader range of host plants, food and shelter requirements, behavioural plasticity and climatic adaptability, surviving under wide-ranging conditions and often colonising vacant niches and new urbanised environments (van Strien et al., 2016).

Finally, increased predation has been suggested as a contributing factor in the decline of large dung beetles in Italy (Carpaneto et al., 2007). Over-collection of specimens has also been suggested in Japan (Nakamura, 2011), but the relative impact of these factors is comparatively minor and geographically confined.

4.1.4. Climate change

The current warming trend, thought by some as the main driver of butterfly and wild bees declines (Bartomeus et al., 2011; Breed et al., 2012; Parmesan et al., 1999), might positively impact on their abundance in temperate regions as they exhibit superior thermal tolerance which - in turn - may benefit their development (Deutsch et al., 2008). In contrast, insects of tropical regions have more narrow thermal thresholds and are particularly susceptible to temperature increases. Hence, global warming has increased the populations of certain butterflies in northern Europe (Kuussaari et al., 2007), expanded their geographical distribution (Isaac et al., 2011; Stefanescu et al., 2011) and caused altitudinal shifts of certain species (Chen et al., 2011; Colwell et al., 2008), yet populations of half of the world's insects are declining counter to that trend (Gilburn et al., 2015).

Global warming has certainly reduced the range of some dragonflies, stoneflies and bumblebees adapted to cold climates and higher latitudes (Ball-Damerow et al., 2014; Jacobson et al., 2018; Tierno de Figueroa et al., 2010), negatively impacted some pollinators in Mediterranean regions such as the beetle *Mylabris nevadensis* (Stefanescu et al., 2018), and might increase the extinction risk of mountainous insect species (Menéndez et al., 2006). There is also clear evidence that climate change is reducing arthropod biomass in the rainforests of Caribbean islands (Lister and Garcia, 2018).

5. Conclusions

This review highlights the dreadful state of insect biodiversity in the world, as almost half of the species are rapidly declining and a third are being threatened with extinction. The information presented here refers mostly to developed countries of Europe and North America (Fig. 1) since those regions have the most comprehensive historical records that allow comparisons of biodiversity on a temporal scale.

Habitat change and pollution are the main drivers of such declines. In particular, the intensification of agriculture over the past six decades stands as the root cause of the problem, and within it the widespread, relentless use of synthetic pesticides is a major driver of insect losses in recent times (Dudley and Alexander, 2017). Given that these factors apply to all countries in the world, insects are not expected to fare differently in tropical and developing countries. The conclusion is clear: unless we change our ways of producing food, insects as a whole will go down the path of extinction in a few decades (Dudley et al., 2017; Fischer et al., 2008; Gomiero et al., 2011). The repercussions this will have for the planet's ecosystems are catastrophic to say the least, as insects are at the structural and functional base of many of the world's ecosystems since their rise at the end of the Devonian period, almost 400 million years ago.

Habitat restoration, coupled with a drastic reduction in agro-chemical inputs and agricultural 'redesign', is probably the most effective way to stop further declines, particularly in areas under intensive agriculture. For example, flower and grassland strips established at the field edge enhance the abundance of wild pollinators (Blaauw and Isaacs, 2014; Hopwood, 2008), and rotation of crops with clover boosts the abundance and diversity of bumblebees (Ekroos et al., 2014; Haaland and Bersier, 2011), which in turn boost crop yield and farm profitability. These 'ecological engineering' tactics not only favour pollinators but also conserve insect natural enemies that are essential for keeping at bay the herbivorous pest species of many crops (Dover et al., 2011; Gurr et al., 2012; Lu et al., 2015). However, for these measures to be effective, it is imperative that current pesticide usage patterns, mainly insecticides and fungicides, are reduced to a minimum as to permit a recovery of insect numbers and their associated 'biological control' services (Heong et al., 2015; Way and Heong, 1994). There is no danger in reducing synthetic insecticides drastically, as they do not contribute significantly to crop yields, but trigger pest resistance, negatively affect food safety and sometimes lower farm revenue (Bredeson and Lundgren, 2018; Lechenet et al., 2017). The judicious implementation of integrated pest management (IPM) in Europe as well as in developing countries of Africa and Asia over the years achieved similar or even greater crop yields (Furlan et al., 2017; Pretty and Bharucha, 2015; Pretty et al., 2011; Thancharoen et al., 2018). Furthermore, in many of the world's farming systems, biological control constitutes an under-used yet cost-effective means to resolve agricultural pest problems while conserving biodiversity both on-farm and beyond the field border (Wyckhuys et al., 2019).

For aquatic insects, rehabilitation of marshlands and improved water quality are a must for the recovery of biodiversity (van Strien et al., 2016). This may require the implementation of effective remediation technologies to clean the existing polluted waters (Arzate et al., 2017; Pascal-Lorber and Laurent, 2011). However, priority should be given to reducing the contamination by runoff and leaching of toxic chemicals, particularly pesticides. Only such conditions can allow the re-colonization of a myriad of discrete species that support essential ecosystem services such as litter-decomposition and nutrient recycling, provide food to fish and other aquatic animals, and are efficient predators of crop pests, aquatic weeds and nuisance mosquitoes.

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