Ecological and habitat restoration for insect conservation

Elise Buisson, Manon C M Hess, Romane Blaya, Tania de Almeida, Natan Huberson, Emile Melloul, Clémentine Mutillod, Léo Rocher, Jean François Alignan, Thierry Dutoit, et al.

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Chapter 15: Ecological and habitat restoration for insect conservation

Elise Buisson[1], Manon C. M. Hess[1,2], Romane Blaya[1], Tania De Almeida[3], Natan Huberson[1], Emile Melloul[1], Clémentine Mutillod[1], Léo Rocher[1], Jean-François Alignan[1], Thierry Dutoit[1], Grégory Mahy[4], Olivier Blight[1]

1. Institut Méditerranéen de Biodiversité et d'Ecologie - IMBE, Avignon Université, Aix Marseille Université, CNRS, IRD, France.
2. Dynamiques et Écologie des Paysages Agriforestiers - DynaFor, Purpan, Toulouse, France.
3. Laboratoire de Génie Civil et géo-Environnement - LGCgE, Université de Lille, IMT Lille Douai, Univ. Artois, Yncrea Hauts-de-France, Lille, France.
4. Biodiversity and Landscape, TERRA Research Center, Gembloux Agro-Bio Tech, University of Liège, Gembloux, Belgium.

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Abstract
Ecological restoration, the process of assisting the recovery of an ecosystem, can benefit insect conservation. The restoration of native plant species is often associated with natural recovery of insects, firstly phytophagous and pollinators. Restoration can also specifically aim at assisting the recovery of a particular insect taxon: meadows reopened after encroachment by pine trees are suitable habitats for an endangered butterfly and the introduction of grazing, prescribed burns, and soil scraping in prairies invaded by exotic grass creates the bare ground patches essential for an endangered beetle. Restoration can also be promoted by the reintroduction of insects that are ecosystem engineers, such as ants or termites. In all cases, the recovery of insect diversity at restored sites is dependent on the level of degradation, the implemented restoration actions, the landscape and regional context, mobility of insect species, and species-specific interactions. Insects have complex life cycles: eggs, larvae, and adults do not share the same habitat requirements and are at different levels in the trophic network. As a result, restoration projects cannot provide an ideal habitat that satisfies the diverse needs of all insects. However, maximizing habitat complexity and heterogeneity is a way to provide a variety of habitats and promote insect diversity.

Keywords: ecological restoration, ecosystem engineers, management, restoration ecology

General background to the topic

Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded or destroyed. It includes any action intended to promote the recovery of an ecosystem, and can thus involve controlling invasive species, conditioning habitats, reintroducing species, and reinforcing populations (Gann et al. 2019). Restoration goals are set following a reference ecosystem, i.e. a native ecosystem representing a non-degraded version of the ecosystem that might have existed on the restoration site had degradation not occurred (Gann et al. 2019). Habitat restoration is more specific and aims at ensuring that the particular combination of resources and environmental conditions that are required by an individual species or group of species to carry out life processes are provided (Miller and Hobbs 2007). It is often used for endangered species. Restoring specific habitats can be included within larger projects considering the recovery of ecosystems. It can also be implemented outside of such context, for example, when artificial burrows are created in natural ecosystems to enhance the density and recruitment success of a local population of a protected species (Grillet et al. 2006).

Given their sensitivity to disturbance and their key role in ecosystem functioning, insects are an interesting model for ecological restoration. A growing number of studies are now using insects as bioindicators of disturbance and in the evaluation of restoration projects. Other studies target insects to assist their own recovery, and to a lower extent, to restore ecosystems. It is therefore necessary to understand the factors that structure the populations and communities of target insects, and the mutualistic relationships that they maintain with plants and other animals to set up effective restoration programmes.

A recent review carried out with the word “restoration” and “insect group (Latin name)” only found 1,293 studies (Coleoptera: 409, Hymenoptera: 261, Lepidoptera: 234, Diptera: 140, Odonata: 88, Hemiptera: 72, Orthoptera: 69, and Isoptera: 20; Wijas and Atkinson 2021). While insects remain understudied within the context of ecological restoration (in comparison 25,271 studies were found when searching “restoration” and “plant”, Web of Science, August 2022), there are still enough projects and research carried out in the field to synthesize the available information. This chapter summarizes the link between restoration and insects in three different ways (Figure 15.1):

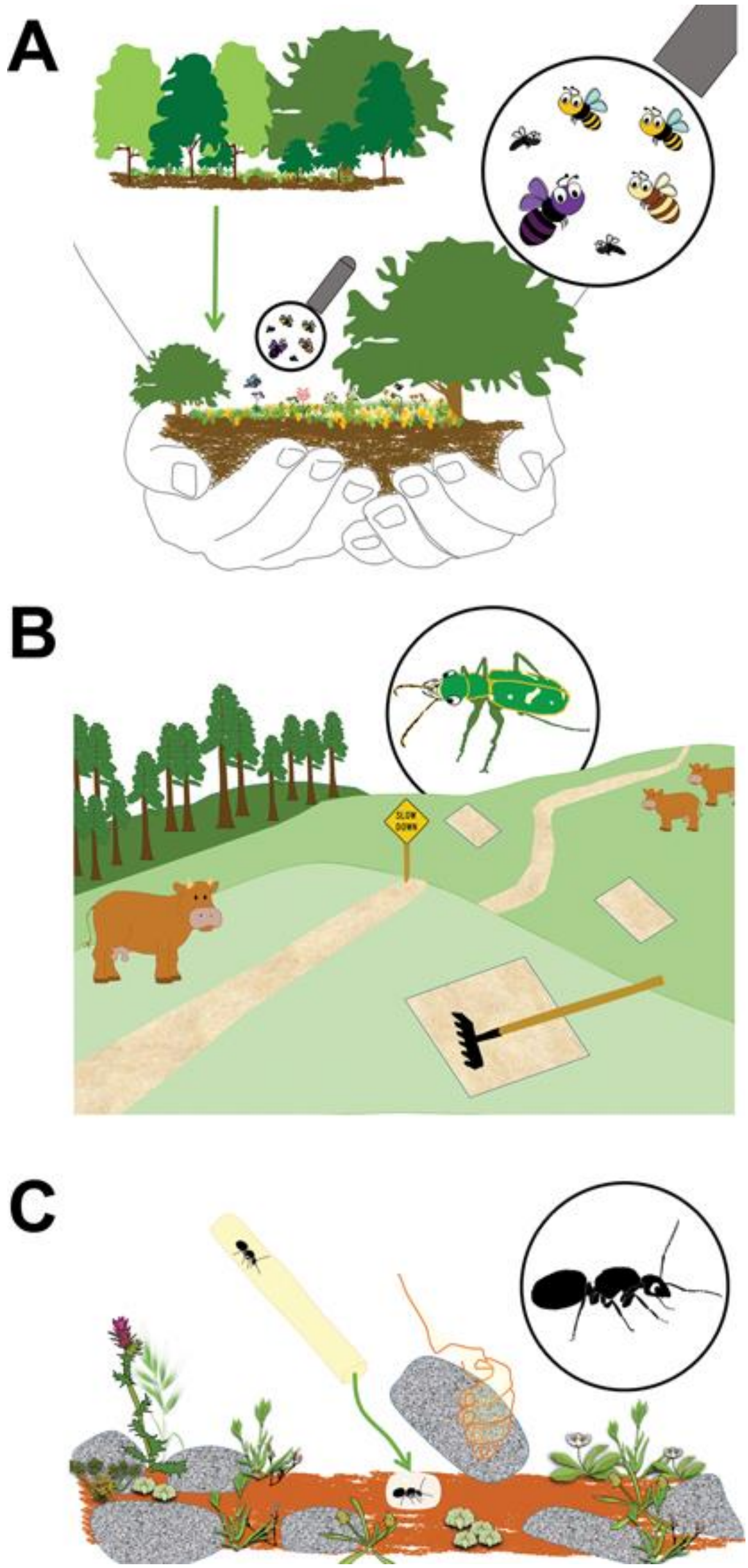

Figure 15.1. *This chapter summarizes the link between restoration and insects in three different ways: (A) Insects contribute to the monitoring of restoration projects: after an ecological restoration project (green arrow) has been implemented (degraded ecosystem on the top, restored ecosystem at the bottom), monitoring is conducted to evaluate restoration success and plan adaptive management. Monitoring can be undertaken on a wide variety of parameters depending on the goals of the restoration project. In this example, pollinators are monitored, as in Lettow et al. 2018. (B) Restoration assists the recovery of target insect taxa: here, the Ohlone tiger beetle's habitat is restored in grass invaded coastal prairies by creating bare-ground patches using cattle grazing and topsoil scraping; it also includes biking speed regulation on trails (Cornelisse et al. 2013a). (C) Insects are used for restoration: restoration is implemented using insects as ecosystem engineers: here harvester ants are reintroduced to a degraded area to help seed dispersal and plant community recovery (Bulot et al. 2014a) (herbaceous plant, cow and bee drawings courtesy of S. Le Stradic and R. Jaunatre).*

1) Once an ecological restoration project has been implemented, monitoring must be conducted in order to evaluate restoration success and plan adaptive management. Monitoring can be undertaken on a wide variety of parameters depending on the goals of the restoration project (Holl and Cairns Jr. 2002). Very often, vegetation is monitored, but the way insects exploit the restored ecosystem compared to the reference ecosystem or compared to the degraded area is increasingly studied. Specific insects may also be used to serve as bioindicators of restoration success or of the restoration of particular ecosystem functions. 2) Restoration can be planned to assist the recovery of a particular insect taxon, whether it is within a larger restoration project or not. In that case, the complete life cycle of the insect must be well described in order to provide the habitats required by all life stages. 3) Restoration can be implemented using insects as ecosystem engineers (Byers et al. 2006), i.e., organisms controlling the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials, leading to modification of habitats (Jones et al. 1994).

Case studies

We present below a few successful case studies according to the outline presented above. More case studies can be found on the Conservation Evidence website (Conservation Evidence 2020).

Insects contribute to the monitoring of restoration projects

Ecological restoration targeting plants usually benefits wider biodiversity, including insects. In this regard, studying biodiversity components other than vegetation provides a better understanding of the functioning of the restored ecosystem and the success of the restoration (e.g., Hugel 2012; Lettow et al. *2*018).

Hugel (2012) presents the impact of native forest restoration on endemic Orthoptera on Rodrigues Island, in the Indian Ocean. The native forest, which only remained in patches on mountain tops and valleys by 1996, was cleared for agriculture and wood production and elsewhere was degraded and invaded by alien plant species. The restoration of Grande Montagne Nature Reserve (25.5 ha) comprised removing invasive plant species and planting over 150,000 native seedlings grown in local nurseries. Fifteen years later, endemic Orthoptera density and diversity were compared between the restored site and the degraded areas. At the restored site, the average density was seven times higher and the average species richness was double that of the degraded areas (Hugel 2012).

Lettow et al*.* (2018) demonstrated the impact of oak savanna restoration on bees. The study site in Michigan, United States of America (USA), was degraded by the suppression of natural fire for several decades leading to encroachment by fire-sensitive tree species whereas the reference ecosystem, an oak savanna, is fire-dependent. The continuous herbaceous vegetation allows low-intensity fires to maintain scattered oak trees (10%–60% canopy cover and low shrub cover) (Lettow et al. 2018). Ecological restoration consisted of non-oak thinning (cut stumps are sprayed with herbicide to prevent resprouting) combined with a spring prescribed fire every two years (Lettow et al. 2014, 2018). Compared with unmanaged degraded areas, restoration succeeded in decreasing canopy cover, increasing light availability, and the diversity of flowering forbs (a mix of pre-existing shade tolerant species, native and exotic ruderals, as well as savanna indicator species) (Lettow et al. 2014) (Figure

15.1A). Restoration efforts also promoted ~~a notable rise in~~ bee abundance, richness, and diversity. Thinning and burning resulted in a distinct bee community after two seasons. This may be due to an increase in nesting resources as illustrated by the high diversity in nesting guilds (nesting in soil, stems, or wood) or to a diversification of diets (oligolectic and polylectic feeding).

Restoration assists in the recovery of target insect taxa

In specific cases, habitat can be restored to assist the recovery of certain species. For example, dead wood is used to restore saproxylic beetle assemblages (Sandström et al. 2019) or flowering shrubs are planted to restore pollinator populations (M'Gonigle et al. 2017). In the three cases presented here, habitats were specifically managed to restore threatened insects: a butterfly (Marttila et al. 1997), a beetle (Cornelisse et al. 2013a), and a damselfly (Tichanek and Tropek 2016).

Marttila et al. (1997) reported the successful reintroduction of an endangered species of butterfly, the Baton Blue butterfly (*Pseudophilotes baton schiffermuelleri*, Bergsträsser 1779), to a site where it had become extinct in Finland due to native tree colonization. Ecological restoration involved the removal of young Scots pine (*Pinus sylvestris* L.), as well as natural recolonization by native plants characteristic of meadows on dry and open eskers, including *Thymus serpyllum* L., its host plant. Two years after the restoration began, 10 female butterflies were translocated. Two years later, 46 individuals were observed on the site. While this reintroduction was a success, natural succession and pine colonization is a constant threat to the site and management is needed every five years. As the restored site is surrounded by pine forests, butterfly emigration is limited, and other clearing patches must be created (Marttila et al. 1997).

The endangered Ohlone tiger beetle (*Cicindela ohlone,* Freitag and Kavanaugh 1993) was found in only five patches of coastal prairies distributed over 24 km² in Santa Cruz County in California (USA), but the protection of its habitat was not enough to prevent its extinction (Cornelisse et al. 2013a). The Ohlone tiger beetle requires patches of bare ground for mating, foraging, and oviposition, which have become scarce due to the exclusion of endogenous disturbances, such as fire, and to invasion by exotic grasses (Cornelisse et al. 2013a). Restoration actions included cattle and horse grazing, prescribed burns, scraping to create bare ground patches, and biking speed regulation on trails (Cornelisse et al. 2013a, b; Arnold and Knisley 2018) (Figure 15.1B). These actions increased its survival rate and population size (Cornelisse et al. 2013a; Arnold and Knisley 2018) and must be continued to maintain populations. Both coastal prairies from where *C. ohlone* was extirpated and coastal prairies where *C. ohlone* was not found can be managed in the same way for potential recolonization or translocation (Cornelisse 2013).

The damselfly, *Coenagrion ornatum* (Selys 1850), is a threatened species of lowland headwater streams in Western and Central Europe. A study on post-mining drainage ditches in the Czech Republic showed that restored ditches with emergent vegetation including *Eleocharis* plant species were an adequate habitat for both larvae and adults (Tichanek and Tropek 2016). The authors therefore recommend the conservation and restoration of such ditches within the rehabilitation of mining sites (Tichanek and Tropek 2016).

Insects are directly used for restoration

Many insects play an engineering role in ecosystems. Insects can build shelters to provide protection for their own larva development. These shelters may be co-occupied or occupied after abandonment influencing other organisms through facilitative interactions (Cornelissen et al. 2016). Some Trichoptera species construct filtration nets in streams to collect organic matter from the water thereby increasing the stability of benthic substrates during flooding (Cardinale et al. 2004). Termites and ants are famous ecosystem engineers providing key soil functions. Termites eat and digest dead vegetation, wood, litter, grass, or dung and build nests, creating biogenic structures (Jouquet et al. 2006; Wijas and Atkinson 2021). They participate in the decomposition of organic matter and nutrient cycling, enhance water infiltration and storage in the soil, and promote bioturbation and microbial development (Jouquet et al. 2006, 2014; Wijas and Atkinson 2021). Ants participate in the recycling of soil nutrients (Frouz and Jilková 2008) and modify soil aeration and porosity (Cerdá and Jurgensen 2008). As predators, they regulate the populations of many other arthropods (Jouquet et al. 2006). Aside from being soil engineers and influencing soil physical and chemical properties, harvester ants, by transporting seeds, influence plant species richness and community composition, accelerating succession processes during restoration (Kovář et al. 2013; De Almeida et al. 2020).

The direct inoculation of termites to degraded sites is difficult because they are difficult to breed (Jouquet et al. 2014). However, if they are found in the surrounding landscape, they can be attracted to the degraded sites by providing appropriate resources, such as mulch or dung, depending on the targeted species (Rouland et al. 2003). Termites can successfully restore compacted or crusted soils, as their burrowing activities increase water infiltration and retention and reduce bulk density (Jouquet et al. 2014; Kaiser et al. 2017). A technique named “Zaï” traditionally uses termites to restore soils in Western Sahel (Burkina Faso, Mali, Niger). It entails digging holes and placing organic matter in the holes (dung mixed with litter, compost, or ashes). Termites build galleries under the organic matter to collect it, thereby allowing water infiltration and the deep rooting of sown or planted species (Roose et al. 1994). This technique is used to improve agricultural production as well as for reforestation (Kaiser et al. 2017).

Ant inoculation was attempted in a degraded Mediterranean grassland by transferring founding queens (Bulot et al. 2014a). The grassland was degraded by an oil pipeline leak. Ecological restoration consisted in polluted soil excavation and just-in-time soil transfer (i.e., with no stockpiling) with the reconstitution of soil horizons from a grassland site planned to be destroyed (Bulot et al. 2014b). *Messor barbarus* L. queens were collected during nuptial flights in the surroundings of the degraded site and each queen was then installed on the site in a small hole in the ground under a stone to protect them from sudden variations in temperature (Bulot et al. 2014a) (Figure 15.1C). Founding queen survival rate reached 56.3% and 35.3% six months and one year after translocation respectively. Broods, worker ants or refuse piles were observed at 12% of the translocation location after one year (Bulot et al. 2014a). Seven years after translocation, nest density was significantly higher in the restored site (263 per ha) than in the surrounding reference grassland (167 per ha) (De Almeida et al. 2020). While the seed bank and the vegetation of the restored site were still different from the reference grassland, restored patches where ants were present have richer seed banks and plant communities than in ant-free patches and were moving towards the reference grassland composition (De Almeida et al. 2020).

Unique solutions to conserve insects

Restoration often requires site- and situation-specific approaches (Hobbs and Norton 1996): channelized rivers can be remeandered, polluted soil excavated and replaced, grazing activity can be excluded or reintroduced, and species planted or translocated. Not all restoration actions can be covered in this chapter considering the number of possible combinations of degradations and the diversity and specificity of ecosystems, but several examples of how insects can be considered are presented below. We present three examples, each representing a different level of restoration intensity according to Whisenant's (1999) conceptual model (Figure 15.2).

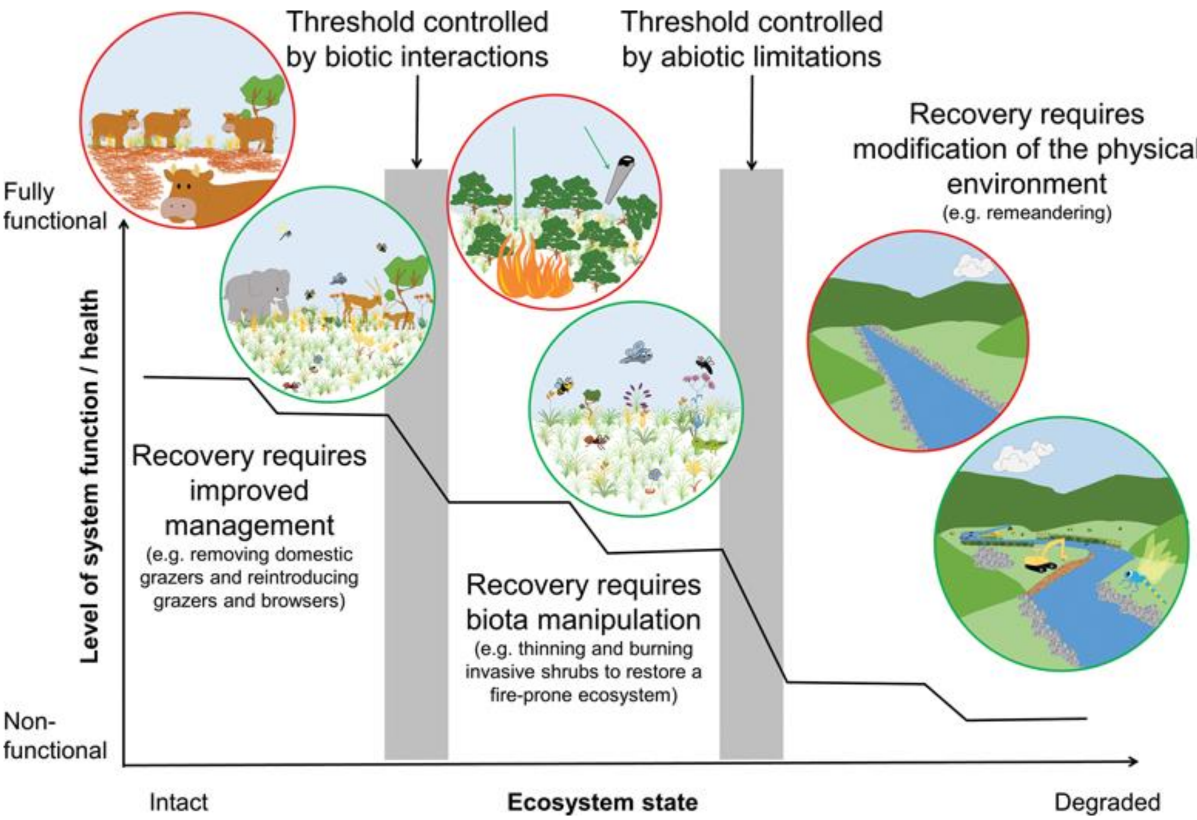

Figure 15.2. *Conceptual model representing ecosystem degradation via two common transition thresholds (biotic interactions and abiotic limitations) that separate degraded ecosystems in three groups (modified from Whisenant 1999). Functional integrity and transition limitations define these groups. The first group did not pass any threshold: ecosystems are not too degraded and recovery only requires removal of the damaging activity and improved management (e.g. switching from domestic herbivore grazing to a suite of native herbivores, grazing and browsing). In the second group, ecosystems passed the biotic interactions threshold and recovery requires manipulation of living-being (e.g. invasive shrub control using thinning and fire). The third group of ecosystems passed both thresholds and recovery first requires modification of the physical environment (e.g. restoration entailing soil preparation, such as river remeadering). Ecosystems circled in red are degraded while ecosystem circled in green are restored (mammal and herbaceous plant drawings courtesy of S. Le Stradic).*

The model represents ecosystem degradation via two common transition thresholds (biotic interactions and abiotic limitations) that categorize degraded ecosystems into three groups. The first group of ecosystems did not pass any threshold: ecosystems are not too degraded, and recovery only requires removal of the damaging activity and improved management. In the second group, ecosystems passed the biotic interactions threshold and recovery requires manipulation of living-being. The third group of ecosystems passed both thresholds (biotic and abiotic) and recovery requires modification of the physical environment before manipulating living-being.

Group 1: Grazing and browsing for insect restoration

Grazing and browsing by domestic or wild animals is often used in restoration to control undesired plants and increase plant species richness (Marchetto et al. 2021) (Figure 15.2). Both types of herbivory have cascading direct and indirect effects on vegetation, soil, and other components of biodiversity (e.g., insects, birds). Herbivores have direct negative effects on insects by inadvertently eating or trampling them (Black et al. 2011) and direct positive effects by providing resources, in the form of dung, carcasses, blood, and live tissues (van Klink et al. 2015). They also have numerous indirect effects on insects *via* their direct effect on vegetation composition and structure (e.g., vegetation height), as well as on soil characteristics, such as compaction or nutrient contents (van Klink et al. 2015). These indirect effects alter environmental conditions and resource availability for insects. For example, herbivores increase the amount of bare ground, which can be beneficial for insect foraging or laying eggs on the ground, such as the Ohlone tiger beetle (Cornelisse et al. 2013a). While herbivores can compete for forage resources with pollinators, they can also help forb-dominated grasslands that support diverse pollinator communities to remain open (Black et al. 2011). The magnitude of the effects of grazing and browsing on insects depends on the insect considered, the ecosystem to be restored, the herbivore(s) used in the restoration project and the grazing/browsing regime.

Group 2: Invasive alien species control for insect restoration

The successful control of invasive alien species helps restoring native biodiversity and ecosystem functions. Insect diversity, although not investigated systematically, is globally improved by invasive alien species management. For instance, the removal of invasive alien trees invading water courses (Samways 2005) or the control of alien ants (Gaigher et al. 2013) resulted in rapid recovery of indigenous insects. The speed of recovery of insect diversity varies according to i) the degree by which the invasive alien species has affected the environment; ii) the connectivity with uninvaded areas presenting intact native insect communities; and iii) the mobility of the insect species. Because the methods used to control invasive alien species and their application protocol (e.g., season of implementation) can substantially influence the success of the control, but also the recovery of native species, including insects, they should be carefully implemented (Hess et al. 2023).

The most common restoration actions to control invasive species include prescribed burning, grazing, the release of chemical compounds (i.e., herbicides), physical removal and mowing, and classical biological control (Hess et al. 2023). They can directly affect the fitness of native populations through death or toxicity (e.g., insecticides; Stanley et al. 2016), competitive displacement, or reduced reproduction. Restoration actions can also induce changes in ecosystem functioning through modification of vegetation composition and structure, disturbing ecological interactions, and indirectly affecting insect diversity (Hess et al. 2023). For example, two herbicides (fluazifop-p-butyl and sethoxydim) were used to control invasive grass species to improve the habitats of several at-risk butterfly species and reverse their decline in Oregon (USA). These herbicides, however, reduce survival, wing size, pupal weight, and development time of the two butterflies *Icaricia icarioides blackmorei* (W. Barnes and McDunnough 1919) and *Pieris rapae* (Linnaeus 1758) through direct toxicity (Russell and Schultz 2010). Another example is the use of prescribed burning to control invasive vegetation in fire-prone ecosystems (Figure 15.2). The considered insect species, site features, climate, fire intensity, and temporal and spatial scale of fires influence insect responses to fire (Kral et al. 2017). These responses are unpredictable at the order or family levels. While fire should not lead to local extinction of native insects adapted to fire-prone ecosystems (Panzer 2002), these responses are linked to the degree of exposure to flames and the mobility of species or life stage (Kral et al. 2017). Before applying any invasive species control treatment, one should have a precise idea of the native species still present on the invaded site (internal native species pool; Fattorini and Halle 2004) in order to choose the method and its application protocol adequately (Hess et al. 2023).

Group 3: Taking insects into consideration when restoration entails soil preparation

Soil preparation is a common first step in restoration. It can consist in ripping, harrowing or tilling the soil (1) breaking sealed soil surfaces (Kinyua et al. 2010), (2) creating microtopography which can contribute to reduce soil erosion, increase the capture of soil and seeds from the surrounding landscape and improve abiotic conditions for germination (Kiehl et al. 2010; Kimiti et al. 2017), (3) limiting competition from an undesired vegetation established on the degraded site (Durbecq et al. 2021). Soil preparation can also consist in topsoil transfer aimed at translocating soil material and its native biota, including the native seed bank, or consist in topsoil removal or soil inversion (i.e. burial of the topsoil under a layer of subsoil) aimed at decreasing soil nutrient content and undesired exotic or weedy seed bank (Buisson et al. 2021a). Finally, soil preparation is most intense where there were major degradations (e.g. oil pipeline leak followed by polluted soil excavation Bulot *et al.* 2014b) or where ecosystems were completely destroyed, such as in mining, quarrying (Legwaila et al. 2015), river channelization requiring remeandering or wetland filling requiring re-creation (Giergiczny et al. 2022) (Figure 2).

Soil must be prepared consistently with the potential internal species pool (i.e., seed bank, bud bank, egg bank, alive individual plants; Fattorini and Halle 2004). For instance, it should not be stockpiled, as direct transfers minimize the colonization by weeds and the loss of native propagule viability, soil structure, or microbial biomass (Buisson et al. 2021a). Soil should be transferred: i) with the reconstitution of soil horizons on restoration sites, ensuring that the topsoil containing the seed bank is placed on top (Bulot et al. 2014b), and ii) at the appropriate season to maximize vegetation recovery from the seed bank (Buisson et al. 2021a). It is now widely admitted that soil preparation is likely to be inappropriate if it hampers vegetation recovery from the seed and bud bank (Buisson et al. 2021b). The internal species pool, comprising microorganisms and invertebrates like insects, is however often overlooked when deciding whether soil preparation is required or determining the suitable timing for such actions. That being said, Fattorini and Halle (2004) explicitly acknowledge the presence of the egg bank in the internal species pool, and certain restoration efforts do take insects into consideration during soil preparation. For example, restored wetland inoculated with remnant wetland soil in the state of New York (USA) showed significantly higher colonization by insects (Brown et al. 1997).

Future considerations for insect conservation

Consideration of insects and their ecology in the design of restoration projects is fundamental to improve insect conservation. The recovery of insect diversity is dependent on the level of degradation of the site to be restored, on the implemented restoration actions, on the landscape and regional context and the mobility of insect species (Hess et al. 2023).

When choosing restoration actions, one must recognize their effect on native insect diversity, as they can directly affect the fitness of insect populations, or indirectly modify ecosystem components and functions, by changing vegetation composition and structure and by disrupting food chains or mutualisms. As insect ecology is highly diverse, it is unlikely that a given restoration action will not affect any native insect species. Precautions can be taken to mitigate their impacts: conserving temporary refugia (e.g., untreated zones, by restoring the site in several phases that allow insects to progressively colonize restored areas), or selecting the appropriate timing for application (e.g., when insects display less vulnerable life-stages, considering insect phenology (Moschetti et al. 2020; Hess et al. 2023)).

"If we build it, they will come" refers to the assumption that community assembly will occur once the physical environment is restored, or that animals will colonize once the vegetation has recovered (Hilderbrand et al. 2005). It has been demonstrated that it is not always true (Hughes 2007; Hölzel et al. 2012) and that restored habitat recolonization by native insects does not only rely on the quality of the restored habitat. It also depends on i) the dispersal capacity of each species (Fisher et al. 2020); ii) the spatial configuration of restored habitats in the landscape, specifically spatial isolation from source habitat (connectivity, habitat features, and matrix permeability); iii) the amount of source habitat in the surroundings of the restored site (Rudnick et al. 2012); and iv) species-specific interactions (e.g., butterfly species of the genus *Phengaris* will survive at a site only if *Myrmica* ants are present as they have a complex lifecycle involving parasitism of an ant nest at the larval stage; Hayes 2015). Protecting pristine ecosystems and adequately choosing the location of the restoration are essential for successful restoration but may have to be complemented with insect translocation (Brown et al. 1997; Hoffmann et al. 2018). Habitat specialists, which are often important targets in restoration projects, face further difficulties in establishing because of their demand for specific habitat conditions (Cristofoli and Mahy 2010). In any case, more attention is needed on insect dispersal capabilities when designing restoration projects (Parkyn and Smith 2011).

Because insects have complex life cycles, no restoration action can provide an ideal habitat for all insects (Black et al. 2011). Nonetheless, although it may not be a universal solution (Palmer et al. 2010), maximizing habitat complexity (i.e., habitat physiognomy, vertical organization) and heterogeneity (i.e., horizontal variation in habitat form, patchiness) in the restoration design offers a means to create diverse habitats for various life stages and foster insect diversity (Larkin et al. 2006).

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