

Addressing global challenges with unconventional insect ecosystem services: Why should humanity care about insect larvae?

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Abstract

1. Ecosystem services are essential for the health of current and future generations and key to the sustainable development of our societies. The role of insects in providing ecosystem services has been increasingly recognized, becoming the focus of several management and conservation initiatives world-wide.
2. However, ecosystem services framework traditionally overlooks the full range of services that can be provided by insects, largely because services provided by life stages other than the insect adult are often neglected.
3. In this paper, I first review the traditional ecosystem services primarily attributed to insects, namely edible insects and mass-rearing for biological control. Next, I provide a collection of unconventional ecosystem services provided by insect larvae which highlights the importance of considering life stage-specific services in a holistic view of the ecosystem services framework.
4. In particular, I discuss recent advances that revealed how insect larvae can degrade plastic, which is one of humanity's greatest environmental pollutants, and how larvae can be used to produce biofuel to help overcome the increasing contribution of the fossil fuel industry to climate change. I then discuss how toxic compounds produced by the larvae of some insects provide potential new medicines for clinical treatment and lastly, I discuss a unique example of how the larval stage of insects is entrenched into the cultural values of Aboriginal communities in Australia.
5. In conclusion, by acknowledging life stage-specific ecosystem services provided by insects, this paper raises awareness of unconventional services that can underpin innovative solutions to contemporary global challenges, which can ultimately help create more sustainable and culturally diverse societies.

KEYWORDS

caterpillars, climate change, edible insects, ethnobiology, grubs, indigenous culture, maggots, renewable energy

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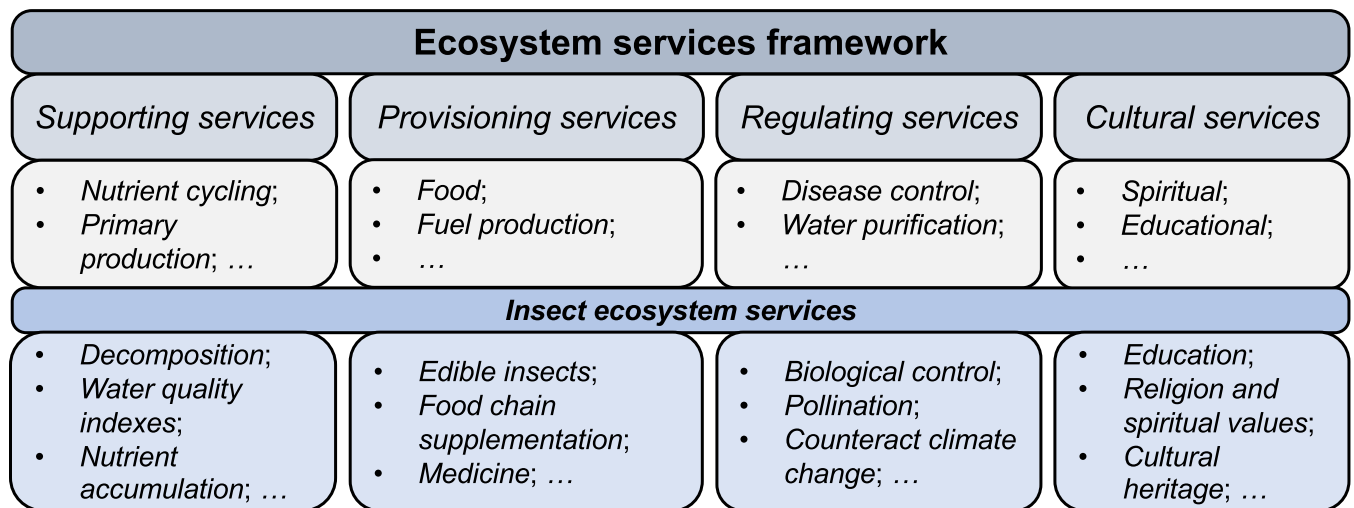
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1 | INTRODUCTION

Exploration of ecosystem services has underpinned the rapid economic development of countries over the previous centuries (Costanza et al., 1997; Millennium Ecosystem Assessment, 2005). This economic growth came at the expense of ecosystem services overexploitation, which has led to the realization that sustainable approaches to harvest the benefits of ecosystem services are needed in order to avoid socio-economic collapse (de Groot et al., 2012; Millennium Ecosystem Assessment, 2005; Whitmee et al., 2015). In this context, it has been recognized that insects play a fundamental role across a wide range of ecosystem services and that the observed insect decline puts significant pressure on ecosystem stability (Noriega et al., 2018; Schowalter, Noriega, & Tscharrntke, 2018). For example, the decline of pollinator species (e.g. bumblebees) poses a major threat to food security in both developed and developing countries (Potts et al., 2010; Vanbergen & the Insect Pollinators Initiative, 2013).

In fact, insects contribute to all types of ecosystems services officially recognized by the Millennium Ecosystem Assessment (MA) namely, *supporting services* (e.g. pollination), *regulating services* (e.g. biological control), *provisioning services* (e.g. honey production, edible insects) and *cultural services* (e.g. tourism related to Monarch butterfly *Danaus plexippus* (Lepidoptera: Nymphalidae) populations; Figure 1; see e.g. Noriega et al., 2018; Prather & Laws, 2018 and references therein). Insects also provide the so called ‘disservices’ which are primarily related to insect pests and disease vectors (Schowalter et al., 2018). Therefore, insects provide many ecosystems services which support (or hinder) socio-economic progress. As a result, failing to acknowledge the significance of insect ecosystem services can have negative implications to the future sustainable development of our societies (Prather & Laws, 2018).

Amongst many traditionally recognized insect ecosystem services, pollination is the most widely known (Schowalter et al., 2018). Pollination is necessary for the majority of plants and underpins more



Sources: Millennium Ecosystem Assessment (2005) and Noriega et al. (2018)

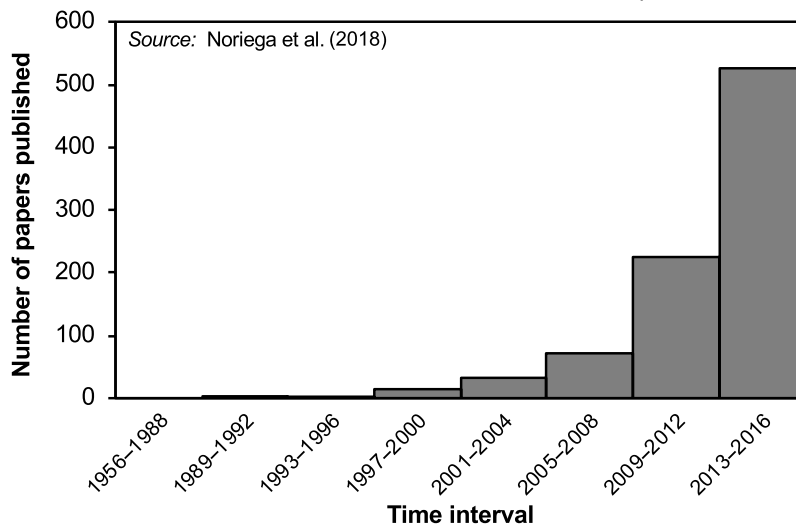


FIGURE 1 Ecosystem services framework. Ecosystem services framework is divided into four categories of services: supporting, provisioning, regulating and cultural services (Millennium Ecosystem Assessment, 2005). Insects provide services across all four categories as exemplified in the figure (Noriega et al., 2018). Note that the recognition of insect ecosystem services resulted in a rapid increase in the number of papers published from 1950s to 2016 (from Noriega et al., 2018)

than one-third of crop production world-wide (Klatt et al., 2014; Klein et al., 2007). Habitat degradation has led to a decline of pollinators in many regions, threatening food production that can lead to economic collapse (Burkle, Marlin, & Knight, 2013; Potts et al., 2010; Vanbergen & the Insect Pollinators Initiative, 2013). Management practices have been devised to support pollinators' biodiversity and growing attention from both the academic and non-academic communities has been given to this issue (e.g. academic: Lindström, Klatt, Smith, & Bommarco, 2018; Taki, Murao, Mitai, & Yamaura, 2018; Vanbergen & the Insect Pollinators Initiative, 2013; non-academic: <https://www.bbc.co.uk/news/science-environment-52399373>). However, these management efforts benefit from the charismatic appeal that pollinators, especially bees and butterflies, has with the community (Fleishman & Murphy, 2009; Heinrich, 2003). Yet, not all insects that provide ecosystem services possess the same charisma of bees and butterflies and can therefore be overlooked. Even amongst species with such charisma, the appeal is largely associated with the adult stage due to their colours and/or 'furry' bodies, while the larval stages are often neglected and even feared. In fact, psychological studies have demonstrated the association between insect larvae and feelings of disgust, fear and anxiety (i.e. 'larvae phobia'; e.g. Hong et al., 2015; Sawchuk, Lohr, Lee, & Tolin, 1999). Thus, it is not surprising that most (if not all) insect flagship species carry the adult stage as 'advertising posters' (Oberhauser & Guiney, 2009). In itself, this adult-focused approach is not necessarily negative since the conservation of the species and species' habitats benefits both the larval and adult stages. But larvae and adults provide different (and sometimes complementary) types of ecosystem services. For example, it is the adult (not the larvae) honeybee that pollinates plants and produces honey. Likewise, it is the elephant fly *Toxorhynchites* sp. (Diptera: Culicidae) larva (not the adult) that predares on other mosquitoes' larvae thereby contributing to the biological control of disease vectors (Linley, 1990; Shaalan & Canyon, 2009). These life stage-specific ecosystem services emerge because the larvae and adults are adapted to perform different functions during insect life cycle and therefore display remarkably different morphologies and ecological traits (Chapman, 2012; Peterson, 1948). Traditionally though, the ecosystem services framework has focused to a large extent on the insect services provided by adults (Prather & Laws, 2018). Failing to recognize life stage-specific ecosystem services can create blindspots that prevent appropriate management and sustainable exploration of the full range of insect ecosystem services available to our societies.

In this paper, I discuss insect ecosystem services through a different lens. First, I review major insect ecosystem services that are explored by our societies with potential for high return-on-investment, namely edible insects and mass-rearing for biological control. Next, I focus on 'unconventional' ecosystem services provided by the larval stage of insects. The services include the role of insect larvae on plastic biodegradation, larval biofuel production, the potential new therapeutic drugs and the significance of insect larvae to Aboriginal culture. These evidences provide an overview of the ways through which unconventional ecosystem services provided by insect larvae can influence how humanity interacts with the planet to foster

more sustainable and culturally diverse societies. The focus on the larval stage does not intend to create an arbitrary division between life stages of an otherwise continuum life cycle, although in evolutionary terms, the separation of life stages is not entirely arbitrary as evolutionary conflict between larval and adult stages are predicted to evolve and have been described in the insect literature (Thompson, 1988; Trivers, 1974). Nor the focus on the larvae intends to claim that earlier life stages are independent from or more important than later life stages. Instead, the focus on the larval stage adopted here is intended to attribute due value to ecosystem services that are provided by the larvae.

2 | TRADITIONAL ECOSYSTEM SERVICES BY INSECTS: NUTRITION AND BIOLOGICAL CONTROL

2.1 | Cultural and provisioning services: Edible insects

Insects are rich in nutrients, particularly protein that can be otherwise expensive and/or in short supply and difficult to obtain (Ramos-Elorduy & Menzel, 1998). Consequently, insects from all families (most commonly Orthopterans, Dipterans, Coleopterans, Lepidopterans and Hymenopterans) are considered a culinary delicacy in many cultures world-wide (DeFoliart, 1999; Vane-Wright, 1991; Figure 2). Africa, America and Asia (largely China and Southeast Asia) are the regions with the highest number of recorded edible species in the world, attesting for the importance of entomophagy (i.e. insect eating) to the culture of these regions (Figure 2). In Mexico for instance, edible insects have been eaten since the Aztecs (del Pino & Ramos-Elorduy, 1997; DePalma, 2001; Ramos-Elorduy et al., 2011). *Escamoles* are the edible larvae and pupae of ants *Liometopum* sp. (Hymenoptera: Formicidae) consumed largely in Mexico City. Similarly, *cuchamás*, the larvae of the moth *Paradirphia fumosa* (Lepidoptera: Saturniidae), are widely consumed in the Zapotitlán region (Ramos-Elorduy et al., 2011). Indigenous people in Australia and groups in Papua and New Guinea are also known to eat insects, which are an important source of nutrients in their diet (Meyer-Rochow, 1973; Si & Turpin, 2015; Yen, 2009, 2010). Likewise, in Africa and Latin America, the traditional culture of eating insects is widespread throughout the continent and plays an important role in nutrient acquisition (Banjo, Lawal, & Songonuga, 2006; Ramos-Elorduy et al., 1997; Siulapwa, Mwambungu, Lungu, & Sichilima, 2014). Because of insects' nutritional value, insect farming is becoming a real alternative to practical nutrient distribution at relatively small production costs (see e.g. Hanboonsong, Jamjanya, & Durst, 2013; Rumpold & Schlüter, 2013). This practice opens up the potential for poorest communities, which are most affected by hunger and poverty, to mitigate nutrient deficiencies and malnutrition (Branca et al., 2020; Popkin, Corvalan, & Grummer-Strawn, 2019; Ramos-Elorduy, 2008). Thus, edible insects might provide an important source of rapid and reliable nutrients to populations world-wide (Van Huis et al., 2013).

FIGURE 2 Edible insects and their potential for supplementing diets. Percentage of recorded edible insect species consumed per region of the planet. Americas and Africa represent the leading regions for the consumption of edible insects. Note the percentage of protein in the larva, compared with raw cattle beef (pink bar). These estimates do not specify whether or not the protein content of the larva is fully digestible in the original publications

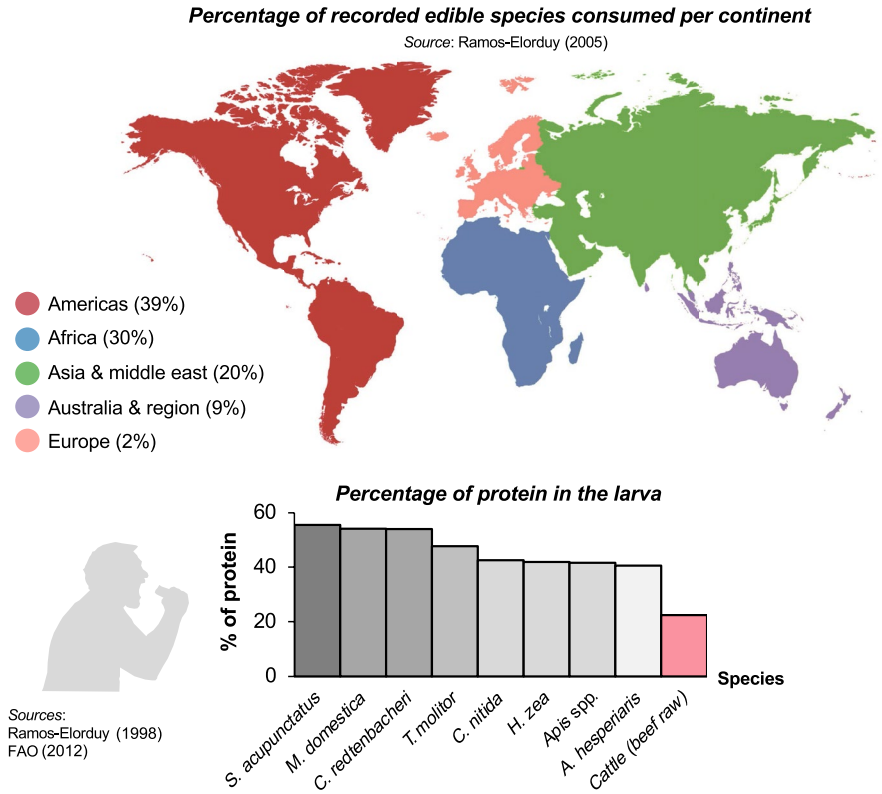
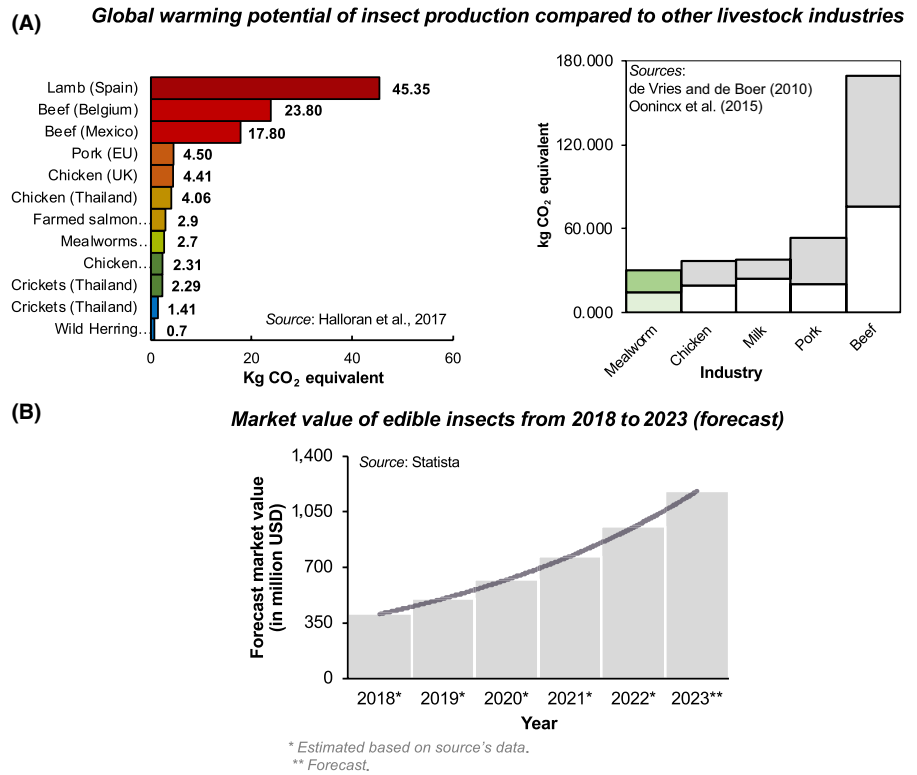


FIGURE 3 Edible insects can reduce greenhouse gases while boosting economic growth. (A) Global warming potential (kg of CO₂ equivalent) of livestock farming compared to mealworms (both panels) as well as crickets (left panel). In general, insect farming has significantly lower global warming potential compared to other livestock species with one exception, the fishing of wild Herring in Norway. Data publicized via <https://sciencenordic.com/agriculture-fisheries-climate-climate-solutions/how-much-more-environmentally-friendly-is-it-to-eat-insects/1445691>. (B) Forecast of the market value (USA) for the edible insect from 2018 to 2023 (in million US dollars). Sources of the data are given within each panel



The culture of entomophagy provides the additional benefit of reducing greenhouse emissions associated with the maintenance of livestock for the meat industry (e.g. de Vries & de Boer, 2010; Halloran, Hanboonsong, Roos, & Bruun, 2017; van Huis & Ooninx, 2017). Recent estimates suggest that the CO₂

production can be up to 20 times lower than livestock industries of beef and lamb (Halloran et al., 2017; see Figure 3a; see also references in <https://www.carboncloud.io/carbondata/>) because insects are more efficient at converting food into biomass, although food conversion rates might vary depending on the life

stage and/or the nutritional composition of the edible insect diet (Berggren, Jansson, & Low, 2019). Nonetheless, rearing edible insects is relatively cheap, making insect farming an attractive business for large-scale production. This has prompted countries to establish official institutions to control and regulate insect production and commercialization. The European Union has initiated an International Platform of Insects for Food and Feed (IPIFF) to advance the production of insects for human and animal consumption (<http://ipiff.org/>). This initiative was taken largely in response to—and in preparation for—the surge of the edible insect market which in the USA is predicted to grow and potentially reach \$1.18 billion USD by 2023 (Figure 3b). Importantly, the growing value of the edible insect market provides a unique opportunity for developing countries in Latin America and Africa, where edible insects are culturally accepted, to exploit this opportunity for economic growth and gain a leading edge on the market.

2.2 | Regulating services: Mass-rearing and biological control

Insects pests and disease vectors are nuisances to humans. The use of pesticides to control pests and vector populations can be detrimental to the wellbeing of humans and the environment (Grewal, Singla, Kamboj, & Dua, 2017; Pimentel et al., 1993). An alternative to pesticides is the sterile insect technique (SIT) which aims to decrease the negative impact of pests and/or vectors by introducing sterile individuals (usually males although in some cases, both sexes) into wild populations (Dyck, Hendrichs, & Robinson, 2006). These sterile males are expected to mate with wild females which will then fail to produce viable offspring, thereby gradually decreasing population numbers (Lees, Gilles, Hendrichs, Vreysen, & Bourtzis, 2015; Zhang, Lees, Xi, Bourtzis, & Gilles, 2016; Figure 4). However, for SIT to yield positive results, millions (perhaps billions) of sterile individuals need

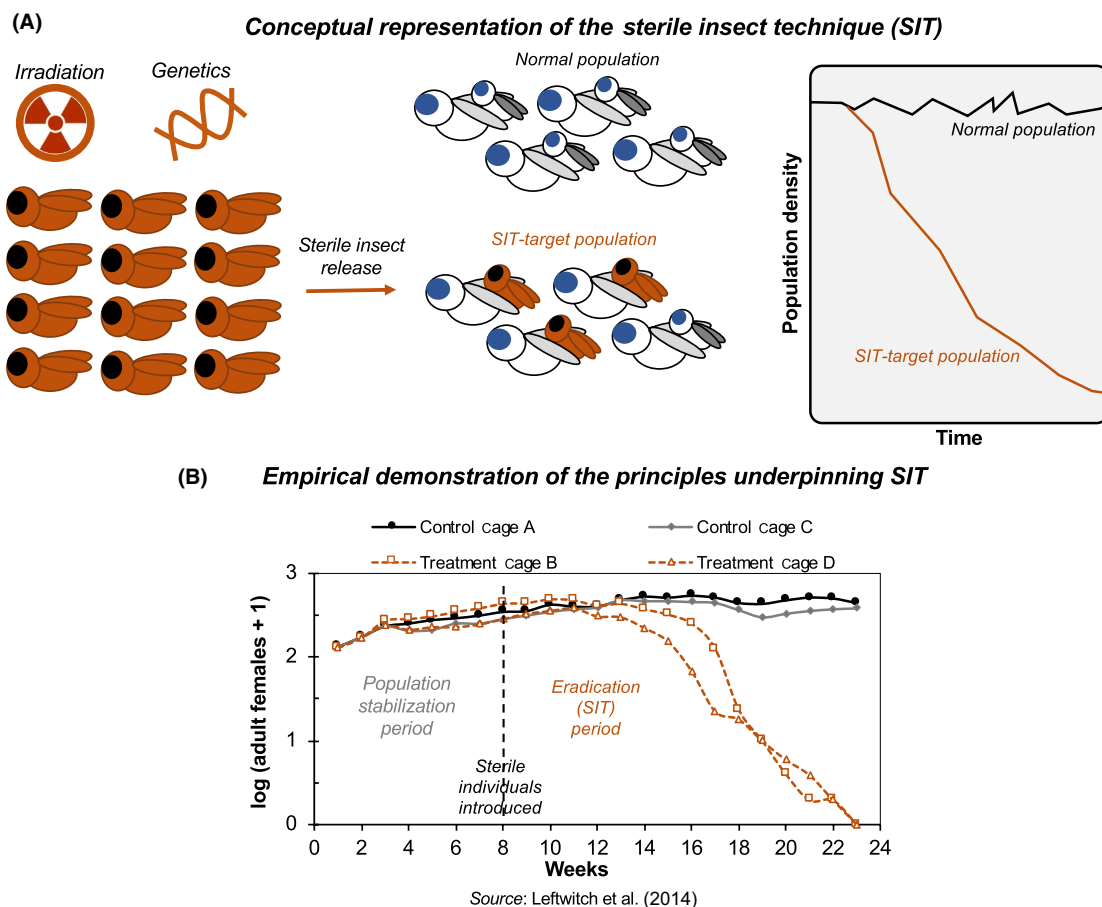


FIGURE 4 Sterile insect technique (SIT) principles. The aim of SIT is for the sterile males to mate with wild females which will then fail to produce viable offspring, thereby gradually decreasing population numbers (Lees et al., 2015; Zhang et al., 2016). SIT has been used to control the populations of many pests such as the medfly *Ceratitis capitata* (Augustinos et al., 2015; Hendrichs, Robinson, Cayol, & Enkerlin, 2002), the Queensland fruit fly *Bactrocera tryoni* (Meats, Duthie, Cliff, & Dominiak, 2003), the olive fly *Bactrocera oleae* (Ant et al., 2012; Estes et al., 2012) and vectors such as *Aedes aegypti* and *Aedes albopictus* (Araújo, Carvalho, Ioshino, Costa-da-Silva, & Capurro, 2015; Bellini et al., 2007; Carvalho et al., 2015). (A) SIT conceptual representation. Sterile individuals of the target species are raised in mass-rearing facilities. Sterility is achieved either by irradiation with X-rays and gamma-rays or by genetic manipulations. Sterile males are released in the wild population (two-sex releases can be performed for some target species). The aim is for sterile males to mate with wild females and cripple successful offspring production. Over time, the SIT-target population should decline in numbers. (B) Example from the literature of the principles and effectiveness of SIT (Leftwich et al., 2014). Control cages did not have the genetic sterilization manipulation; Treatment cages experienced SIT with genetically sterilized males

to be released in a given area and period of time (e.g. Esteva & Mo Yang, 2005; Ito, 1977). These unprecedented numbers of sterile individuals can only be obtained through the mass-rearing of the target species in specialized facilities ('factories'). In the factories, mass-rearing fundamentally requires the optimization of the conditions for individual growth (e.g. larval density and diet of colonies; Cerutti, Bigler, Eden, & Bosshart, 1992; Chang, 2009; Kaspi, Mossinson, Drezner, Kamensky, & Yuval, 2002; Khan, 2013; Moadeli, Taylor, & Ponton, 2017), which is crucial for two reasons. First, research has shown that insects' developmental conditions plays a major role on determining life-history traits and fitness of adults—sterile or not (Engels & Sauer, 2007). If the conditions are poor or sub-optimal, sterile adults are bound to have low fitness and fail to fulfil their role after release, meaning that the SIT program will likely fail to attain its objectives. Second, mass-rearing factories are costly (Caceres, Rendon, & Andrew, 2012) and if conditions are not optimized, mass-rearing factories are likely to experience a significant loss of capital on waste (e.g. needless excess of larval diets). This will affect the cost-benefit of running the factory due to an unprofitable business model, which in turn becomes too expensive for the private and/or public sectors to fund its activities, ultimately impacting economic growth, food security and disease control. Overall, though insect mass-rearing for biological control provides an important ecosystem service to mitigate the negative effects of pests and disease vectors.

Interestingly, mass-rearing for biological control provides the methodology and infra-structure which could underpin the up-scaling of the edible insect production and growth of edible insect markets (Hanboonsong et al., 2013; Morales-Ramos, Rojas, & Shapiro-Ilan, 2014). This is because in theory, mass-rearing is a viable way to produce millions of edible insects needed to support, in an affordable way, the dietary needs of local communities. This possibility remains to be explored. However, two factors currently limit human's potential to couple mass-rearing edible insect production: an *intrinsic* and an *extrinsic* factor. The intrinsic factor refers to the biology of the target edible insect species and is largely inflexible. For instance, species with long life cycles are unlikely to be profitable for commercialization given the long lagging period of laborious (and costly) work between the start of the process and the end product. Thus, only edible insect species with fast life cycles are likely suitable for a profitable mass-rearing program (Durst, Johnson, Leslie, & Shono, 2010). The extrinsic factor refers to societies' perception on the matter of replacing traditional protein sources for edible insects; this is therefore flexible (although difficult to change). In fact, market models revealed that consumers' perception and acceptance of edible insects is the main barrier for edible insect commercialization (DeFoliart, 1999; Rich, 2006). Therefore, both intrinsic and extrinsic factors are hurdles that need to be overcome to allow for the commercialization of edible insects in profitable scales. More research is needed on the life-history traits, dietary needs and biology of edible insects world-wide to select the best candidates for the market and identify new species that can fulfil the market's demands in an affordable way (Durst et al., 2010; see Box 1 of 'Outstanding Questions').

BOX 1 Outstanding questions

Regulating, provisioning and supporting services

- What are the most appropriate edible insect species for large-scale production in a profitable fashion?
- What are the potential risks and benefits—to individuals, societies and the economy—of large-scale edible insect commercialization? Moreover, what are the potential unintended ecosystems disservices of large-scale edible insect commercialization?
- What are the nutritional consequences of insect feeding for health and wellbeing?
- Can edible insects mitigate the burden of malnutrition in regions with nutritional deficiencies?
- What is (if any) the most profitable business model for supporting large-scale mass-rearing of insect larvae for SIT and/or insect-as-food?
- Can SIT factory operation models be adapted for the production of edible larvae of other insect species?
- Can the use of larvae to degrade plastic be scaled-up to match the vast plastic production and use of the 21st century?
- Is it possible to couple the processes of larval plastic degradation and larval biofuel production to convert plastic into renewable energy through larval nutrition?
- What are the larval diets and larval nutrient requirements to maximize biofuel production yield and quality?
- Is larval biofuel production a profitable alternative to non-renewable energy?
- What is the molecular profile and function of the toxins in the venom of *Lonomia* and *Perreyia* species?

Cultural services

- What cultural services are present in indigenous communities and is it possible to translate their cultural value into economic currencies to fit the ecosystem services framework?
- Is it possible to catalogue cultural services across indigenous communities to gain insights into their sustainable relationship with nature?

3 | UNCONVENTIONAL ECOSYSTEM SERVICES: THE ROLE OF INSECT LARVAE

In addition to the traditional services described above, insects can help humanity address current challenges in unconventional ways. As mentioned in Section 1, morphological and ecological differences between insect life stages open up the possibility for ecosystem services to be delivered by both larval and adult stages. Yet, the majority of described insect ecosystem services that are exclusive of—or attributed primarily to—adults. This includes for

example pollination, ecotourism and biological control via SIT (e.g. Dyck et al., 2006; Noriega et al., 2018; Prather & Laws, 2018). Only in few cases are ecosystem services provided by the larvae highlighted, mostly within the contexts of edible insects (Ramos-Elorduy et al., 2011) or wound healing practices in medicine (Shi & Shofler, 2014). Despite this, there is astounding diversity of insects that possess a larval stage during development (also known as 'holometabolous insects', Figure 5) and therefore is likely that at least some larvae can provide life stage-specific ecosystems services to humankind. Below, I describe examples of a wide range of ecosystems services that are provided by insect larvae. Acknowledging these services—and more broadly, the opportunity to explore life stage-specific ecosystems services—can prove useful for the future sustainable development of culturally diverse societies.

3.1 | Supporting services: Plastic-degrading larva

Plastic is one of the most practical yet environmentally destructive inventions of humankind. Up to a trillion plastic bags are

used world-wide per year, with only one in 200 being recycled (<https://conservingnow.com/plastic-bag-consumption-facts/>). More than >90% of plastic production relies on polyethylene (PE) and polypropylene (PP; <https://www.plasticseurope.org/en>), which make these compounds the primary target of waste management and recycling to mitigate the environmental burdens of plastic. It turns out that insect larvae (and their gut bacteria) can degrade PE (Yang et al., 2015; but see also Weber, Pusch, & Opatz, 2017; Figure 6a). Two studies have recently shown that caterpillars of two wax moth species (i.e. *Plodia interpunctella* (Lepidoptera: Pyralidae; Yang, Yang, Wu, Zhao, & Jiang, 2014) and *Galleria mellonella* (Lepidoptera: Pyralidae; Bombelli, Howe, & Bertocchini, 2017) can rapidly degrade PE into ethylene glycol (the product of PE degradation). Larvae can also degrade polystyrene (PS) and Styrofoam as recently shown in *Tenebrio molitor* larvae (Coleoptera: Tenebrionidae). These results demonstrate that larvae can provide an important supporting ecosystem service by acting as a bio-degrading agent of plastic, thereby opening up the potential to help humanity mitigate the serious environmental threats of plastic pollution.

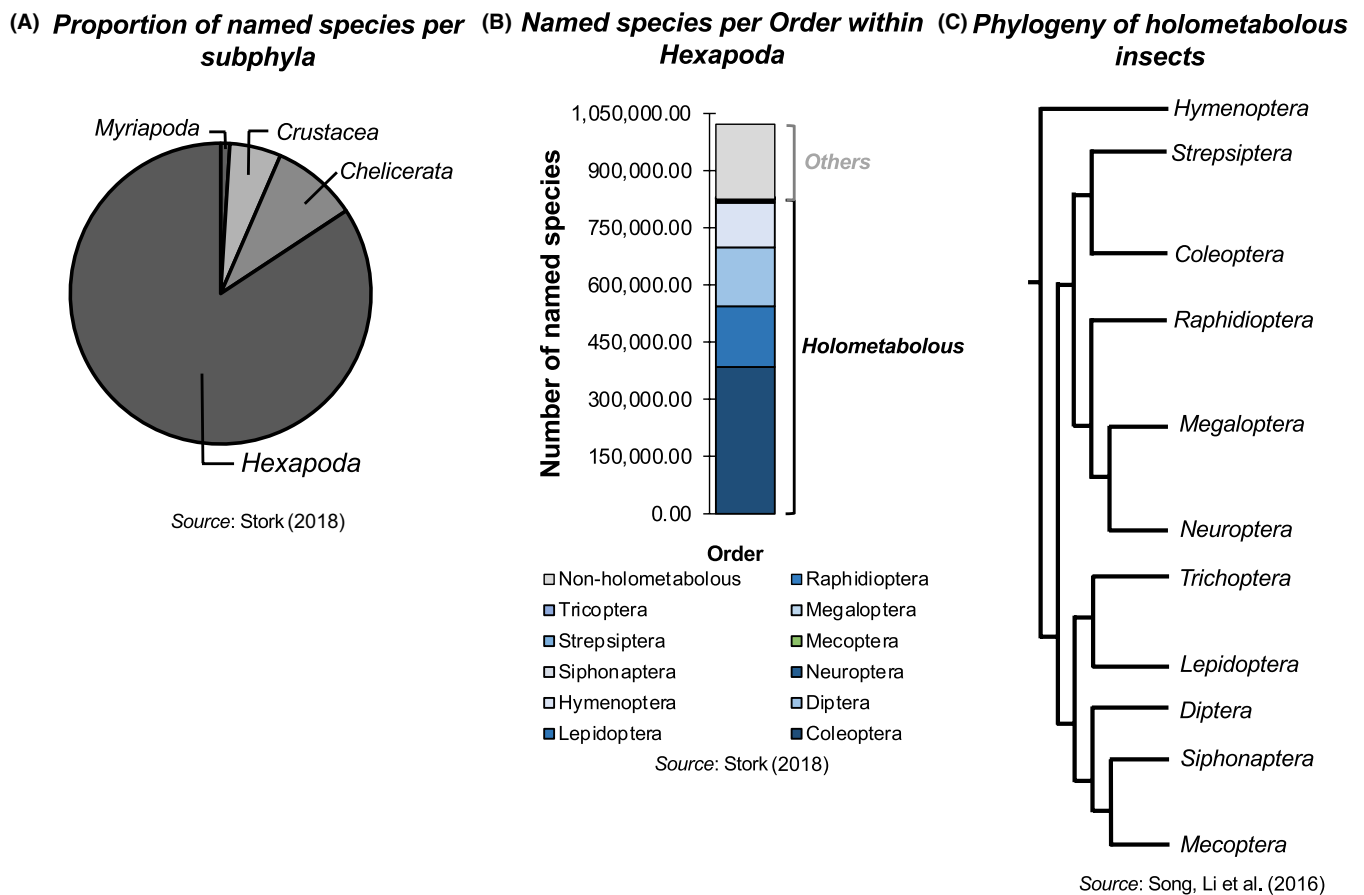


FIGURE 5 Overview of holometabolous insects. (A) Visual representation of the proportion of named species of (living) arthropods. (B) The number of named species per Order within Hexapoda. Note that holometabolous insects represent the vast majority of named species. Most holometabolous species (816,000) belong to four major Orders: Coleoptera (beetles; 387,000), Lepidoptera (moths and butterflies; 157,000), Diptera (flies; 155,000) and Hymenoptera (bees and ants; 117,000) (Stork, 2018 and references therein). Other holometabolous insects Orders include Neuroptera (5,868), Siphonaptera (2,075), Mecoptera (757), Strepsiptera (609), Megaloptera (354), Tricoptera (354) and Raphidioptera (254); (C) Phylogenetic relationship amongst holometabolous insects constructed with nuclear genes (Peters et al., 2014)

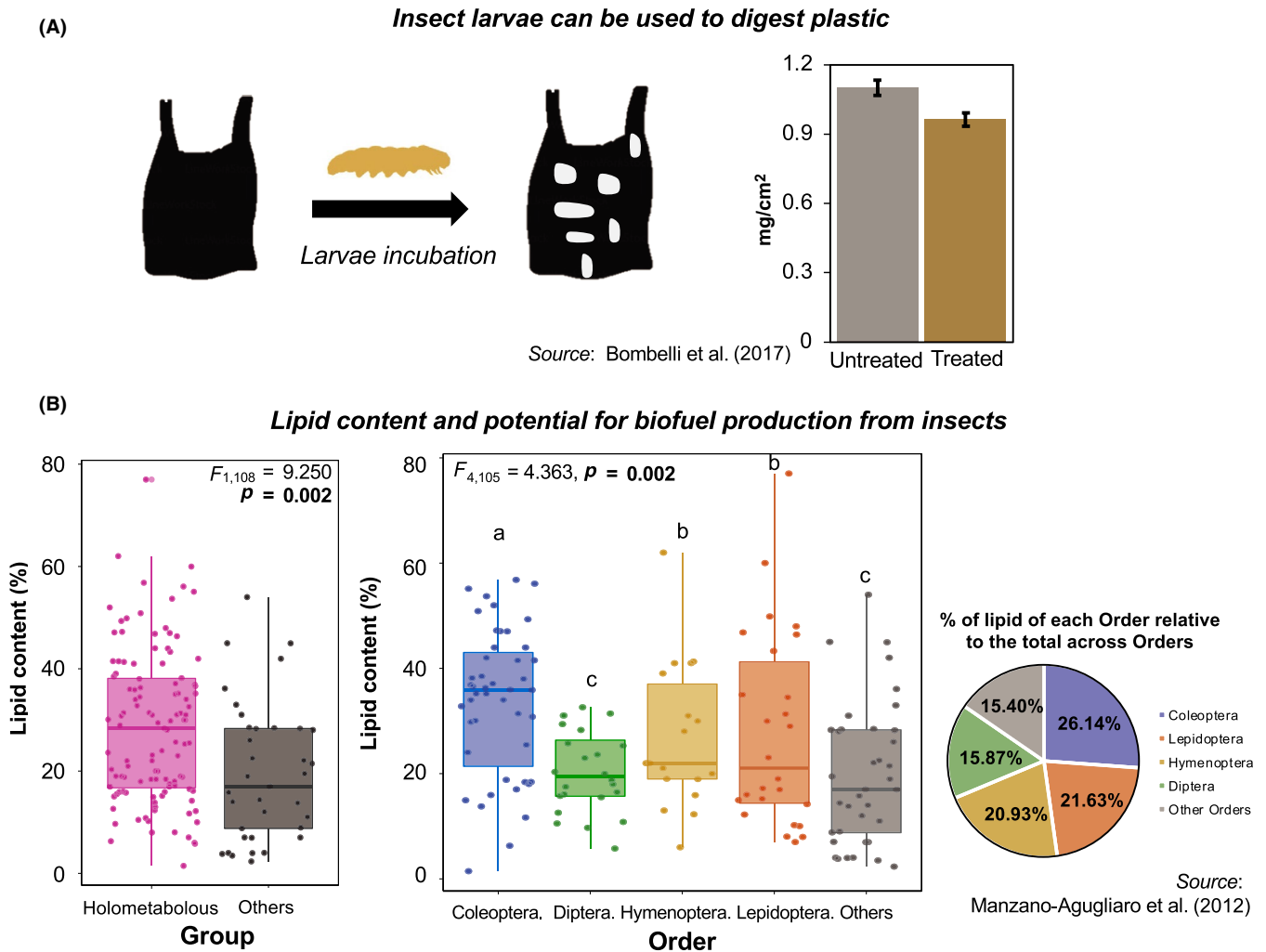


FIGURE 6 Larvae can degrade plastic as well as be used to produce biofuel. (A) Larva of wax moths can degrade plastic. Gravimetric data (right panel) shows the loss in mass of plastic bags after incubation with the larvae. (B) Lipid content (%) present in holometabolous insects compared with non-holometabolous insects (left panel) as well as a comparison of lipid content by main holometabolous insect Orders (right panel). F -values and p -values were obtained using a GLM regression with Poisson family and *quasi* extension with square-root link function in R. Letters represent differences between groups from Student–Newman–Keuls (SNK) posthoc test from the *AGRICOLAE* package in R (Mendiburu & Simon, 2015; R Core Team, 2019). Representativity displays the percentage of lipid storage per group relative to the total percentage of lipid storage, highlighting Orders with greatest percentage of fat storage and, consequently, highest potential for biofuel production. Complete table of lipid content is given in Data S1

3.2 | Provisioning services: Larval biofuel production

Burning non-renewable energies (e.g. fossil fuels) is a major contributing factor to climate change (Jakob & Hilaire, 2015; McGlade & Ekins, 2015). New approaches designed to produce cleaner and renewable energy sources are urgently needed (Ellabban, Abu-Rub, & Blaabjerg, 2014). An innovative approach involves chemically modifying and utilizing the extractable fat from insects, particularly the larvae, as biofuel (Li, Zheng, Cai, et al., 2011; Li, Zheng, Qiu, et al., 2011; Zheng, Li, Zhang, & Yu, 2012). Holometabolous insects have relatively higher percentage of fat stored (Figure 6b), which can translate into higher biofuel yield (Manzano-Agugliaro et al., 2012). Amongst holometabolous insects, the percentage of fat stored can vary greatly between Orders (Manzano-Agugliaro et al., 2012),

whereby on average, Coleopterans have a higher percentage of fat followed by Hymenoptera and Lepidoptera with intermediate levels and Dipterans with the lowest percentage of fat which is comparable to non-holometabolous insects (Figure 4b). Notably, the larvae of some species can have unexpected high percentages of fat as seen in the wasp *Polistes instabilis* (Hymenoptera: Vespidae) which has a fat percentage of >60% and a staggering 77% in the moth *Phasus triangularis* (Lepidoptera: Hepialidae; Ramos-Elorduy et al., 1997). This suggests that larvae are an unprecedented source of fat for biofuel production and a promising way to move forward into the renewable energy era (Gold, Tomberlin, Diener, Zurbrügg, & Mathys, 2018; Manzano-Agugliaro et al., 2012; Souza, Seabra, & Nogueira, 2018).

One way to produce larval biofuel is through the recycling of organic waste and livestock manure (supporting ecosystem service; Li, Zheng, Cai, et al., 2011; Varelles, 2019), although this approach

is unlikely to succeed for the larvae of all species. Having said that, cattle, pig and chicken manure can be used for growing larvae of the black soldier fly *Hermetia illucens* (Diptera: Stratiomyidae; Li, Zheng, Cai, et al., 2011). Chicken manure—which has highest ratio of nitrogen-to-carbon ('N:C ratio') amongst these animals (Huang et al., 2017)—led to the highest larval biofuel yield (Li, Zheng, Cai, et al., 2011; Data S2), suggesting that manure nutritional value influences biofuel yield and potentially, biofuel quality. Further studies in this field are needed. Nonetheless, the provisioning (biofuel production) and supporting (manure recycling) ecosystem services provided by the larvae can become the 'go-to' mechanism to convert organic waste and manure into a useful clean-energy product.

3.3 | Provisioning services: Larvae, life and death

In South America, the larvae of two moth species of the *Lonomia* genus [i.e. *L. obliqua* and *L. achelous* (Lepidoptera: Saturniidae); Figure 7a] have been associated with haemorrhage and death in humans (Arocha-Piñango & Guerrero, 2001; Chudzinski-Tavassi, Camargo, & Fernandes, 1999; Schmitberger et al., 2013; Zannin et al., 2003). The larva's venom has paradoxical effects. On the one hand, the venom act in vivo as procoagulant via the prothombin activator protein (Lopap) and the Factor X activator (Losac), resulting in systemic coagulation (Levi, 2001). On the other hand, this systemic coagulation is followed by depletion of coagulant factors due to fibrinolytic activity (also known as 'consumption coagulopathy', Levi, 2001) which increases the risk of haemorrhage (i.e. haemorrhagic

syndrome; Alvarez Flores, Zannin, & Chudzinski-Tavassi, 2010; Berger et al., 2010; Carrijo-Carvalho & Chudzinski-Tavassi, 2007). The clots induced by the procoagulant activity of the venom can also contribute to blockage of minor veins and arteries thereby inducing organ failure and aggravating the clinical symptoms of the patient (Alvarez Flores et al., 2010). While the venom is a complex cocktail of molecules with a variety of functions, the venom's compounds are now being studied as a model for the mechanisms underpinning haemorrhagic syndrome and thrombosis, opening up new possibilities to develop treatments to improve blood coagulation using (principles drawn from) the larvae's venom properties (Ramos, Gonçalves, Ribeiro, Rocha Campos, & Sant'Anna, 2004; Veiga, Ribeiro, Guimarães, & Francischetti, 2005). Other species also possess toxic compounds such as the sawfly *Perreyia flavipes* (Hymenoptera: Pergidae) which has been implicated in natural intoxication of livestock and thus presents an unexplored study organism for the discovery of novel compounds with putative clinical properties (Dutra, Riet-Correa, Mendez, & Paiva, 1997; Raymundo et al., 2012; Soares et al., 2001).

3.4 | Cultural services: Insect larvae in Aboriginal culture

Cultural services are perhaps the hardest to define in scope and impact within the framework of ecosystem services (e.g. Daniel, Muhar, Arnberger, et al., 2012; Daniel, Muhar, Aznar, et al., 2012; Kirchoff, 2012). Nonetheless, there are clear instances where



FIGURE 7 Unconventional ecosystem services in medicine and cultural heritage. (A) The poisonous *Lonomia obliqua* caterpillar (Lepidoptera: Saturniidae; Location: Curitiba, Paraná, Brazil). Credits: Anuska Nardelli. (B) Case moth *Metura elongatus* (Lepidoptera: Psychidae) specimen (Location: Ryde, New South Wales, Australia). Credits: Juliano Morimoto

cultural ecosystem services provide the window to better understand the culture of a society. The elements of these cultural services—e.g. the agents or heroes of stories—can provide a unique perspective into the way through which societies interact with their version of the world. A clear example of this cultural service can be found in Aboriginal culture in Australia. Aboriginal and Torres Strait Island culture relies on storytelling to make sense of the world around (Pfister, 2000). Amongst many stories (also known as 'Dreamtime stories'), the larvae of an insect is the essence of at least one, which features the case-moth *Metura elongatus* (Lepidoptera: Psychidae) (Figure 7b):

A Queensland hunter went on a long journey, taking his small son with him. It was hard for the little boy to keep up with his father, and day by day he grew thinner and weaker. Then came the rains. They fell without stopping until rivers rose and the land became one vast swamp. The little boy became ill. The only thing his father could do was to build a rough shelter of bark and branches of trees to keep the rain off him. Their food supplies had long been exhausted, and the man knew that his son would die if he was not given nourishing food quickly.

He tucked the boy up in his kangaroo-skin rug and splashed through the marsh in search of game. It was not easy to find in the flooded land, but after several days he found a possum and killed it with his spear. He hurried back to the gunyah [an Aboriginal hut] he had built, fearful that he might find his son lying there dead from starvation.

He arrived at the clearing, which he recognized by the broken branches of trees and the little mound that rose above the water, but of the gunyah and his son there was no sign. He could not understand what had happened. He had been prepared to find his son's body, but the last thing he imagined was that it, and the little gunyah that sheltered it, would have disappeared as through by magic.

He leaned against a tree. His hand came in contact with a loose knob of bark and twigs on the trunk. He looked at it idly and then, with a sudden sense of shock, more closely, for it was a replica of the little gunyah he had built to shelter his son. He opened it with trembling fingers. Inside the case lay the white body of a grub, and he knew that the spirits had taken pity on the boy and saved him from death.

To this day the grub of the case-moth always has a gunyah which it builds to protect it, and remind it of how, long ago, a father cared enough for his son

to build a shelter for him while he sought for food. (Source: http://rmwebed.com.au/web_resources/ab_culture/dreamt_case_Moth.htm).

Cultural services are likely to be common amongst indigenous communities, yet unknown to modern societies. Stories such as this provide invaluable insights into the relationship between indigenous communities and the environment, serving as unique cultural ecosystem services that still need to be widely acknowledged and protected.

4 | CONCLUSION

Ecosystems services provide an important framework to bridge the intrinsic value of natural resources with socio-economic monetized systems (Millennium Ecosystem Assessment, 2005). Insects play a pivotal role across many of the provisioning, regulating, supporting and cultural services that are categorized within the ecosystem services framework (Noriega et al., 2018). Yet, most traditional ecosystems services provided by insects are associated primarily with the adult stage (Prather & Laws, 2018; Schowalter et al., 2018). By describing unconventional ecosystem services provided by insect larvae, this paper highlights the importance of understanding and recognizing life stage-specific insect ecosystem services. It is likely that early developmental stages of non-holometabolous insects and vertebrates (e.g. fish, anurans) can also provide additional ecosystem services than those provided by adults (e.g. DeGarady & Halbrook, 2006; Firmiano et al., 2017; Igulu et al., 2014; Laegdsgaard & Johnson, 2001). Therefore, the holistic perspective of ecosystem services presented here is essential for the sustainable development of societies that recognize and cherish the complex relationship of humanity with all elements of its environment. This holistic view is significant above and beyond any limitations of the ecosystem services framework (e.g. Schröter & van Oudenhoven, 2016; Silvertown, 2015; Wilson & Law, 2016) because it integrates the diversity of functions and cultural knowledge that can be found across societies. In the long-term, such holistic view and the appreciation of the diversity of ecosystem services available to humanity might be the key for our success in addressing major global challenges while fostering culturally diverse societies.

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CONFLICT OF INTEREST

The author has no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available in this manuscript and the referenced literature.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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