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Bats and rice: promoting integrated pest
management to enhance biodiversity conservation

Carme Tuneu-Corral

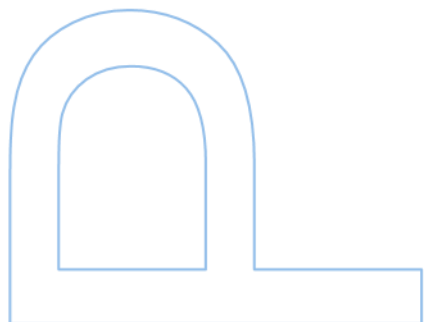
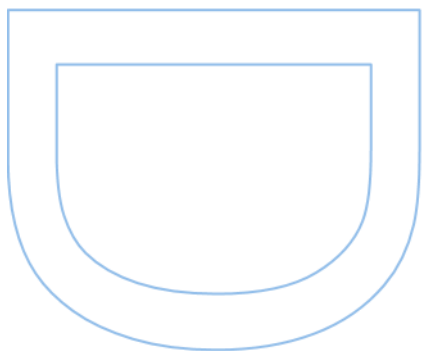
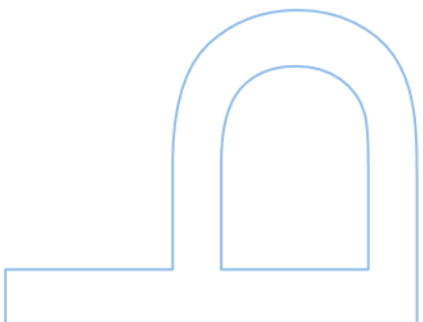
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Doctoral Program in Biodiversity, Genetics and Evolution
Faculty of Sciences of the University of Porto, Department of Biology
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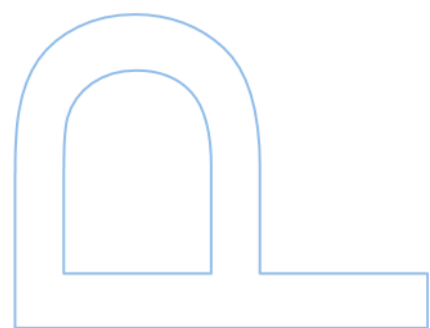
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*A la meva mare i al meu pare,
les persones més inspiradores que tinc al costat.*

Foreword

In compliance with the no. 2 of article 4 of the General Regulation of Third Cycles of the University of Porto and with the article 31 of the Decree-Law no. 74/2006 of 24 March, with the alteration introduced by the Decree-Law no. 230/2009, of 14 September, the results of already published works were totally used and included in some of the chapters of this dissertation. As these works were performed in collaboration with other authors, the candidate clarifies that, in all these works, participated in obtaining, analysing, and discussing the results, as well as in the writing of the published forms.

The Faculty of Sciences of the University of Porto was the home institution of the candidate, and the work was supervised by Dr. Adrià López-Baucells and co-supervised by Dr. Hugo Rebelo and Dr. Mar Cabeza. The work was developed at CIBIO-InBIO, Research Center in Biodiversity and Genetic Resources, Vairão, Portugal; as well as at the Natural Sciences Museum of Granollers (as a member of the BiBio research group), Granollers, Spain.

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It has been four years since I embarked on this PhD project. Four years that have flown by, a testament to both the joy and hard work involved. Four years full of learning, experiences, a pandemic, lockdowns, travelling, challenges, setbacks, solutions, and adventure. I started my PhD in March 2020, just as Covid-19 arrived in Europe. With a first expedition to Madagascar planned and flights already booked, this pandemic brought significant changes in the initial conception and structure of my project, which was originally intended to be conducted entirely in Madagascar. This country's borders remained closed for nearly two years, which forced me to seek for alternative plans and scenarios to redirect my research. However, with the unconditional support of a great team, family, friends and institutions, this thesis has turned out to be a beautiful project of which I am very proud.

Firstly, I would like to express my immense gratitude to the **FCT** for the financial support in the form a PhD grant that provided me with a salary during four years. I am deeply thankful to **Nestlé** and the **Ministry of Science and Innovation of the Spanish Government**, which funded fieldwork in Spain, and **National Geographic Society**, **Bat Conservation International**, and **Barcelona Zoo Foundation** for funding fieldwork expeditions in Madagascar. I also want to thank the **British Ecological Society**, the **BIODIV PhD Program** of the University of Porto and **CIBIO-BIOPOLIS**, for providing financial assistance to which enabled me to attend some of the most important international conferences during the development of my thesis. Without the support of all these institutions this thesis would not have been possible.

Behind this project there is a lot of effort, hard work, perseverance, motivation, enjoyment, confidence, and passion. I learned all this qualities at home, with my family. Aquest projecte no hauria set possible sense molt d'esforç i feina dura, perseverança, motivació, diversió, confiança, i passió. I tot això no ho he après a cap a escola ni a cap universitat, això ho he après a casa, amb la meva **família**. Gràcies **Mama i Papa** per ensenyar-me tots els valors que avui considero fonamentals i indispensables a la meva vida. No existeixen paraules suficients per agrair tot el que heu fet i feu per mi. De vosaltres he après les grans lliçons: m'heu ensenyat que perseguir allò que realment vull, allò que m'apassiona i em fa feliç, és una obligació. Tot i les incomptables vegades que us he fet patir anant a llocs recòndits del món (Llatinoamèrica, Nepal, Camerun, Zàmbia, Namíbia, Madagascar...) sempre heu respectat les meves decisions i m'heu donat recolzament infinit. M'heu encoratjat i animat en els moments difícils, m'heu escoltat i m'heu donat la confiança necessària per seguir avançant, perquè heu cregut en mi. Gràcies per ser com sou, les persones amb el cor més gran que conec i a qui més admiro. **Lluís**, el germà gran que sempre ha cuidat de les nenes,

un dels meus grans referents durant tota la meva infància i adolescència, del que he après molt més del que es pensa. Per mi ets una persona molt important i un gran recolzament. Gràcies per ser-hi sempre que no he necessitat! Estic molt orgullosa de tenir-te al costat. **Maria**, la meva germana, la meva bessona, i la meva millor amiga. No hi ha persona al planeta amb qui estigui més connectada, amb la que comparteixi i empatitzi tant. Amb tu hem descobert la vida agafades de la mà, compartint la passió per la natura. Gràcies pel teu suport infinit, per tants riures, llàgrimes i abraçades. Gràcies per ser-hi sempre! Gracias **abuelo y abuela**, i **gràcies iaia Maria i avi Lluís**. Allà on sigueu, sento que heu set i sou guies que m'heu transmès grans valors en la meva infància, i que ho seguïu fent ara a través del meus pares, els vostres fills. Ells em segueixen donant les lliçons de vida i d'amor incondicional que vosaltres els hi vau ensenyar. Gràcies **Lili**, per ser també un referent per mi quan era petita i per ensenyar-me amb passió tantes coses. Els ocells de Madagascar t'encantarien! Gràcies **tietia Lourdes**, per la teva energia, sempre ajudant desinteressadament, sempre donant bons consells i transmetent bona vibra. Gràcies cosinet **Martí**, per tant moments de petits, i tantes abraçades de grans. I gràcies també a les millors companyes que podien trobar els joves de la família, **Anna i Gabi**! Gràcies també a la **Pili**, a en **David** i la **Marta**, per viure amb il·lusió totes les aventures que m'ha portat aquest doctorat. Em sento la persona més afortunada del món tenint la família que tinc al costat. Gràcies un cop més, sense tots vosaltres res del que estic fent hagués set possible. Us estimo fins al cel!

També hi ha família que, tot i que no és de sang, és imprescindible en la vida d'una mateixa. Persones amb qui he crescut, après, i viscut moments que quedaran gravats per sempre en la memòria. Amb qui he compartit infinites converses, reflexions i experiències de vida, de les bones i també de les no tant bones. Però sempre fent-nos costat. Persones amb qui la complicitat és infinita. Aquella gent amb el do d'espantar tristeses i preocupacions. Aquella gent que et fa feliç. Aquesta és la meva altra família de Centelles. Gràcies **Petxines** i gràcies a les meves estimades germanes i germans de la família **M&Ms. Núria**, això també va per tu. Gràcies per creure en mi i en aquest projecte. Gràcies per recolzar-me en totes les meves aventures i peripècies, i sobretot per ser un oasi de calma i desconexió, on la principal moneda de canvi és un palique, una filosofada que arregli el món, un petó o una abraçada. Per molt lluny que vagi, sempre se'm dibuixa un somriure a la cara quan us penso. Compartir la vida i part d'aquest projecte amb vosaltres, és un plaer que multiplica la felicitat. Sou un tresor que estimo amb tot el meu cor!

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una se senti que està exprimint la vida al màxim. Gràcies per ser-hi, per encoratjar-me quan ho he necessitat, per viure amb il·lusió el meu projecte i creure en que tot això val la pena. Gràcies per les expedicions furgoneteres tant a la muntanya com al mar, escalades, esquíades, acampades, i tantes altres aventures que son com una alenada d'aire fresc. Per les converses, la complicitat i també per les in comptables festes que fan que tornis a casa rebenat però revessant de vida (**Baró, Èric**, va per vosaltres també), gràcies! Sou d'aquella gent que fa vibrar, i sense vosaltres aquest camí hagués sigut un molt més pedregós. Us estimo!

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It has been almost 14 years since I first set foot in the university. I still remember that feeling of starting a new stage: new people, the big city, the faculty, great professors... The five wonderful years I spent at the Faculty of Biology at the University of Barcelona also marked a before and after. There, I deepened my passion for nature and conservation, together with great people whom I admire very much today. **Lorena, Laura, Claudia and Ana**, the first good friendships of that time. The kind that take care of you and with whom you laugh day in and day out. Thank you for such good times! **Bioclica**, where should I start with you? **Joan, Ainara, Xavi, Gerard, Miquel, Nacho, Edu, Anna, Violeta, Laura, Grego, Andrea**. Amazing, crazy and brilliant souls. We have a good collection of unforgettable moments everywhere: at the faculty, in the field, in wild and crazy parties, in Euskal Herria, or in our annual Christmas gatherings. You all have also been an inspiration and support throughout a long period of my life. Thank you for so many experiences, and for all those to come! Here I also want to thank the friends I met during my master's. Super motivated and talented people, with amazing life projects that have also been of great inspiration and admiration. Thanks **Albert, Carlos, Auxi, Pepo, Pau, Aida, Cami, Eladia, Mónica, Rodrigo, Lucas, Ana, Bet**. I hope our paths cross again someday!

Throughout my career as a student and biologist, there are some crucial pieces that gave firm footing to my first steps in the world of research: my mentors. I'm sure I would not be here today, submitting my PhD thesis, if I had not met **Marcelo H. Cassini** and **Diana Szteren**, great researchers and wonderful people who gave me the opportunity to work on behavioural ecology of sea lions and fur seals in Cabo Polonio (Uruguay). This experience opened my mind, and catapulted my motivation to continue doing wildlife conservation projects. I was 22 and that was my first real research project. While working in a paradise of sand, water, sun, and wildlife, I realised that yes, that was my passion, that made me the happiest human being in the planet, and that was what I wanted to dedicate my life to. I was the luckiest person in the world to meet you two, Marcelo and Diana. You guided me, supported me and took great care of me in Argentina and Uruguay, and also whenever I needed it once I returned to Catalonia. For the trust you placed in me, and for all that you taught me, I thank you enormously. From South America I jump now to Africa: thanks **Serge Kamgang** for letting me join your project on chimpanzee conservation in Cameroon. That was a mind-blowing and tough experience in equal parts, which made me a stronger, fighter, independent and more self-confident person. I am sure all this has benefited me during this period as a PhD student. **Iris and Elise**, empowered women working on great cats, you gave me a lesson in courage, comradeship and hard work in Cameroon. Meeting you made a big difference to my experience there and motivated me to keep fighting for what I wanted. Thank you so much!

I keep talking about great mentors, but there is a reason why I start a new paragraph: the world of bats begins. In 2018 and almost by chance, I had the privilege to join the bat team of the **Natural Sciences Museum of Granollers**. It was a small group of just four people, **Carles, Xevi, Adrià and Maria**, but their energy, motivation, ambition and enthusiasm felt like that of 400. At that time, I was looking for projects related to marine mammals or sharks, but then, yes, bats stole my heart. When you meet someone who lives and communicates their passion with such intensity, with eyes shining bright, it is impossible not to let it rub off on you. Thanks to these four amazing freaks I got into the fascinating world of bats, a universe where the more you learn, the more it attracts you, and the more you realise how much you have left to discover. Thank you Adrià, Maria, Carles and Xevi for teaching me so much, for believing in what you do, and for trusting me from day one. The truth is that bats were not the only ones that stole my heart. The bat group grew quickly, and we created a REAL family composed by many bat nerds. I learned hand by hand with this incredible people. We have shared wonderful projects and amazing fieldwork expeditions, and spent most of our day-to-day life, helping and supporting each other unconditionally (except when we play *futbolín*, then we are happily cruel, merciless and evil). You all are the best thing of doing science. Thanks **David** (I'll never forget our adventures in Madagascar), **Alba, Laura, Estel, Adrià Jr, Carol, Esther, Sergi, Diana,**

Marina, Cristina. In fact, our family extends beyond bats. We have formed a beautiful multidisciplinary team that has brought together even more geeks (birds of a feather flock together), without whom life at the museum would not be the same. Thanks **César, Carmeta B., Marc, Lúdia, Andreu, Clàudia, Tina, Constan, Eric M., Eric S., Ferran, Laura J., Lucia, Anna.** And of course, thanks **Toni Arrizabalaga**, for believing in us and in our crazy projects.

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chauves-souris, et à tous ceux qui se sont intéressés à ce que nous faisons. J'espère que nous nous reverrons très bientôt à Madagascar. Misaotra betsaka!

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Per últim, vull dedicar-li unes paraules a una persona molt important que va aparèixer just a l'inici d'aquest projecte. Una persona que també ha viscut el dia a dia d'aquest doctorat, que

ha conegut tot el seu recorregut amb les dues cares de la moneda: les bones i les no tant bones. Una persona que ha celebrat amb orgull els bons moments, i que ha endolcit els més difícils. Gràcies per creure en mi i en aquest projecte esbojarrat, i per recordar-me que jo podia arribar allà on em proposés. **Txel**, amb tu aquests quatre anys han sigut dels millors capítols de la meva vida. Gràcies pel teu suport incondicional i per tota la paciència, especialment en aquests darrers mesos. Tu sempre hi has sigut. Però sobretot, gràcies per respirar amb la mateixa il·lusió que jo aquest somni, i per emocionar-te amb cada descobriment. Després de tots els entrebancs inicials del projecte, poder-lo fer realitat ha estat espectacular, i compartir una part de l'aventura a Madagascar amb tu ha set la cirereta del pastís. Gràcies per ser-hi sempre i per fer aquest camí més apassionant. T'estimo.

Resumo

Ocupando quase 40% da superfície terrestre, a agricultura é essencial para a segurança alimentar e para o rendimento de áreas rurais. Um dos principais desafios que os agricultores enfrentam é lidar com as pragas agrícolas, especialmente os insetos, que causam perdas significativas nas culturas todos os anos. A nível mundial, o dano causado devido a pragas foi estimado em 18-40% do rendimento, e prevê-se que as alterações climáticas exacerbem estes efeitos. Nos países desenvolvidos, a intensificação da agricultura e a dependência dos pesticidas como principal método de controlo de pragas conduziram a repercussões indesejadas e imprevistas, tais como problemas associados à contaminação ambiental e elevados custos para a saúde humana. Nas regiões em desenvolvimento, as perdas agrícolas são muitas vezes compensadas pelo corte de floresta primária para criar novos terrenos para cultivo, sendo a desflorestação e a conversão do habitat os principais motores da perda de biodiversidade nestas áreas.

O arroz é o principal alimento para mais de metade da população mundial e estima-se que só as pragas de insetos provoquem perdas de cerca de 15% da produção mundial de arroz. Para resolver isto, a Gestão Integrada de pragas (GIP) tornou-se cada vez mais importante para impulsionar práticas sustentáveis de gestão de pragas. Uma estratégia eficaz de GIP é o controlo biológico, que promove a presença de inimigos naturais das pragas, como os morcegos, de forma a regular as populações de pragas. A maioria das espécies de morcegos são predadores vorazes de artrópodes, desempenhando um papel importante na agricultura através da redução dos níveis de pragas e dos danos nas plantações agrícolas, evitando assim também perdas económicas. Nas últimas décadas, um número crescente de estudos tem-se focado na avaliação dos serviços de ecossistemas que os morcegos prestam enquanto controladores de pragas agrícolas. No entanto, pouco se sabe sobre o seu papel nos arrozais e a magnitude dos benefícios que trazem como supressores de pragas desta cultura de importância mundial.

Esta tese pretende preencher algumas destas lacunas de conhecimento, avaliando os serviços de supressão de pragas mediados por morcegos em agrossistemas, com especial ênfase no arroz, e promover práticas sustentáveis que melhorem a biodiversidade através da conservação dos morcegos. Especificamente, pretendi (i) avaliar o estado do conhecimento do papel dos morcegos como inimigos naturais de pragas agrícolas a nível global, fornecendo recomendações para aumentar o seu potencial supressor em agrossistemas, (ii) quantificar os benefícios económicos dos morcegos como predadores de uma das pragas do arroz mais importantes no mundo: a traça da Broca-listrada-do-caule-do-arroz (*Chilo suppressalis*), (iii) investigar o efeito dos ultrassons dos morcegos na produção de ovos desta praga do arroz e,

finalmente, (iv) compreender o papel das áreas protegidas na provisão de serviços de supressão de pragas mediados por morcegos em plantações de arroz e outros agrossistemas fora das fronteiras destas áreas. O trabalho apresentado nesta tese foi realizado ao longo de quatro anos (2020 – 2024), incluindo vários períodos de recolha de dados no campo realizados em duas áreas de estudo: Espanha, um dos maiores países produtores de arroz da Europa, e Madagáscar, uma ilha fortemente dependente da agricultura de subsistência e da produção de arroz.

Para atingir o primeiro objetivo, realizei uma revisão sistemática da literatura para avaliar o estado atual do conhecimento e identificar as principais lacunas na compreensão dos serviços ecossistémicos prestados pelos morcegos como supressores de pragas em agrossistemas a nível global. Compilei da literatura científica também medidas de conservação e recomendações de gestão que podem favorecer a prestação deste importante serviço de ecossistema. Além disso, produzi uma rede global de interações entre morcegos e pragas de insetos, com 2.308 díades presas-predadores documentadas em todo o mundo. Para o segundo e terceiro objetivos da tese, realizei trabalho de campo em arrozais na Espanha. Utilizei quatro estruturas de exclusão para quantificar os benefícios económicos dos morcegos como predadores de *C. suppressalis*. Na ausência de morcegos, os danos nas plantas devido a esta praga duplicaram. Os meus resultados sugerem que os morcegos podem evitar perdas nas colheitas de quase 70 kg [4 – 147 kg] de arroz por hectare, o que pode traduzir-se numa poupança económica de 56€ [3 – 165€] por hectare e por ano. Extrapolando estas estimativas para a escala nacional da Espanha, os morcegos poderão potencialmente poupar até 7,6 mil toneladas de arroz, o que equivale a mais de 6 milhões de euros anuais. Por outro lado, para investigar o efeito da emissão de ultrassons por parte dos morcegos no sucesso reprodutivo da *C. suppressalis*, capturei um total de 188 traças e mantive-as em cativeiro durante toda a sua fase adulta. Metade das traças capturadas foram expostas a gravações acústicas que continham diversos chamamentos de ecolocalização de morcegos, enquanto a outra metade foi mantida numa sala de controlo sem a transmissão destes ultrassons. Esta experiência permitiu comparar a produção de ovos das fêmeas entre ambos os tratamentos. Observei que na presença de ultrassons de morcegos havia um menor número de ovos, sendo este número reduzido para metade. Estes resultados sugerem que os morcegos podem suprimir as pragas não só pela predação direta, mas também pela redução indireta do sucesso reprodutivo das populações de pragas através da emissão de ultrassons.

Por fim, estudei o papel das áreas protegidas de Madagáscar na prestação de serviços de supressão de pragas mediados por morcegos em paisagens rurais próximas. Capturei morcegos insetívoros dentro e fora de três áreas protegidas e recolhi amostras fecais para

estudar a sua dieta utilizando metabarcoding de ADN. Os meus resultados revelaram que a maioria dos morcegos insectívoros, tanto as espécies que usam exclusivamente áreas protegidas como as espécies sinantrópicas, consomem não só pragas importantes do arroz e de outras culturas, mas também vetores de doenças relevantes, como a malária. Os meus resultados sugerem que muitas espécies de morcegos que se abrigam em áreas protegidas (principalmente morcegos que vivem em grutas) podem ter a capacidade de voo para se deslocarem para locais de alimentação nas paisagens agrícolas próximas, contribuindo para a supressão de pragas de insetos e para a redução de vetores de doenças. Assim, as áreas protegidas não são apenas fundamentais para a conservação dos habitats naturais e da sua biodiversidade largamente endémica, mas também servem provavelmente como uma fonte importante de serviços ecossistémicos mediados por morcegos para as comunidades rurais para além das suas fronteiras.

Esta tese realça o papel fundamental dos morcegos nos sistemas agrícolas, destacando os seus contributos significativos para a agricultura sustentável. Para além disto, fornece ferramentas de referência para agricultores, gestores da paisagem, governos e outras partes interessadas em promover e aplicar práticas ecológicas para gerir os insetos nocivos através da conservação dos morcegos. No entanto, são necessários maiores esforços na síntese e divulgação dos resultados científicos em formatos acessíveis para influenciar eficazmente os decisores políticos e os gestores da paisagem. A gestão adaptativa e as abordagens baseadas na comunidade são essenciais para uma conservação eficaz, juntamente com estratégias interdisciplinares, como o uso de certificados ecológicos e a integração das ciências sociais. Finalmente, esta investigação apela a uma maior sensibilização, educação e apoio político para promover a agricultura sustentável e garantir a segurança alimentar a longo prazo, beneficiando tanto os ecossistemas como o bem-estar humano.

Palavras-chave: morcego, agroecossistema, controlo biológico de pragas, revisão sistemática, produção de arroz, interações multitróficas, ovoposição, dimensão acústica, avaliação económica, agricultura de subsistência, conservação da biodiversidade, Espanha, Madagáscar

Abstract

Covering nearly 40% of Earth's surface, agriculture is essential for food security and rural income. One of the main challenges farmers face is dealing with agricultural pests, especially insects, which cause significant harvest losses each year. Yield loss due to pests has been estimated at 18-40% globally, and climate change is expected to exacerbate these effects. In developed countries, agriculture intensification and the reliance on pesticides as the primary method of pest control has led to unintended and unforeseen repercussions, including evident problems of environmental contamination and high human health costs. In developing regions, crop losses are often compensated by cutting down primary forest to create new lands for cultivation, being deforestation and land-use conversion the main drivers of biodiversity loss in these areas.

Rice is the main staple food for over half the world's population and insect pests alone are estimated to cause losses of about 15% of the global rice production. To address this, Integrated Pest Management (IPM) has become increasingly important for boosting sustainable pest management practices. One effective IPM strategy is biological control, which promotes the presence of natural pest enemies, such as bats, in order to regulate pest populations. Most bat species are voracious predators of arthropods, playing an important role in agriculture by reducing pest levels and crop damage, and thereby also preventing economic losses worldwide. In recent decades, an increasing number of studies have focused on the assessment of the ecosystem services bats provide as controllers of agricultural pests. However, little is known about their role in rice paddies, and the magnitude of the benefits they bring as insect pest suppressors of this globally important crop.

This thesis aim to fill some of these knowledge gaps by evaluating bat-mediated pest suppression services in agrosystems, with a special focus on rice, and to promote sustainable practices that enhance biodiversity through bat conservation. Specifically, I aimed to (i) assess the state of knowledge of the bats' role as natural enemies of agricultural pests at a global level, providing recommendation for enhancing their suppressive potential in agrosystems, (ii) quantify the economic benefits of bats as predators of one of the most widespread rice pests in the world, the striped rice stem borer moth (*Chilo suppressalis*), (iii) investigate the effect of bat ultrasounds on the egg production of this rice pest, and finally to (iv) understand the role of protected areas in the provisioning of bat-mediated pest suppression services in rice plantations and other agrosystems beyond their borders. The work presented in this thesis has been carried out over four years (2020 – 2024), including several periods of field data collection conducted in two very different study areas: Spain, one of the largest rice-producing

countries in Europe, and Madagascar, an island heavily reliant on subsistence agriculture and rice production.

To achieve the first objective, I conducted a systematic literature review to assess the current state of knowledge and identify the main gaps in understanding the ecosystem services provided by bats as pest suppressors in agrosystems globally. I also compiled conservation measures and management recommendations from scientific literature that may favour the delivery of this important ecosystem service. Additionally, I provided a global network of interactions between bats and insect pests, with 2308 documented prey-predator dyads from around the world. For the second and third objectives, I carried out fieldwork experiments in rice paddies of Spain. In one hand, I used four exclosures to quantify the economic benefits of bats as predators of *C. suppressalis*. In the absence of bats, the plant damage observed due to this pest doubled. My results suggested that bats might prevent crop losses of nearly 70 kg [4 – 147 kg] of rice per hectare, which can be translated to an economic saving of 56€ [3 – 165 €] per hectare each year. Extrapolating these estimates to the national scale, bats could potentially save up to 7.6 thousand tonnes of rice, amounting to over 6 million euros annually in Spain alone. In the other hand, to investigate the effect of bat ultrasounds on the reproductive success *C. suppressalis*, I captured a total of 188 moths and kept them in captivity cages throughout their entire adult stage. Half of the moths were exposed to acoustic recordings containing numerous bat echolocation calls, while the other half were kept in a control room without ultrasound broadcasting. This experimental set-up allowed me to evaluate the egg-production of females from both treatments. I observed that the clutches were smaller in the presence of bat ultrasounds, with the number of eggs laid in each clutch being almost halved. These results suggested that bats may suppress pests not only by direct predation, but also by indirectly reducing the reproductive success of pest populations through the emission of ultrasounds.

Finally, I studied the role of protected areas of Madagascar in providing bat-mediated pest suppression services in nearby rural landscapes. I captured insectivorous bats inside and outside three protected areas and collected faecal samples to study their diet using DNA metabarcoding. My findings revealed that most insectivorous bats, both those roosting exclusively in protected areas and the synanthropic species, consumed not only important pests of rice and other crops, but also vectors of relevant diseases such as malaria. My results suggest that many bat species roosting in protected areas (mostly cave-dwelling bats) may have the flight capacity to move to feeding sites in the nearby agricultural landscapes, contributing to the suppression of pest insects and reduction of disease vectors. Therefore, protected areas are not only paramount for conserving natural habitats and their largely

endemic biodiversity, but they also likely serve as an important source of essential bat-mediated ecosystem services for rural communities beyond their borders.

This thesis underscores the pivotal role of bats in agricultural systems, highlighting their significant contributions to sustainable farming. It provides reference tools for farmers, land managers, governments and other stakeholders to promote and apply eco-friendly practices to manage harmful insects through bat conservation. However, there is still a need for increased efforts in synthesising and disseminating scientific findings in accessible formats to influence policymakers and land managers. Adaptive management and community-based approaches are essential for effective conservation, alongside interdisciplinary strategies such as eco-labelling and integrations of social sciences. This research calls for greater awareness, education, and political support to foster sustainable agriculture and ensure long-term food security, benefiting both ecosystems and human well-being.

Keywords: bat, agroecosystem, biological pest control, systematic review, rice production, multitrophic interactions, oviposition, acoustic dimension, economic valuation, subsistence agriculture, biodiversity conservation, Spain, Madagascar

Table of Contents

Foreword	iii
Acknowledgements	iv
Resumo	xi
Abstract	xiv
List of Tables	xx
List of Figures	xxii
Chapter 1 – General Introduction	1
1.1. Agriculture and evolution of the global human population growth.....	2
1.2. Agriculture vs nature conservation: farming intensification, forest loss and the Sixth Mass Extinction	3
1.3. Arthropod pests, Integrated Pest Management (IPM) and biological control	6
1.4. Bats, rice and pest suppression: the role of bats as insect predators	7
1.5. Knowledge gaps and research opportunities	9
1.6. General objective and thesis outline	11
1.7. Study system	12
1.8. References	14
Chapter 2 – Bat pest suppression at a global level.....	20
2.1. Introduction.....	22
2.2. Materials and methods	24
2.2.1. Bats as insect pest suppressors in agroecosystems	24
2.2.2. Bat–insect pest interactions	24
2.3. Results	26
2.3.1. Bats as insect pest suppressors in agroecosystems	26
2.3.2. Bat–insect pest interactions	31
2.4. Discussion	34
2.4.1. Bats as insect pest suppressors in agroecosystems	34
2.4.2. Bat–insect pest interactions	42
2.5. Conclusions	42
2.6. Acknowledgements.....	43
2.7. References	43
Chapter 3 – Quantification of bat-mediated rice pest suppression	60
3.1. Introduction.....	62
3.2. Materials and methods	65

3.2.1.	Study area	65
3.2.2.	Experimental exclosures installation	66
3.2.3.	Rice damage assessment.....	68
3.2.4.	Bat predation of the striped rice stem borer moth.....	70
3.2.5.	Economic quantification: Avoided yield loss and economic estimation	71
3.3.	Results	72
3.3.1.	Top-down effect of bat predation on pest populations	72
3.3.2.	Avoided yield loss and economic quantification of bat ecosystem services ..	75
3.4.	Discussion	75
3.4.1.	Top-down effect of bat predation on pest populations	77
3.4.2.	Avoided yield loss and economic quantification of bat ecosystem services ..	79
3.4.3.	Experiment limitations.....	80
3.4.4.	Implications for farmers and bat conservation	81
3.5.	Conclusions	82
3.6.	Acknowledgements.....	82
3.7.	References	83
Chapter 4 – Pest suppression effect of bat ultrasounds	91	
4.1.	Introduction.....	93
4.2.	Materials and meethods	95
4.2.1.	Study area	95
4.2.2.	Experimental enclosures.....	96
4.2.3.	Nocturnal soundscape recording and broadcast	96
4.2.4.	Moth captures	98
4.2.5.	Experimental design	98
4.2.6.	Statistical analyses	99
4.3.	Results	100
4.4.	Discussion	103
4.4.1.	Landscape of fear	103
4.4.2.	Integrated Pest Management.....	104
4.4.3.	Study limitations.....	105
4.5.	Conclusions	107
4.6.	Acknowledgements.....	107
4.7.	References	108
Chapter 5 – Protected areas and bat pest control in Madagascar	112	

5.1. Introduction.....	114
5.2. Materials and methods	116
5.2.1. Study area	116
5.2.2. Bat captures and faecal sample collection	118
5.2.3. DNA extraction and PCR amplification	119
5.2.4. Bioinformatic analyses	120
5.2.5. Diet description and statistical analyses.....	121
5.3. Results	122
5.3.1. General description of bat diet	122
5.3.2. Agricultural pest and disease vector consumption by insectivorous bats....	127
5.4. Discussion	134
5.4.1. General description of bat diet	134
5.4.2. Agricultural pest and disease vector consumption by insectivorous bats....	135
5.5. Conclusions	139
5.6. Acknowledgements.....	139
5.7. References	140
Chapter 6 – General discussion	149
6.1. Key findings.....	150
6.2. Integrating scientific research and ecosystem services in applied conservation planning.....	152
6.3. Engagement of local communities through biocultural approaches.....	154
6.4. Empowering bat conservation through general public involvement and national leadership.....	157
6.5. Eco-labelling strategies for sustainable agriculture: local realities and global perspectives	159
6.6. Concluding remarks.....	161
6.7. References	163
Appendix A – Supplementary Information	166
7.1. Supplementary information for Article I	167
7.2. Supplementary information for Article II	174
7.3. Supplementary information for Article III	184
7.4. Supplementary information for Article IV	187
Appendix B – Other publications during the PhD.....	190

List of Tables

Table 2.1. Agroecosystem types studied in the 66 articles located by our first literature search (LS1). Some articles considered more than one agroecosystem, and hence the total percentage does not sum to 100. 28

Table 2.2. Articles assessing the economic value of the ecosystem services provided by bats as agricultural insect pest suppressors organised by country and type of crop. Where valuations were made in the original study in other currencies these have been converted to US \$. Method: ACM, avoided cost model; BT, bene fit transfer model; EE, exclosure experiment. Bt, genetically modified pest-resistant variety..... 29

Table 2.3. Recommendation measures to enhance bat activity in agroecosystems taken from the reviewed articles. AS indicates the number of articles supporting each measure. Since more than one action was often recommended in a single article, the sum of the percentages is > 100. 30

Table 2.4. Bat species, IUCN conservation status and the number of agricultural insect pest species they were reported to consume. Data are only shown for bat species reported to consume more than 10 insect pest species; see Table A1.5 for the full list. IUCN categories: DD, Data Deficient; EN, Endangered; LC, Least Concern; NT, Near Threatened; VU, Vulnerable..... 32

Table 3.1. Relationship between “infested rice stems” and (i) Treatment (Control/Exclosure) and (ii) Julian day modelled with a GLMM with a Poisson distribution (N = 32), assessed in our sampling site in Huesca (Spain). 72

Table 3.2. Estimated values of cumulative plant damage (number of infested plants) over the entire study period in the plots (400m²) for each treatment and block. The difference in crop damage as well as the percentage of increased damage between treatments, have also been included in the table. 73

Table 3.3. Economic quantification of the ecosystem services provided by bats in the study area (Huesca, Spain) as suppressors of the striped rice stem borer moth. The values have been calculated considering (i) the treatment plot area (400m²), (ii) one hectare (ha) and (iii) the total area of rice plantations in Spain (109,411 ha). The amount of rice and euros saved by bats have been estimated based on the results obtained in each block, including also an average value of all four scenarios. Note that these values are expressed in kilograms (kg) and euros € when considering a surface of 400m² and 1 hectare, and in thousands of tonnes (KT) of rice and millions of euros (M€) when assessing the total area of rice crops in Spain. 76

Table 4.1. Generalised Linear Mixed Model (glmm.TMB) results for the model with the lowest AICc value assessing the effect of ‘treatment’ (control/ultrasounds) and ‘time’ on ‘clutch size’ (number of eggs in each clutch). Predictors with significant results (p-value < 0.05) are highlighted in bold, which indicates significant effects on the size of the egg clutches..... 102

Table 5.1. Number of distinct families, genera, and species found in bat faecal samples summarised to arthropod order level. Number of samples in which they occur, frequency of occurrence (FOO), percentage of occurrence (POO) and distinct OTUs detected for each arthropod order are also provided. 123

Table 5.2. Weighted percentage of occurrence (wPOO) of each arthropod order in the diet of the different bat species captured in the study. The values in brackets next to each species' name are the total samples collected for that species. The shaded rows show the values for *Chaerephon leucogaster* and *Mops leucostigma*, the two species captured exclusively outside protected areas. 124

Table 5.3. Summary of the number of distinct pests and disease vectors detected in the dry and wet seasons, along with their frequency of occurrence (%FOO) in the diet of the different bat species. Note that species are listed in descending order based on the total number of pests and disease vectors they consume. In the %FOO column, the number of samples collected for each species is shown in brackets. The shaded rows show the values for *Chaerephon leucogaster* and *Mops leucostigma*, the two only species captured exclusively outside protected areas..... 128

Table 5.4. Number of samples per bat species and %FOO in brackets for all identified agricultural pests (known and potential). Known and potential rice pest species are highlighted with an asterisk. The shaded columns show the values of pest detection outside protected areas, belonging to *Chaerephon leucogaster* and *Mops leucostigma*..... 131

Table 5.5. Number of samples per bat species and %FOO in brackets for all identified disease vectors (known and potential). The shaded columns show the values of pest detection outside protected areas, belonging to *Chaerephon leucogaster* and *Mops leucostigma*. 133

List of Figures

Figure 1.1 Global human population growth 10,000 BCE – 2000 CE. This graphic has been modified from OurWorldinData.org. Based on estimates by the History Database of the Global Environment (HYDE) and the United Nations. Licensed under CC-BY-SA by the author Maz Roser.	3
Figure 1.2. Forest burning to expand rice paddies in the surroundings of the Ranomafana National Park, Madagascar. © Adrià López-Baucells	4
Figure 1.3. Large-scale soybean harvest in Brazil. © Shutterstock/Haboski	5
Figure 1.4. Malagasy white-bellied free-tailed bat (<i>Chaerephon leucogaster</i>), endemic to Madagascar, foraging in a rice growing area. © Adrià López-Baucells & Joan de la Malla	8
Figure 1.5. Caterpillars damaging rice plants in Ramomafana, Madagascar. © Joan de la Malla	9
Figure 1.6. Farmer harvesting rice, the main staple food for Malagasy population, Madagascar. © Adrià López-Baucells.....	10
Figure 1.7. Study areas covered in this thesis. A) Agricultural region where the village of Alcolea de Cinca is located (province of Huesca, northeastern Spain), and where fieldwork corresponding to Chapter 3 and Chapter 4 was conducted in 2021. B) Sampling area for Chapter 5, located in DIANA region, in northern Madagascar. The rectangles indicate the three protected areas visited in 2022-2023, from top to bottom: Protected Harmonious Landscape of Ambohitra'Antsingy French Mountain, Amber Mountain National Park, Ankarana Special Reserve.	13
Figure 2.1. Geographic distribution of studies assessing the ecosystem services provided by bats as suppressors of agricultural insect pests.	27
Figure 2.2. Recommendation measures provided in the scientific literature to enhance the efficiency of ecosystem services provided by bats as pest suppressors. To highlight their importance in future research, bat diet assessment, searching for proof of bat ecosystem services, and economic assessment of pest suppression have also been included.	31
Figure 2.3. Food web illustrating the proportions of pest insect taxa (left) consumed by different bat genera (right).	33
Figure 2.4. The proportion of pest species types (categorised by the crop type they attack) detected in the diet of bats in the different habitats surveyed in the articles reviewed in the second literature search (LS2). Data are expressed as a percentage of pest species types.	34
Figure 3.1. Location of the study area (on the left) and configuration of the blocks studied (block 1 'B1', block 2 'B2', block 3 'B3', and block 4 'B4'), consisting of paired 'Control' (orange square) and 'Exclusion' (orange grid) plots (on the right). The bat icons show the old barn where the colony of common pipistrelles (<i>Pipistrellus pipistrellus</i>) was found roosting under the roof.....	66
Figure 3.2. Experimental enclosure structures. A) Frontal view of one of the 400m ² enclosures installed in the rice paddies of our study area (Alcolea de Cinca, Spain); B) Aerial view of the rice paddies with two of the enclosures installed.	67

Figure 3.3. Plant affectation by the striped rice borer moth. Examples of infested rice plants identified over the course of the experiments: A) Typical white rice spike of a plant infested by *C. suppressalis*; B) Stem of a rice plant collected in the field and infested by *C. suppressalis*. Adult females lay eggs on rice plants' leaves, sometimes with more than 200 eggs per laying (Maes, 2022; Ramoneda and De Haro Vera, 1988). After hatching, larvae enter the stems to feed by drilling them. The arrow on the right points to the entrance hole of the larva(e), and the arrow on the left points to the exit hole; C) Caterpillar of *C. suppressalis* found in a rice plant cane of our study area; D) Adult moth of *C. suppressalis* captured in our study area. 69

Figure 3.4. Total number of rice plants infested by *C. suppressalis* depending on the two treatments (Control/Exclosure), considering the values recorded in all blocks during the entire study period in Alcolea de Cinca (Spain). 'Control' shows the total number of infested plants recorded in the four plots (400 m² each) where bats were not excluded, and 'Exclosure' shows the total value of infested plants registered in the four plots (400 m² each) where bats were excluded. In each boxplot, the thick horizontal black bar represents the median of the data, while the lower and upper horizontal thin black bars represent the first and third quartile, respectively. The lower whiskers cover the 25% lowest values and the upper whiskers the highest 25% of the values recorded for each treatment..... 73

Figure 3.5. Crop damage registered throughout the study period. (A) Mean values of crop damage detected in Control plots (in presence of bats) and Exclosure plots (in absence of bats) on the four dates sampled, (B) Cumulative mean values of damaged rice plants in Control plots (in presence of bats) and Exclosure plots (in absence on bats) over time. 74

Figure 4.1 Key elements to conduct the captivity experiment to quantify the behavioural responses of *C. suppressalis* towards bat echolocation calls: A) 1m³ enclosure with a living rice plant, corrugated cardboard (green and brown), wax paper, water container (behind the brown corrugated cardboard) and a small bowl with water and sugar (in the middle); and B) one of the lures used to broadcast the nocturnal soundscape (including bat echolocation calls) recorded in rice paddies..... 97

Figure 4.2. Reproductive organs of *C. suppressalis* moths were used to identify the sex of all adults included in the study. The identification features were the ovipositor of the females, and the claspers for the males. A) ovipositor of a female with two eggs still attached; B) male claspers. These images were obtained using a binocular loupe with 10X/20X magnification. 99

Figure 4.3. Some of the egg clutches found in the captivity enclosures. The first two pictures (A, B) show clutches on rice leaves, and the third (C) is an egg clutch laid on green corrugated cardboard. The last picture (D) was taken through the binocular loupe (10X/20X magnification), showing a zoomed view of the eggs grouped in the previous clutch on the green corrugated cardboard..... 101

Figure 4.4. Significant differences in clutch size (n° of eggs / clutch) were found between experimental treatments 'Control' and 'Ultrasounds'. Significance was tested using a Generalised Linear Mixed Model (GLMM). In each boxplot, the thick horizontal bar represents the median of the data, while the lower and upper horizontal thin bars represent the first and third quartile, respectively. The lower whiskers cover the 25% lowest values and the upper whiskers the highest 25% of the values recorded for each treatment. * indicates significance with p-value ≤ 0.05. 102

Figure 5.1. Study area and location of the three protected areas sampled in this study: Amber Mountain National Park, Ankarana Special Reserve and Harmonious Protected Landscape of Ambohitra'Antsingy French Mountain, located within the DIANA Region. The black lines represent the perimeter of each protected area, the red-shaded polygons indicate the area where sampling points were concentrated within the protected areas, and the yellow points indicate the location of the rural areas where bats were surveyed.....	117
Figure 5.2. A) Illustration of the wPOO for each arthropod order found in the diet the bat species studied; B) Nonmetric multidimensional scaling (NMDS) ordination of the arthropod order composition in the diet of different bat families. Each dot represents an individual faecal sample or a group of faecal samples with very similar or identical NMDS scores, coloured according to the taxonomic family to which it belongs.	125
Figure 5.3. Food-web showing associations (wPOO) between insectivorous bat species (left) and prey items summarised at the order level (right). Interactions are illustrated in different colours according to the different bat species. Connecting bar width represents the percentage of interactions between each bat species and each arthropod order.	126
Figure 5.4. Effect of season on pest and disease vector predation. A) Number of pests and disease vectors consumed per bat species in dry and wet seasons. In each boxplot, the dashed horizontal black bar represents the mean of the data, while the continuous horizontal black bars represent, from lower to upper position, the first quartile, the median and the third quartile, respectively. The lower whiskers cover the 25% lowest values and the upper whiskers the highest 25% of the values recorded in each season. B) Principal Coordinates Analysis (PCoA) plot of the pest composition in the diet of bat species during the dry and wet seasons. Each small triangle and circle represents a bat species, coloured according to season. ...	129
Figure 6.1. Malagasy woman cultivating rice, Madagascar. © Adrià López-Baucells	152
Figure 6.2. Rufous trident bat (<i>Triaenops menamena</i>) in Ankarana Special Reserve. In the study described in Chapter 5, this Madagascar endemic species was reported to roost exclusively in protected areas and prey on numerous agricultural pests and disease vectors. ©Adrià López-Baucells.....	154
Figure 6.3. Bat box installed next to rice paddies in Ambatolahy village, Madagascar. © Adrià López-Baucells	156
Figure 6.4. Matthieu (one of the main collaborators of the project) leading the environmental talks in the schools of Ranomafana (Madagascar), and I, showing one of the bat boxes that were installed in the village. © Adrià López-Baucells.....	157
Figure 6.5. Researchers from the GCC lab (University of Helsinki, Finland) exchanging knowledge and experiences with farmers from Ranomafana village (Madagascar), regarding rice damage, pests and insectivorous bats in 2018. © Adrià López-Baucells.	158
Figure 6.6. Farmer and owner of a small vanilla plantation in southern Madagascar. © Adrià López-Baucells	160
Figure 6.7. Photomontage created by combining multiple photos of a Soprano pipistrelle bat (<i>Pipistrellus pygmaeus</i>) chasing a striped rice stem borer moth (<i>Chilo suppressalis</i>) in rice paddies in Spain. © Oriol Massana Valeriano & Adrià López-Baucells	161
Figure 6.8. Peters' wrinkle-lipped bat (<i>Mormopterus jugularis</i>) flying over rice paddies in Madagascar. © Adrià López-Baucells.....	162

Chapter 1 – General Introduction



Starry sky from the Tsingy of Ankarana, Madagascar. © Adrià López-Baucells

1.1. Agriculture and evolution of the global human population growth

Earth's ecosystems have been changing for millions of years, always in a constant transition mediated by different forces such as climate, tectonic activity or sea level variation. However, in the more recent history of the planet, humans have become the main cause of landscape transformation, with its inherent impact on ecosystem functioning and services, biodiversity patterns and climate (Boivin et al., 2016; Ruddiman et al., 2015; Smith and Zeder, 2013).

Homo sapiens appeared in Africa about 300,000 years ago, living in nomadic hunter-gatherer groups. The Neolithic Revolution was marked by the emergence of agriculture about 10,000 years ago, when human societies were already established in all habitable regions of the world, with an estimated global population of 6 million people (Raven and Wagner, 2021; Stephens et al., 2019). Land cultivation and animal domestication allowed to gradually increase the size of settlements, forming small villages first, and towns and cities later, as food production and storage techniques became more sophisticated. Global population growth soared, so that there were about 100 million people by 2000 BCE, and 250 million over the first century CE (Fig. 1.1) (Raven and Wagner, 2021). Between mid-17th century and 1900, the Second Agricultural Revolution took place in Europe, followed by the First Industrial Revolution, involving the mechanisation of agricultural production, advances in transportation, development of large-scale irrigation, and changes to consumption patterns of agricultural goods. These events caused an exponential population growth, surpassing 1 billion people in the 19th century. The Second Industrial Revolution and the subsequent Green Revolution at the beginning of the 20th century made this growth curve even more exponential, with a demographic explosion that multiplied the world's population from 1.65 billion in 1900 to more than 6 billion in 2000 (Cohen, 1995a; Raven and Wagner, 2021). As a consequence of this massive growth, human impacts on Earth also increased and became more widespread, with large areas of the planet already being transformed for agriculture, pasture or urbanisation (Stephens et al., 2019). In the 21st century, this value has increased by 2 billions in less than 25 years, bringing the world's population to over 8 billions, and projected to reach 10 billion and 20 billion by 2050 and 2100, respectively (Cohen, 1995a,b; Raven and Wagner, 2021).

Modern levels of human population growth have been made possible by advances in medicine, industrial and technological development, and large-scale agriculture and livestock macro-farming to supply food, albeit very unevenly across regions and hemispheres. What has been progress for mankind is actually having very high environmental costs, altering the natural functioning of all ecological processes on the planet (Boivin et al., 2016; Kaplan et al., 2011; Ruddiman et al., 2015; Smith and Zeder, 2013). Agricultural land use is one of the main drivers of the anthropogenic global change, and it is responsible for greenhouse gas emissions

related to global warming, soil erosion and overexploitation, widespread habitat fragmentation, deforestation, as well as species introductions, invasions, and extinctions (Boivin et al., 2016; Ellis, 2011; Ellis et al., 2013; Fuller et al., 2011; Kaplan et al., 2011; Ruddiman et al., 2016).

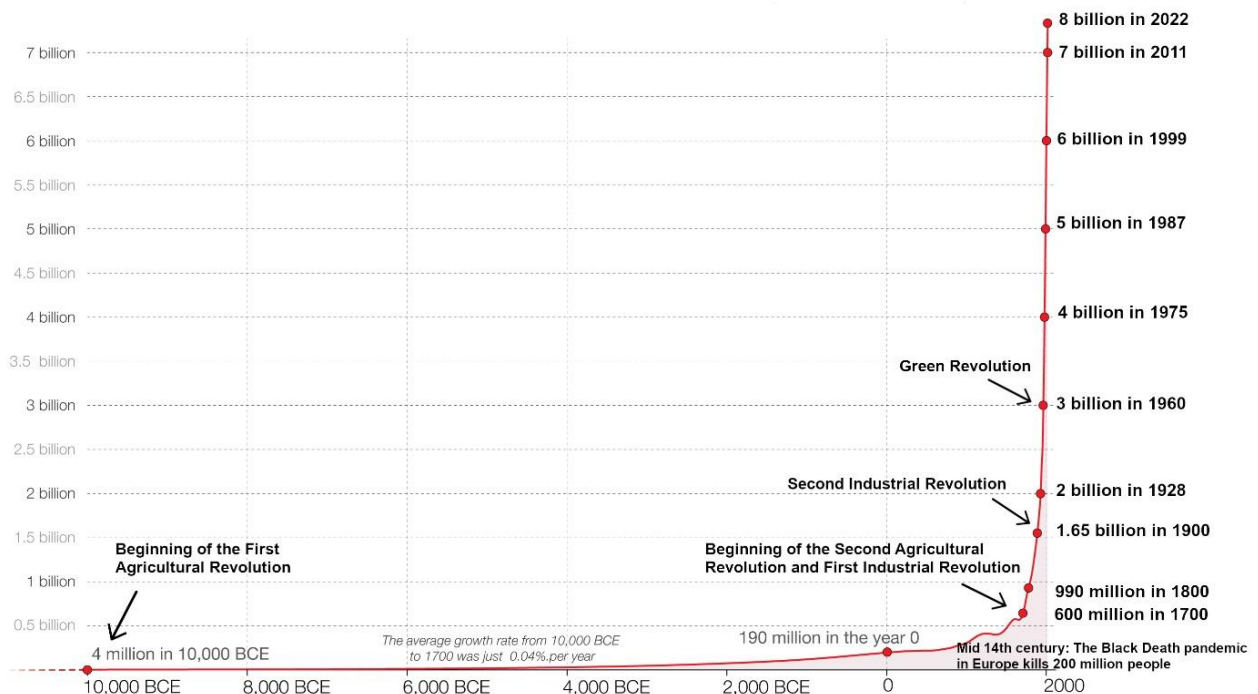


Figure 1.1 Global human population growth 10,000 BCE – 2000 CE. This graphic has been modified from OurWorldinData.org. Based on estimates by the History Database of the Global Environment (HYDE) and the United Nations. Licensed under CC-BY-SA by the author Maz Roser.

1.2. Agriculture vs nature conservation: farming intensification, forest loss and the Sixth Mass Extinction

Agricultural practices have significantly changed in recent decades, especially in the northern hemisphere and after World War II (Raven and Wagner, 2021). As a consequence of the migration of rural populations to cities, those farmers who remained in rural areas often work now on a much larger scale, replacing mixed cropping with extensive areas of monocultures and removing weeds, hedgerows or any other landscape structure to increase arable land. The intensification of agriculture has been facilitated by the industrialisation of farming methods, which has drastically reduced the effort and time needed to cultivate large extensions of crop fields. The application of significant amounts of fertilisers, insecticides and herbicides was promoted to increase crop yield, leading to land overexploitation and degradation, and thus, creating a dependency on these products. Additionally, toxins embedded in agrochemicals started to accumulate in soil, crops or leach into groundwater

systems, threatening public health and harming plant, animal and microbial communities (Hossain et al., 2020; Rani et al., 2021; Raven and Wagner, 2021; Sharma et al., 2019; Sharma and Singhvi, 2017).

Agriculture intensification and expansion are major drivers of habitat destruction and biodiversity loss worldwide (Emmerson et al., 2016; Foley et al., 2005; Pereira et al., 2012; Zabel et al., 2019). The growing demand for food supplies has led to large-scale deforestation, including clearing intact primary forests, particularly in tropical and subtropical areas (Raven and Wagner, 2021). Between 1980 and 2000, 55% of the new agricultural areas were created from primary forests in the tropics (Gibbs et al., 2010). Low income and food security issues in these areas are strongly correlated with the conversion of forests to croplands, often encroaching on the boundaries of protected areas in an attempt to meet food demands (Fig. 1.2) (Jha and Bawa, 2006; Raven and Wagner, 2021; Tscharntke et al., 2012). Globally, the total forest area declined by 3% between 1990 and 2015. While forests are expanding in Europe, North America, the Caribbean, East Asia, and Western-Central Asia; uncontrolled tree felling is taking place in Central and South America, South and Southeast Asia and all regions of Africa (Keenan et al., 2015). This deforestation is often driven by commercial



Figure 1.2. Forest burning to expand rice paddies in the surroundings of the Ranomafana National Park, Madagascar. © Adrià López-Baucells

farmland to export products such as oil palm, coffee or soya (De Sy et al., 2019, 2015) (Fig. 1.3). In 2018, a report published by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services stated that less than 25% of the land surface has remained free from substantial human activity, a value that is expected to fall below 10% by 2050. Considering the global human population projections for the coming decades, the situation is further exacerbated, with tropical and subtropical forests particularly at risk (Cincotta et al., 2000; Raven and Wagner, 2021).



Figure 1.3. Large-scale soybean harvest in Brazil. © Shutterstock/Haboski

Biodiversity loss is occurring at unprecedented rates in human history, and highly unusual in planet's history. With several hundreds of species already documented as extinct (especially over the last 500 years), there is increasing evidence that we are at the early stages of the Earth's Sixth Mass Extinction, the first one induced by humans (Barnosky et al., 2011; Ceballos et al., 2015; Dirzo et al., 2014). The rate of many species' populations loss is even more accelerated, foreshadowing the most likely fate of numerous species still present on the planet (Ceballos et al., 2017). Most species under threat play crucial roles in ecosystems, providing important benefits and essential services to the planet and to our societies, such as carbon sequestration, nutrient recycling, crop pollination, or arthropod populations' regulation (Ceballos et al., 2015; Gascon et al., 2015; Rehman et al., 2022). Thus, the massive loss of

biodiversity threatens the balance of the Earth's ecosystems on which life depends and, consequently, also the survival of our civilisation (Ceballos et al., 2015; Zabel et al., 2019). The need to protect nature and establish sustainable ways to manage natural resources is more evident than ever, and must be addressed with the highest priority.

1.3. Arthropod pests, Integrated Pest Management (IPM) and biological control

Modern, industrialised farming exacerbates its own challenges by creating ideal conditions for arthropod pests. This occurs due to the cultivation of large extensions of genetically uniform monocultures, characterised by dense plantings and competitive cultivation practices, making agrosystems particularly vulnerable to arthropod infestations (Culliney, 2014). Moreover, when this happens, instead of allowing natural processes to restore equilibrium, which may result in yield losses, artificial measures are employed to control pests. This artificial intervention disrupts the natural balance of the ecosystem and perpetuates the input of energy, nutrients, and other resources to maintain production levels (Schowalter, 2007).

Dependence on pesticides as the primary method of pest control has led to unintended and unforeseen repercussions, in addition to evident problems of environmental contamination and high costs to human health (Rani et al., 2021; Thacker, 2002). This includes the development of resistance among the main targeted pests and the disruption of natural predator populations, leading to outbreaks of secondary pests. In fact, it is estimated that approximately 50% of the arthropod pests currently controlled with pesticides worldwide became pests as a direct result of the use of these agrochemicals (Thacker, 2002).

Considering the worst-case scenario with higher percentage losses of key cereals and other crops, the global economic impact of arthropods surpasses \$470 billion annually, being responsible for around 13-26% of crops losses worldwide (Boxall, 2001; Culliney, 2014; Oerke, 2006; Pimentel, 1997; Yudelman et al., 1998). However, this estimate is likely to underestimate the actual extent of crop damage due to the absence of data from developing countries. Integrated Pest Management (IPM) was developed in response to the escalating use of synthetic pesticides, and has increasingly gained importance in recent decades as a more sustainable approach to preventing and managing multiple plant pests (Dent, 2000; Peshin and Dhawan, 2009). The IPM strategy consists of applying diverse practices simultaneously and synergistically to manage multiple pests. Instead of aiming to eradicate harmful organisms, IPM seeks to keep them below economically damaging levels. It therefore establishes economic or treatment thresholds for pesticide use, which are applied as a last resort, while promoting and enhancing ecosystem services such as natural pest predation (Alwang et al., 2019; Ehler, 2006; FAO, 2024).

Biological control or biocontrol is one of the most studied methods of IPM, involving the use of living organisms to manage pest populations, and thereby reduce their impact on crops (Stenberg, 2017; Stenberg et al., 2021). Natural enemies of insects, such as predators, parasitoids, and pathogens, play an essential role in regulating the densities of harmful species. Important achievements in the application of biocontrol strategies include the use of the entomopathogenic bacterium *Bacillus thuringiensis* and baculovirus to combat the cotton bollworm *Helicoverpa armigera* since its official detection in Brazil in 2012, when caused substantial damage to corn, cotton and soy (Parra, 2023). Another successful example in the Mediterranean basin involved the use of hemipteran predators to efficiently manage emerging insect pests like the South American pinworm *Tuta absoluta*, which was causing severe damage to tomato crops (Urbaneja et al., 2012). Understanding the relationship between natural enemies of arthropod herbivores and their potential to suppress pests is essential for grasping the value of biodiversity and its role providing ecosystem services.

1.4. Bats, rice and pest suppression: the role of bats as insect predators

Bats, the second most diverse group of mammals worldwide, inhabit all continents and ecosystem types except for polar regions. With over 1,400 described species, bats exhibit a broad spectrum of behaviours and dietary preferences, feeding from insects, fruits and nectar to small vertebrates, seeds and, in a few species, blood (Frick et al., 2020; Simmons and Cirranello, 2022). This makes bats providers of essential ecosystem services such as pollination, seed dispersion, or arthropod regulation (Kunz et al., 2011), the latter being the focus of this thesis. Despite their ecological importance, widespread deforestation and habitat degradation pose major threats to bat populations globally, especially due to their low reproductive rate and longevity (Voigt and Kingston, 2015). In fact, approximately one-third of bat species are considered threatened or data deficient by the IUCN, while more than half exhibit unclear or declining population trends (IUCN, 2024; Voigt and Kingston, 2015).

Possessing a highly evolved echolocating system, insectivorous bats are considered some of the world's most voracious predators, being crucial in the regulation of arthropod populations (Kalka and Kalko, 2006; Kunz et al., 2011; Kunz and Stern, 1995). In agricultural areas, bats act as natural enemies of many harmful insects, providing very valuable ecosystem services as predators of crop pests (Tuneu-Corral et al., 2023) (Fig. 1.4). Many authors have highlighted the important ecological role of bats in agrosystems, saving large amounts of money to farmers, land managers and governments (Kolkert et al., 2021; Maine and Boyles, 2015; Taylor et al., 2018). In addition, published evidence reports non-consumptive effects of bats, related to the perception of predatory risk by insect species with tympanic organs

capable of detecting echolocating bats (Gillam et al., 2011; Huang et al., 2003; Huang and Subramanyam, 2004; Nakano et al., 2022). These tympanate species may alter their normal behaviour when detecting foraging bats, which can negatively affect insect reproductive success, thereby enhancing pest suppression.



Figure 1.4. Malagasy white-bellied free-tailed bat (*Chaerephon leucogaster*), endemic to Madagascar, foraging in a rice growing area. © Adrià López-Baucells & Joan de la Malla

Rice (*Oryza sativa*) is the most important staple food for over half of the world's population, playing a crucial role in food security (Gnanamanickam, 2009; Maclean et al., 2013). In the developing world, rice provides 27% of the dietary energy supply and 20% of the dietary protein intake (Sanint, 2004). In Asia, it accounts for up to 85% of all cereal crops produced and supplies up to 80% of the daily caloric intake per person (Papademetriou, 2000; Timmer, 2010). In sub-Saharan Africa, rice consumption is growing faster than any other food staple, with an estimated 6% increase per year (Saito et al., 2015); and in Latin America, consumption has tripled in the last century (Sanint, 2004). However, rice crops are frequently damaged by pests, especially by insects, resulting in losses of about 15% of the world's rice production (Fig. 1.5) (Sharma et al., 2017). Global rice demands are expected to continue rising, but at the same time crop losses due to pests are also expected to increase due to global warming. In fact, some models show that when the average global surface temperature rises by 2°C, the average increase in rice yield losses due to insect pests will be 19%, leading to total losses

estimated at millions of tonnes per year (Deutsch et al., 2018). In light of this, several efforts have been committed worldwide to develop sustainable pest management strategies such as biocontrol to enhance rice production while ensuring human well-being.



Figure 1.5. Caterpillars damaging rice plants in Ramomafana, Madagascar. © Joan de la Malla

1.5. Knowledge gaps and research opportunities

While there is growing evidence of the relevance of bats as natural enemies of pest insects in agriculture, significant knowledge gaps remain. For instance, there is a lack of comprehensive assessments gathering evidence-based conservation strategies that effectively promote bat presence in agrosystems. There is also a notable absence of appropriate recommendations, guidelines, and protocols to assist farmers in adopting sustainable pest management practices that integrate bats (Adams and Sandbrook, 2013).

In addition, there is insufficient information on the specific contribution of bats as pest suppressors in many crop types. Despite the critical role rice plays in food security worldwide, just a few studies have evaluated the contribution of bats as controllers of harmful insects affecting this crop (Bhalla et al., 2023; Wanger et al., 2014). To date, no study conducted directly on rice plantations has successfully quantified the economic value of the benefits bats

provide as rice pest consumers anywhere in the world. Thus, an accurate valuation of this ecosystem service is broadly required by rice growers and their agricultural institutions.

Insectivorous bat species use echolocation to orientate in the dark and to detect and pursue prey in flight. Predator-prey coevolution is a major driver of the emergence of auditory systems in many arthropod species, particularly moths, enabling them to detect ultrasounds emitted by bats and change their normal behaviour to reduce predation risk. Most research on bat-mediated pest suppression has only assessed their role as predators without considering the effect that ultrasounds might exert on insect species with tympanic organs. Studying the potential effect of ultrasounds on rice pests is a pending task of great importance if we want to better understand the ecological role of bats in rice paddies and other agrosystems.

The study of this essential ecosystem service becomes even more relevant in developing countries (predominantly located in the tropics and subtropics), where, in most cases, human communities are heavily reliant on subsistence agriculture (Fig. 1.6). As a consequence of the high deforestation rates in these regions, natural protected areas have become crucial refuges for biodiversity and, therefore, key elements for the conservation and maintenance of their associated ecosystem services. However, little is known about the role of protected areas in enhancing bat-mediated pest suppression, which could be essential for agriculture and rural communities in these regions.



Figure 1.6. Farmer harvesting rice, the main staple food for Malagasy population, Madagascar. © Adrià López-Baucells

1.6. General objective and thesis outline

The work presented in this thesis addresses key knowledge gaps identified in the previous section. The main objective of this research was to enhance the understanding of the ecosystem services provided by bats as natural insect predators in agrosystems, with a special focus on the study of their role as consumers of rice pests. Specifically, I wanted to (i) assess the global state of knowledge on the bat-mediated pest suppression in agrosystems, and provide recommendations for promoting their suppressive potential, (ii) economically quantify the benefits bats provide as natural enemies of one of the most widespread rice pests in the world, the striped rice stem borer moth (*Chilo suppressalis*), (iii) study the effect of bat ultrasounds on the egg production of the same pest insect, and finally (iv) evaluate the role of protected areas as sources of bat-mediated pest suppression services beyond their borders.

Thus, this thesis has been structured into six chapters. The initial chapter, or Chapter 1, is a general introduction that contextualises the work conducted in this thesis.

Chapter 2 (published in *Biological Reviews*. Tuneu-Corral et al., 2023) is a systematic review that evaluated the state of knowledge on the ecosystem services provided by bats as pest suppressors at a global scale. It also brings together recommendations and strategies for farmers, land managers and other stakeholders to promote and favour bat populations in agricultural systems. In addition, this publication presents a first bat-pest interaction network that summarises a total of 2308 associations between bat species and agricultural pests documented in the literature.

Chapter 3 (published in *Ecosystem Services*. Tuneu-Corral et al., 2024) investigated the role of bats in suppressing the striped rice stem borer moth (*C. suppressalis*). For this purpose, I developed exclusion experiments in rice paddies to assess plant damage and yield loss in the presence or absence of bats. For the first time using this method, I economically quantified the benefits they provide as consumers of this pest insect, estimating the rice and monetary saving attributed to insectivorous bats. This research underscores the importance of implementing management measures that support bat populations in agrosystems as part of the IPM strategy to reduce harmful insects in an ecological and sustainable manner.

Chapter 4 (submitted to *Pest Management Science*) aimed to evaluate the non-consumptive effects of bats on insect pest populations in rice paddies. To achieve this, I conducted an acoustic experiment to determine whether the presence of bat ultrasounds in the environment affects the egg production of *C. suppressalis*, a moth species with tympanic organs. I observed that females exposed to bat ultrasounds laid significantly fewer eggs than those not exposed to ultrasound broadcasting. The findings of this chapter support the hypothesis that bats may

suppress pests simply by emitting ultrasonic pulses, which may negatively affect insect reproductive success, thereby reducing crop damage and economic losses in rice paddies.

Chapter 5 (submitted to *Agriculture, Ecosystems & Environment*) focused on Madagascar, one of the world's poorest and most biodiverse countries. In this chapter, I evaluated the role of protected areas in providing bat-mediated pest suppression services to surrounding rural communities. To accomplish this, I carried out a diet assessment of insectivorous bats using molecular techniques, revealing that agricultural pests and disease vectors are part of the diet of most bats species. Considering their home ranges and the distances between their natural roosts inside protected areas and croplands, I suggest that certain bat species likely contribute to pest suppression and disease vector reduction in rural villages.

Chapter 6 served as a general discussion to integrate the topics and interpretations explored throughout this thesis, highlighting the major findings, main conclusions, and outlining the next steps and future research challenges arising from this study.

1.7. Study system

The work presented in this thesis has been carried out throughout four years (2020 – 2024). Except for Chapter 2, the other three chapters were built upon several periods of field data collection conducted in two very different study areas: Spain and Madagascar.

Rice plantations in Spain account for 30% of the EU's rice production, being the second-largest rice-producing country in Europe (Gómez De Barreda et al., 2021). The main pest insect damaging this crop is the striped rice stem borer moth (*C. suppressalis*), annually damaging a million hectares of rice across Australasia, Asia, and Europe (Heinrichs and Muniappan, 2017; Maes, 2022). This Lepidopteran species was detected in Spain in 1933. Since 1950, farmers have employed synthetic insecticides to manage this insect, often through aerial applications. In 1988, the first sexual confusion treatment test was performed using pheromones, a practice that has been increasingly used as an effective and eco-friendly pest control method. Since 2006, sexual confusion has become the primary strategy adopted in some rice-growing areas of Spain, and treatment thresholds have been established to limit the use of agrochemical insecticides.

However, in the province of Huesca, in northeastern Spain, rice growers do not use sexual confusion treatments. Despite recent years showing less severe impacts from *C. suppressalis* on crops, pest densities and plant damage levels are usually higher compared to other regions. This makes Huesca province a suitable scenario to investigate the potential of bats

in suppressing the striped rice stem borer moth. Data collection for Chapter 3 and Chapter 4 was conducted during a five-month fieldwork season (June – October 2021) in a rice plantation located in Alcolea de Cinca, an important producing area in this province (Fig. 1.7A).

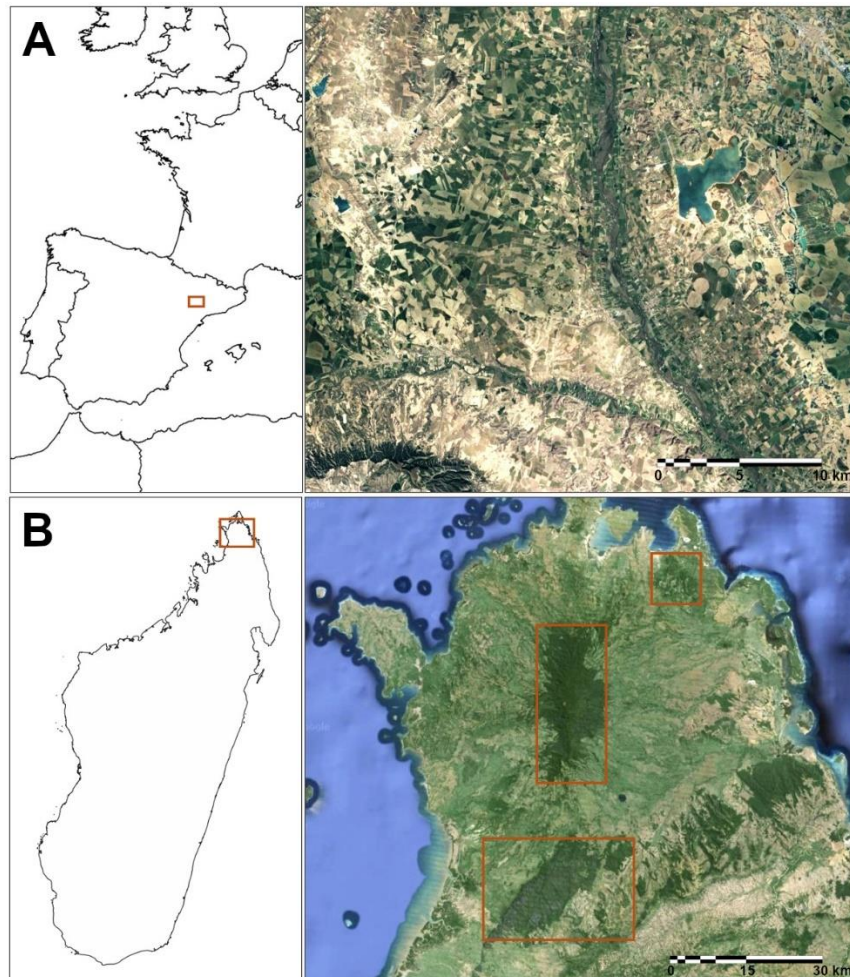


Figure 1.7. Study areas covered in this thesis. A) Agricultural region where the village of Alcolea de Cinca is located (province of Huesca, northeastern Spain), and where fieldwork corresponding to Chapter 3 and Chapter 4 was conducted in 2021. B) Sampling area for Chapter 5, located in DIANA region, in northern Madagascar. The rectangles indicate the three protected areas visited in 2022-2023, from top to bottom: Protected Harmonious Landscape of Ambohitr'Antsingy French Mountain, Amber Mountain National Park, Ankarana Special Reserve.

Chapter 5 was conducted in Madagascar, renowned for its extraordinary biodiversity yet facing severe economic challenges. The Malagasy population relies heavily on subsistence agriculture, exacerbated by rapid population growth and limited economic alternatives. This situation is leading to widespread conversion of forests into arable land, keeping deforestation rates high (Jarosz, 2004; Scales, 2014; Suzzi-Simmons, 2023). I conducted two fieldwork expeditions in DIANA region, in northern Madagascar (Fig. 1.7B), covering both the dry and wet seasons (October-November 2022, and May-June 2023). I collected faecal samples from insectivorous bat species in three protected areas (Amber Mountain National Park, Ankarana

Special Reserve and Protected Harmonious Landscape of Ambohitra'Antsingy French Mountain) and nearby rural villages to investigate their diet composition. This research encompassed various types of ecosystems, including caves, humid montane forests, dry deciduous forests or agricultural landscapes.

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Chapter 2 – Bat pest suppression at a global level



Commerson's leaf-nosed bat (*Macronycteris commersonii*), Madagascar © Adrià López-Baucells

Article I

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Article I – Pest suppression by bats and management strategies to favour it: a global review

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Abstract

Fighting insect pests is a major challenge for agriculture worldwide, and biological control and integrated pest management constitute well-recognised, cost-effective ways to prevent and overcome this problem. Bats are important arthropod predators globally and, in recent decades, an increasing number of studies have focused on the role of bats as natural enemies of agricultural pests. This review assesses the state of knowledge of the ecosystem services provided by bats as pest consumers at a global level and provides recommendations that may favour the efficiency of pest predation by bats. Through a systematic review, we assess evidence for predation, the top-down effect of bats on crops and the economic value of ecosystem services these mammals provide, describing the different methodological approaches used in a total of 66 reviewed articles and 18 agroecosystem types. We also provide a list of detailed conservation measures and management recommendations found in the scientific literature that may favour the delivery of this important ecosystem service, including actions aimed at restoring bat populations in agroecosystems. The most frequent recommendations include increasing habitat heterogeneity, providing additional roosts, and implementing laws to protect bats and reduce agrochemical use. However, very little evidence is available on the direct consequences of these practices on bat insectivory in farmland. Additionally, through a second in-depth systematic review of scientific articles focused on bat diet and, as part of the ongoing European Cost Action project CA18107, we provide a complete list of 2308 documented interactions between bat species and their respective insect pest prey. These pertain to 81 bat species belonging to 36 different genera preying upon 760 insect pests from 14 orders in agroecosystems and other habitats such as forest or urban areas. The

data set is publicly available and updatable. Key words: agriculture, Chiroptera, ecosystem services, forestry, integrated pest management, pest suppression.

Key words

Agriculture, Chiroptera, ecosystem services, forestry, integrated pest management, pest suppression.

2.1. Introduction

One of the major challenges for agriculture, both locally and globally, is the prevalence of herbivorous insect pests (Oerke, 2006; Savary et al., 2019). Although standardised information on crop losses is difficult to compile, global crop losses due to herbivorous arthropod pests has been estimated at 25–50%, reaching much higher values in several regions, such as in sorghum plantations in Kenya (88% yield loss) and rice fields in the Philippines (66% yield loss), in both cases due to moth species of the genus *Chilo* (Myers et al., 2017; Pimentel et al., 1978; Savary et al., 2019). To overcome this problem, conventional agriculture adopts pesticides despite their well-known adverse consequences such as alteration of ecosystem dynamics, the development of toxicity resistance by pests, and human health risks (Carvalho, 2006). In contrast, organic farming has developed chemical-free management systems to deal with pests (Zehnder et al., 2007). Among the multiple strategies applied in organic farming, the use of the pest control services provided by natural predators of insects such as bats and birds has become increasingly popular (Olmos-Moya et al., 2022; Puig-Montserrat et al., 2015).

Chiroptera is the second most biodiverse group of mammals with >1460 species worldwide (Burgin et al., 2018; Simmons and Cirranello, 2022). Most bat species are insectivores, consuming up to 70–84% of their body mass in insects each night (Kalka and Kalko, 2006; Kunz et al., 2011; Kurta et al., 1989), and sometimes up to 100% (Kunz and Stern, 1995). Bats use different hunting strategies depending on their foraging guilds, some species specialising on flying insects (aerial-hawking bats) and others seizing prey directly from the foliage or ground (gleaning bats). Several authors have reported the vital ecosystem services provided by bats as insect pest suppressors, which are beneficial for both ecosystems and farmers (e.g. Cleveland et al., 2006; Kemp et al., 2019; Kunz et al., 2011; Leelapaibul et al., 2005; Linden et al., 2019; Puig-Montserrat et al., 2015). Efforts have been made to quantify the importance of these ecosystem services, despite the difficulty of valuing them. For instance, Boyles et al. (2011) valued the pest suppression services provided by bats at \$22.6 billion/year in cotton

fields in the USA; Wanger et al. (2014) estimated that bats prevent losses of more than \$1.2 million each year in the rice fields of Thailand, and Taylor et al. (2018) calculated that annual costs of around \$613/ha in the macadamia orchards of South Africa are avoided due to the presence of bats.

Integrated pest management (IPM) is an ecosystem-based strategy increasingly adopted to prevent and fight agricultural pests (Stenberg, 2017). It consists of using multiple techniques to regulate pests cost effectively, encouraging biological control, pesticide reduction, and sustainable practices to reduce ecological and human health impacts (Dent, 2000; Ehler, 2006; Kogan, 1998; Stenberg, 2017). IPM is based on different interacting management elements that create either synergistic or antagonistic effects when applied simultaneously in farmlands (Stenberg, 2017). Use of IPM practices attempts to restrict damage levels due to pests below a certain economic threshold, reducing the need for pesticides and thus protecting the environment (Alwang et al., 2019; Vreysen and Hendrichs, 2007). However, evaluating the efficiency of any conservation interventions is essential to understand what works and what does not (see Sutherland et al., 2013).

Despite the potential benefits of bats as natural enemies of insect pests in agriculture, there remains a lack of information on their provision of ecosystem services and for evidence-based conservation strategies, as well as appropriate recommendations, guidelines, and protocols to help farmers adopt sustainable practices (Adams and Sandbrook, 2013). There is also a considerable knowledge gap regarding the diet of most insectivorous bat species, limiting our understanding of which species prey upon a given pest and the magnitude of pest suppression they provide (Boyles et al., 2013). The complexity of identifying prey at the species level in bat faeces using traditional methods (i.e. visual inspection) has hampered progress for decades, but recent improvements in molecular technologies now offer potential for a more precise picture of bat–pest interactions. Quantifying their ecosystem services, however, remains challenging due to a lack of suitable methods to extrapolate the true abundance of prey from such genetic analyses, the difficulty of detecting predatory bats from acoustic surveys, and due to the inherent complexity of designing experiments to assess pest suppression/control by aerial vertebrates such as bats.

The aim of this study was to provide an assessment of the state of knowledge on the role of bats as pest suppressors at a global level, summarise the available evidence, and provide recommendations on how to enhance the efficiency of bat pest suppression in agriculture. We conducted a review of the ecosystem services provided by insectivorous bats in different agroecosystems, and specifically: (i) examined the crop types covered, the pest species detected, and the bat species involved; (ii) assessed whether the reviewed studies provided evidence for predation of insect pests, demonstrated a top-down effect of bat predation on

crops, and economically quantified the benefits of bats to agriculture; (iii) summarised conservation measures, actions, and agricultural recommendations documented in the scientific literature to favour bat foraging as a form of natural pest suppression; (iv) from a second review focused on bat diet, provided a complete list of known interactions between bat species and pest insect species worldwide which we made publicly available in an online open repository.

2.2. Materials and methods

2.2.1. Bats as insect pest suppressors in agroecosystems

We conducted a first literature search (LS1) in ISI Web of Science of indexed articles and book chapters in English, using the following terms in the TOPIC field (searching both the title and the abstract): ‘agricultur*’, ‘pest’, ‘insect*’ and ‘bat*’ or ‘bats’. The search was performed by CTC in October 2022 obtaining 173 references, of which only 66 of were considered for the review after checking the whole text (see online Supporting information, Fig. A1.1). We only included articles directly studying and assessing the effect of bats as pest controllers, either as direct predators of one or several pests (providing or not evidence of predation), evaluating their effect as top predators or quantifying economically their suppressive effect. We excluded any work that only mentioned the potential of bats as insect pest suppressors as an indirect topic of their research. For each of the included studies (see Table A1.1), we extracted information following a semi-structured questionnaire: (i) the year and country where the study was performed; (ii) the agroecosystem type studied; (iii) the insect pest species detected and the bat species on which the study was focused; (iv) whether predation of bats upon pest species was demonstrated; (v) whether the study demonstrated a top-down effect of bats on that agroecosystem; (vi) whether the benefits of bat ecosystem services were quantified economically, and what methods were used to estimate the economic value of bats as pest suppressors; and (vii) the conservation and management strategies proposed in the articles and their potential application.

2.2.2. Bat–insect pest interactions

We compiled a comprehensive list of agricultural insect pests occurring in temperate and tropical regions. Since no more recent public documents or published lists were available, we extracted the main agricultural insect pests cited in Hill (1983, 1987). Note that species might be considered pests in certain regions while not in others, meaning that this comprehensive list will need careful review by entomologists and local or regional experts for use in agricultural management.

We assembled a first list of 1236 insect pest species or genera extracted from Hill (1987, 1983). We then conducted a second literature search (LS2) in the ISI Web of Science using the R package *wosr*. We searched for any indexed document containing the following terms in the topic field: 'pest species name' AND 'bat*', where 'pest species name' refers to each of the 1236 species in Table A1.2. After the first check of the articles found, we added 562 new pest species to the first list, which were not included in Hill (1987, 1983) but were studied in the papers found. The updated list consisting of 1798 insect pest species then was used to perform the same literature search with the R package 'wosr'. In addition, we also performed three literature searches including the following terms: (i) 'bat' or 'bats', 'diet*', and 'insect*'; (ii) 'bat' or 'bats', 'predat*', and 'insect*'; (iii) 'bat' or 'bats', 'diet*', and 'arthropod*'. We identified a total of 3620 articles, of which only 366 were assessed for eligibility. Of the latter, we finally retained only those that identified bat prey at the genus or species level (N = 95) (see Fig. A1.2).

For each article, the following information was extracted: year, country, habitat type, diet assessment methods, bat species, and pest species consumed. For the variable 'habitat type' we considered five categories: agricultural (dominated by agricultural lands), forested (dominated by woodlands and forests), urban (landscape dominated by urban areas), others (when the habitat described in the study did not match the above categories; e.g. desert, grasslands), not specified (when the authors mentioned the study area or the specific place without describing the habitat in which it is found). The variable 'diet assessment methods' considered the methods applied by authors in order to study the diet of bats: 'acoustics and insect remains' (when authors combined acoustic recordings and analysis of insect remains discarded by hunting bats), 'acoustics and visual' (when authors combined acoustic recordings and visual observations), 'insect remains' (when authors used insect remains discarded by bats), 'DNA faeces' (when authors studied DNA extracted from faeces), 'DNA stomach' (when authors studied DNA extracted from stomach contents), 'faeces dissection' (when authors dissected faecal samples to study insect remains).

Predator and prey information was organised into two data sets. In the first data set, we recorded each bat species with the insect pest species it consumed, and the method used to confirm predation (see Table A1.3). In the latter, for each pest species known to be preyed upon by bats, we recorded the crop types they affected (see Table A1.4). Crop types were classified into several categories for analysis: cereals (e.g. wheat, maize, corn, rice, barley, sorghum); forest (e.g. beech, oak, poplar, willow); fruit crops (e.g. apple, pear, apricot, strawberry, cranberry); grasses (e.g. sugarcane, turfs, pastures); legumes (e.g. pea, bean, alfalfa, soybean); ornamental (e.g. garden species); other (cotton, tea, tobacco, hop, flax, rubber tree, hemp, peppermint, jute, rapeseed, kenaf, ashwagandha, mushrooms,

honeybees); stored products (e.g. stored cereals, stored tobacco, dried fruits); and vegetables (e.g. tomato, lettuce, spinach, potato, onion).

To present our findings graphically, we created food webs using the function *plotweb* of the R package 'bipartite', to show the interactions between different bat genera and insect pest orders consumed by them. We finally assessed the distribution of these insect pest orders according to the different crop types affected and the different habitats surveyed. All analyses were carried out with R software version 4.0.3 (R Core Team, 2022).

We performed all systematic reviews following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (O'Dea et al., 2021).

2.3. Results

2.3.1. Bats as insect pest suppressors in agroecosystems

We retrieved 66 articles in LS1 published from 1995 to 2022 (Fig. A1.1), with the publishing rate for these articles showing a clear positive trend with time (Fig. A1.3). The studies were conducted in 25 countries, primarily in North America (USA and Mexico; 27 articles, 40.9%), Europe (especially southern Europe; 11 articles, 16.7%), and southeast Asia (Thailand, Malaysia, Indonesia, and the Philippines; seven articles, 10.6%) (Fig. 2.1). Almost no studies were found for north and central Asia (only one published article for India). We found clear knowledge gaps for the African continent, where seven studies assessing the role of bats as pest suppressors have been carried out: five in South Africa, and one each in Madagascar and Senegal. A similar focus on only a few regions was found for Central and South America and the Caribbean islands: the ecosystem services of bats as pest suppressors have been assessed only in Brazil (three articles), Costa Rica (two articles), Chile (one article) and Peru (one article).

Of a total of 18 agroecosystem types surveyed, cotton was the most studied (22.7%), followed by rice (13.6%), coffee (7.6%), corn (7.6%), fruit trees (7.6%), macadamia (7.6%), and vineyards (7.6%) (Table 2.1). A considerable proportion of articles (16.7%) did not specify the crop types cultivated in the study area.

(a) Predation, top-down effect, and economic value assessment

The 66 reviewed articles reported that 102 bat species preyed upon a total of 208 pest species (Table A1.1). Only half of the studies (33 articles) demonstrated that bats feed on these agricultural pests, while the remaining articles, although declaring a focus on bats as pest

consumers, did not provide evidence for predation. Methods used to confirm predation included molecular techniques (DNA barcoding and metabarcoding) to analyse bat diets (28/33 articles, 84.8%) or visual identification of insect parts from faeces using stereo or digital microscopy (4/33 articles, 12.1%). Only 13 out of the 66 articles (19.7%) provided evidence for a top-down effect of bats on harvest or yield, in all cases by comparing the damage recorded in crops from which the bats had been experimentally excluded with control plots that were fully accessible. Economic quantification of the ecosystem services delivered by bats was provided by only 18 (27.3%) of the 66 studies, for several regions of the world and for different crop types. Seventeen of these studies contained an explicit calculation of the economic benefits provided by bats as pest suppressors, or sufficient information to perform this calculation (Table 2.2).

The most common method used to calculate the economic value of ecosystem services provided by bats was an avoided cost model (62.7%, N = 11), which estimates avoided costs related to reduced crop damage and/or pesticide use; only four articles (23.5%) used exclusion experiments to calculate economic benefits, and two articles (11.8%) applied a benefit transfer model, which uses the same calculations as the avoided cost model but with published data from other studies.

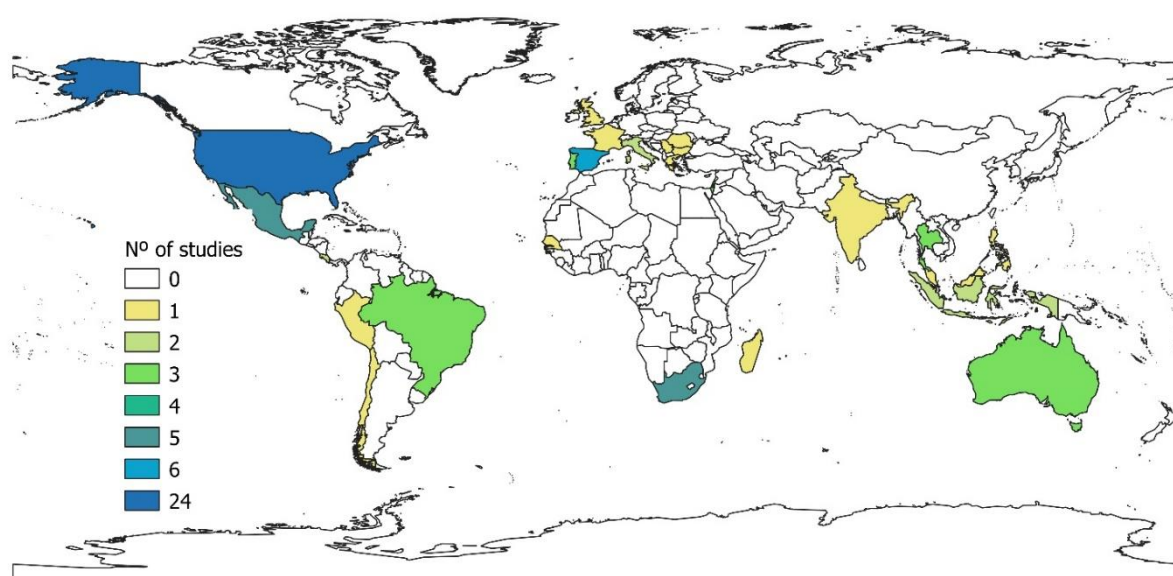


Figure 2.1. Geographic distribution of studies assessing the ecosystem services provided by bats as suppressors of agricultural insect pests.

(b) Integrated pest management – guidelines to enhance bat activity in agroecosystems

We classified the suggestions provided in the consulted literature into seven different groups (Table 2.3, Fig. 2.2).

Table 2.1. Agroecosystem types studied in the 66 articles located by our first literature search (LS1). Some articles considered more than one agroecosystem, and hence the total percentage does not sum to 100.

Agroecosystem	Number of articles	References
Cotton	15 (22.7%)	Cleveland <i>et al.</i> (2006); Federico <i>et al.</i> (2008); Boyles <i>et al.</i> (2011); Lopez-Hoffman <i>et al.</i> (2014, 2017); Wiederholt <i>et al.</i> (2015, 2017); Davidai <i>et al.</i> (2015); Medellin <i>et al.</i> (2017); Krauel <i>et al.</i> (2018); Cohen <i>et al.</i> (2020); Kolkert <i>et al.</i> (2020a, 2020b, 2021); Korine <i>et al.</i> (2020)
Not specified	11 (16.7%)	Whitaker (1995); Agosta and Morton (2003); McCracken <i>et al.</i> (2012); Valentin <i>et al.</i> (2016); Aizpurua <i>et al.</i> (2018); Kahnonitch <i>et al.</i> (2018); Olimpi and Philpott (2018); Hughes <i>et al.</i> (2021); Mata <i>et al.</i> (2021); Ancilloto <i>et al.</i> (2022); O'Rourke <i>et al.</i> (2022)
Rice	9 (13.6%)	Leelapaibul <i>et al.</i> (2005); Wanger <i>et al.</i> (2014); Puig-Montserrat <i>et al.</i> (2015, 2020); Srilopan <i>et al.</i> (2018); Kemp <i>et al.</i> (2019); Sedlock <i>et al.</i> (2019); Montauban <i>et al.</i> (2021); Bhalla <i>et al.</i> (2023)
Coffee	5 (7.6%)	Williams-Guillen <i>et al.</i> (2008); Karp <i>et al.</i> (2013); Karp and Daily (2014); Libran-Embid <i>et al.</i> (2017); Schmitt <i>et al.</i> (2021)
Corn	5 (7.6%)	Maine and Boyles (2015); Davidai <i>et al.</i> (2015); Krauel <i>et al.</i> (2018); Harms <i>et al.</i> (2020); Whitby <i>et al.</i> (2020)
Macadamia	5 (7.6%)	Taylor <i>et al.</i> (2017, 2018); Weier <i>et al.</i> (2018, 2019); Linden <i>et al.</i> (2019)
Vineyard	5 (7.6%)	Baroja <i>et al.</i> (2019); Polyakov <i>et al.</i> (2019); Rodríguez-San Pedro <i>et al.</i> (2020); Charbonnier <i>et al.</i> (2021); Baroja <i>et al.</i> (2021)
Fruit trees	5 (7.6.1%)	Maslo <i>et al.</i> (2017, 2022); Denan <i>et al.</i> (2020); Harms <i>et al.</i> (2020); Murphy and Ament (2022)
Cacao	4 (6.1%)	Maas <i>et al.</i> (2013); Cassano <i>et al.</i> (2016); Gras <i>et al.</i> (2016); Vansynghel <i>et al.</i> (2022)
Soybean	3 (4.5%)	Krauel <i>et al.</i> (2018); Harms <i>et al.</i> (2020); Whitby <i>et al.</i> (2020)
Pecan	2 (3.0%)	Brown <i>et al.</i> (2015); Braun de Torrez <i>et al.</i> (2019)
Sorghum	2 (3.0%)	Davidai <i>et al.</i> (2015); Krauel <i>et al.</i> (2018)
Alfalfa	1 (1.5%)	Whitby <i>et al.</i> (2020)
Oil palm	1 (1.5%)	Denan <i>et al.</i> (2020)
Olive	1 (1.5%)	Costa <i>et al.</i> (2020)
Rubber tree	1 (1.5%)	Denan <i>et al.</i> (2020)
Sugarcane	1 (1.5%)	Leelapaibul <i>et al.</i> (2005)
Vegetables	1 (1.5%)	Harms <i>et al.</i> (2020)
Urban areas	1 (1.5%)	Aguiar <i>et al.</i> (2021)

Table 2.2. Articles assessing the economic value of the ecosystem services provided by bats as agricultural insect pest suppressors organised by country and type of crop. Where valuations were made in the original study in other currencies these have been converted to US \$. Method: ACM, avoided cost model; BT, bene fit transfer model; EE, exclosure experiment. Bt, genetically modified pest-resistant variety.

Country	Agrosystem	USD\$/ha/year	Total amount (USD\$/year)	Method	Reference
USA	Cotton	\$183.11* [\$29.90 – \$426.26] *	\$741,000 [\$121,000 – \$1,725,000]	ACM	Cleveland <i>et al.</i> (2006)
USA	Cotton	<i>Conventional cotton</i> Pesticide use: \$86 Non-pesticide use: \$683	<i>Bt cotton</i> Pesticide use: \$46 Non-pesticide use: \$214	ACM	Federico <i>et al.</i> (2008)
USA	Cotton	\$182.90* [\$29.66 – \$427.58] *	\$22.9 billion [\$3.7 billion – \$53 billion]	BT	Boyles <i>et al.</i> (2011)
USA	Cotton	\$34.05* [\$66.65 (1990) – \$13.58 (2008)] *	\$12.24 million [\$23.96 million (1990) – \$4.88 million (2008)]	ACM	López-Hoffman <i>et al.</i> (2014)
USA and Mexico	Cotton	–	\$11.67 million	ACM	Wiederholt <i>et al.</i> (2015)
USA	Cotton	[\$0.01 – \$8.06]	\$12.24 million	BT	Wiederholt <i>et al.</i> (2017)
USA and Mexico	Cotton	[\$0.01 – \$8.06]	\$12.88 million	ACM	López-Hoffman <i>et al.</i> (2017)
Australia	Cotton	<i>Dryland Bt cotton</i> \$99 – \$126	<i>Irrigated Bt-cotton</i> \$286 – \$361	ACM	Kolkert <i>et al.</i> (2021)
South Africa	Macadamia	\$56.81 – \$138.91	\$1.42 million – \$3.48 million	ACM	Taylor <i>et al.</i> (2018)
South Africa	Macadamia	\$2421.61 (exclusion of bats and nocturnal birds)	–	EE	Linden <i>et al.</i> (2019)
Thailand	Rice paddies	–	\$1.21 million [\$0.48 – \$1.95]*	ACM	Wanger <i>et al.</i> (2014)
Spain	Rice paddies	\$25.18	–	ACM	Puig-Montserrat <i>et al.</i> (2015)
Indonesia	Cacao	\$730 (exclusion of birds and bats)	–	EE	Maas <i>et al.</i> (2013)

			> \$1 billion			
			Conventional corn \$851 million	Bt corn \$150 million		
USA	Corn	\$7.88 (conventional corn)			EE	Maine & Boyles (2015)
Brazil	Corn	\$94	\$390.6 million		ACM	Aguiar <i>et al.</i> (2021)
Chile	Vineyard	\$188 – \$248	–		EE	Rodríguez-San Pedro <i>et al.</i> (2020)
UK	Apple	\$372 – \$731	–		ACM	Murphy & Ament (2022)

*Calculated using values found in the article.

Table 2.3. Recommendation measures to enhance bat activity in agroecosystems taken from the reviewed articles. AS indicates the number of articles supporting each measure. Since more than one action was often recommended in a single article, the sum of the percentages is > 100.

Action focus		Measures proposed	AS	%
1	Landscape heterogeneity	Increasing landscape heterogeneity to improve arthropod diversity and bat activity (e.g. hedgerows, patches of natural vegetation, higher diversity of cover types, connectivity with natural areas)	24	36.3
2	Legislation	Improving appropriate conservation legislation and protection measures (e.g. monitoring programs, protection of bat roosts, cave protection initiatives, control of artificial light, habitat conservation, reducing mortality from wind farms)	21	31.8
3	Roost availability	Installing artificial bat roosts (e.g. bat boxes) to attract bats	19	28.8
4	Agrochemical use	Improving pesticide management (e.g. reduction of chemical pesticide use, scheduling use with regard to bat activity patterns, promotion of organic farming)	13	19.7
5	Water sources	Increasing proximity of water sources or the use of safe water troughs	6	9.1
6	Education	Supporting education initiatives to inform landowners and the wider public about the benefits and economic value of ecosystem services provided by bats in agroecosystems	5	7.6
7	Bat lures	Broadcasting feeding buzzes or social calls to attract bats to agroecosystems	1	1.5

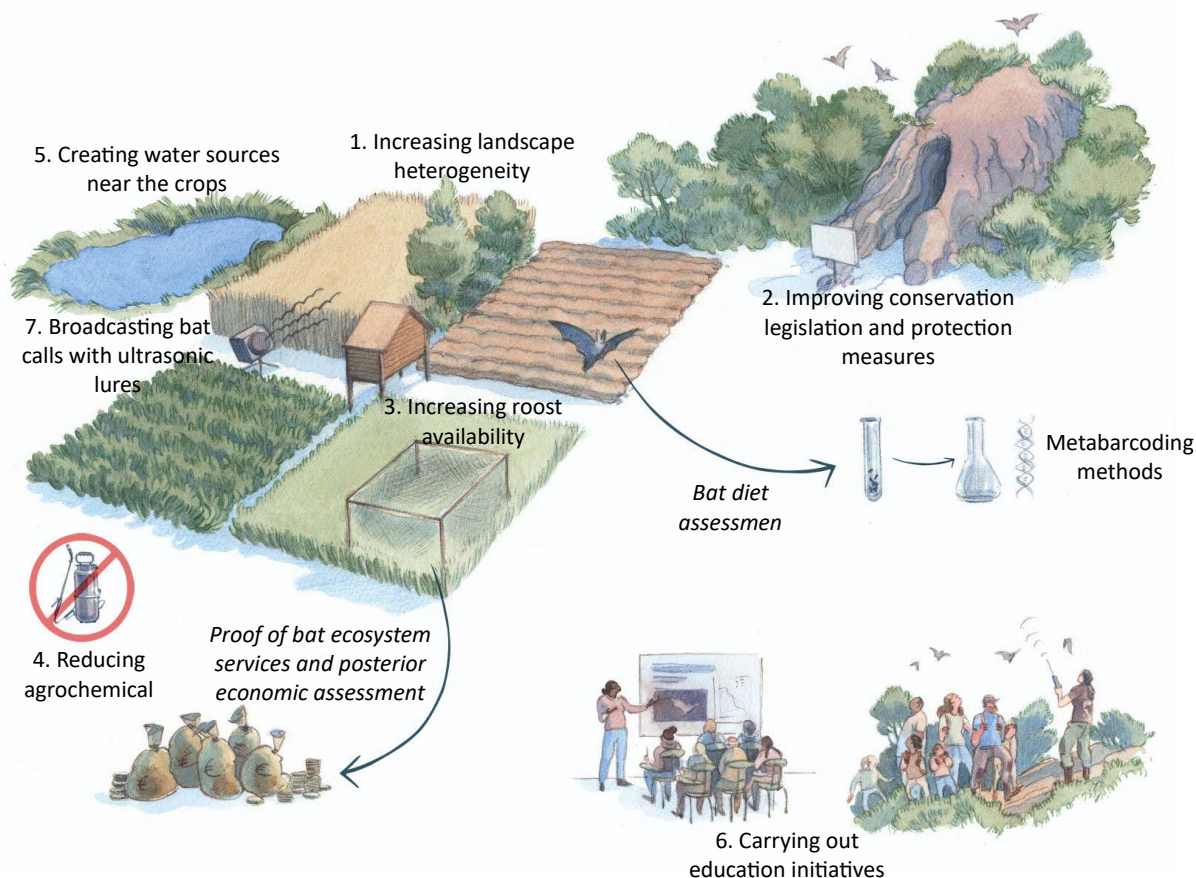


Figure 2.2. Recommendation measures provided in the scientific literature to enhance the efficiency of ecosystem services provided by bats as pest suppressors. To highlight their importance in future research, bat diet assessment, searching for proof of bat ecosystem services, and economic assessment of pest suppression have also been included.

2.3.2. Bat–insect pest interactions

We found 95 papers in the second literature search (LS2) that documented prey identity at the species or genus level (Fig. A1.2). We provide a complete list of 2308 recorded interactions between bat predator species and insect prey worldwide in Table A1.3.

In total, 81 bat species belonging to 36 genera and six families were listed as consumers of insect pests (Table 2.4 and Table A1.5). A total of 694 species and 66 genera of agricultural pests belonging to 14 different orders were detected as bat prey (see Table A1.3, <https://doi.org/10.5281/zenodo.7821119>). The bat genera reported most often to eat agricultural insect pests were *Myotis* (31.2%), *Rhinolophus* (17.3%), *Eptesicus* (13.2%), and *Pipistrellus* (10.5%), with *Plecotus*, *Tadarida*, *Miniopterus*, *Lasiurus*, *Barbastella*, *Nycticeius*, and *Antrozous* reported in fewer studies (<5% each). Table 2.4 shows the number of agricultural pests consumed by each bat species, with *Myotis lucifugus* consuming the highest number of pest species (201 species; 26.4% of all pests detected). Different studies identified

the consumed pest species through one or a combination of techniques including: DNA extraction from faeces (69.8%), visual identification from faeces dissection (18.3%), acoustics (8.4%), visual observations (5.4%), insect remains found on the ground (5.4%) or DNA extraction from stomach contents (2.2%). The largest proportion of pest species was from the order Lepidoptera (59.2%), members of which were consumed by almost all bat genera, followed by Coleoptera (13.9%), Diptera (11.1%), Hemiptera (10.7%), and Orthoptera (2.2%) (Fig. 2.3). The prey species belonging to these orders are pests of economically important crops such as fruits, vegetables, and cereals (Fig. A1.4).

Table 2.4. Bat species, IUCN conservation status and the number of agricultural insect pest species they were reported to consume. Data are only shown for bat species reported to consume more than 10 insect pest species; see Table A1.5 for the full list. IUCN categories: DD, Data Deficient; EN, Endangered; LC, Least Concern; NT, Near Threatened; VU, Vulnerable.

Bat species	IUCN category	Number of pest species consumed
<i>Myotis lucifugus</i>	EN	201
<i>Eptesicus fuscus</i>	LC	180
<i>Myotis escaleraei</i>	LC	139
<i>Rhinolophus hipposideros</i>	LC	113
<i>Myotis crypticus</i>	DD	111
<i>Pipistrellus pipistrellus</i>	LC	102
<i>Rhinolophus euryale</i>	NT	97
<i>Pipistrellus kuhlii</i>	LC	78
<i>Eptesicus serotinus</i>	LC	67
<i>Miniopterus schreibersii</i>	VU	62
<i>Myotis daubentonii</i>	LC	56
<i>Plecotus auritus</i>	LC	54
<i>Rhinolophus ferrumequinum</i>	LC	49
<i>Tadarida teniotis</i>	LC	47
<i>Plecotus austriacus</i>	NT	39
<i>Tadarida brasiliensis</i>	LC	38
<i>Barbastella barbastellus</i>	NT	35
<i>Lasiurus borealis</i>	LC	30
<i>Myotis mystacinus</i>	LC	29
<i>Nycticeius humeralis</i>	LC	26
<i>Lasiurus seminolus</i>	LC	20
<i>Myotis austroriparius</i>	LC	20
<i>Myotis brandtii</i>	LC	19
<i>Taphozous mauritanus</i>	LC	19
<i>Eptesicus nilssonii</i>	LC	18
<i>Myotis emarginatus</i>	LC	18
<i>Antrozous pallidus</i>	LC	17
<i>Rhinolophus mehelyi</i>	VU	16
<i>Eptesicus isabellinus</i>	LC	15
<i>Pipistrellus pygmaeus</i>	LC	15
<i>Myotis bechsteinii</i>	NT	12

<i>Myotis myotis/blythii</i>	LC	12
<i>Myotis nattereri</i>	LC	12
<i>Murina ussuriensis</i>	LC	11
<i>Corynorhinus townsendii ingens</i>	LC	10

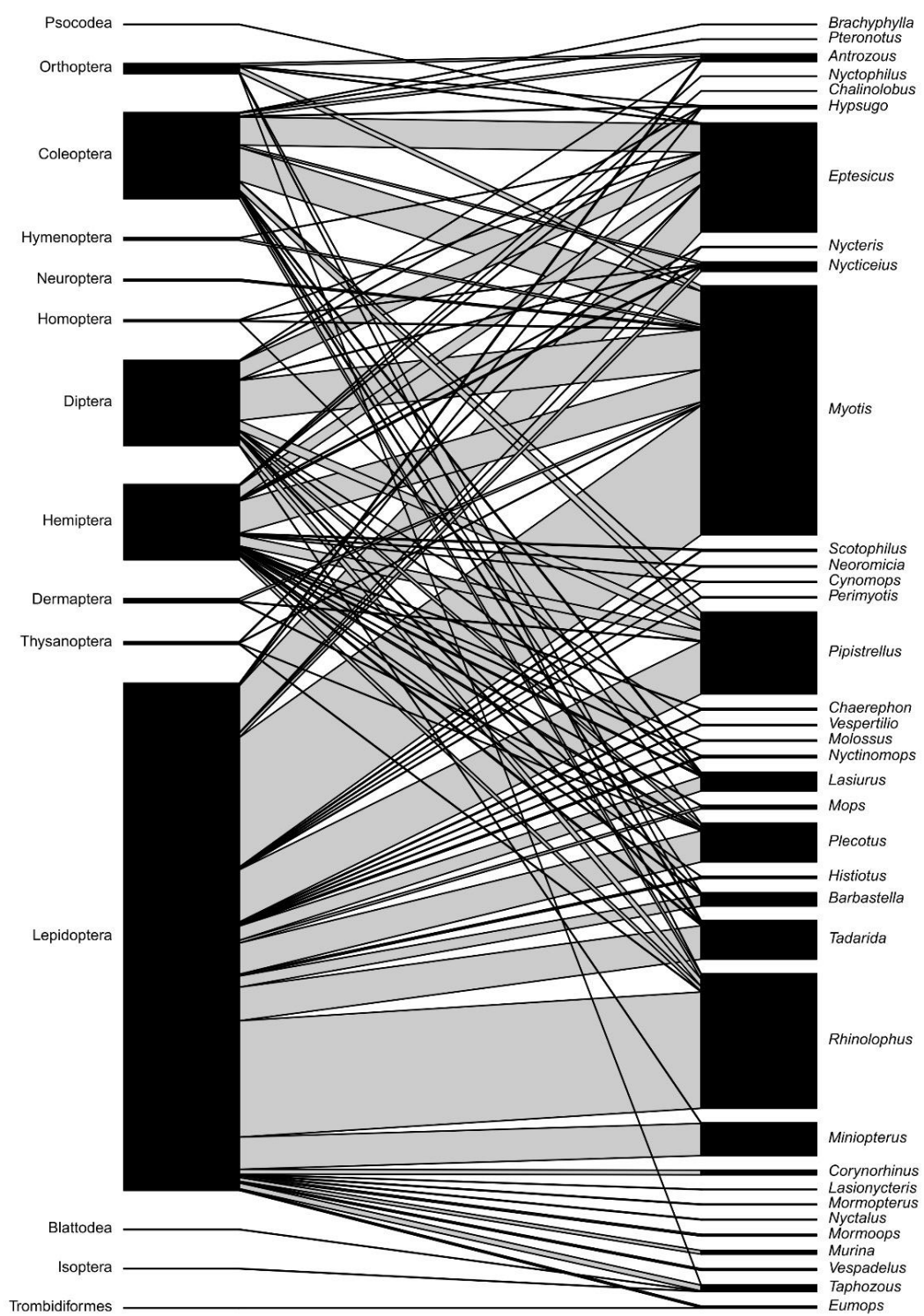


Figure 2.3. Food web illustrating the proportions of pest insect taxa (left) consumed by different bat genera (right).

We also assessed whether the type of habitat (agricultural, forested, urban, others, not specified) in which the studies were carried out affected the pest types detected in bat diets. As shown in Fig. 2.4, the proportions of different types of pests categorised by the crop they attack are similar across the different surveyed habitats.

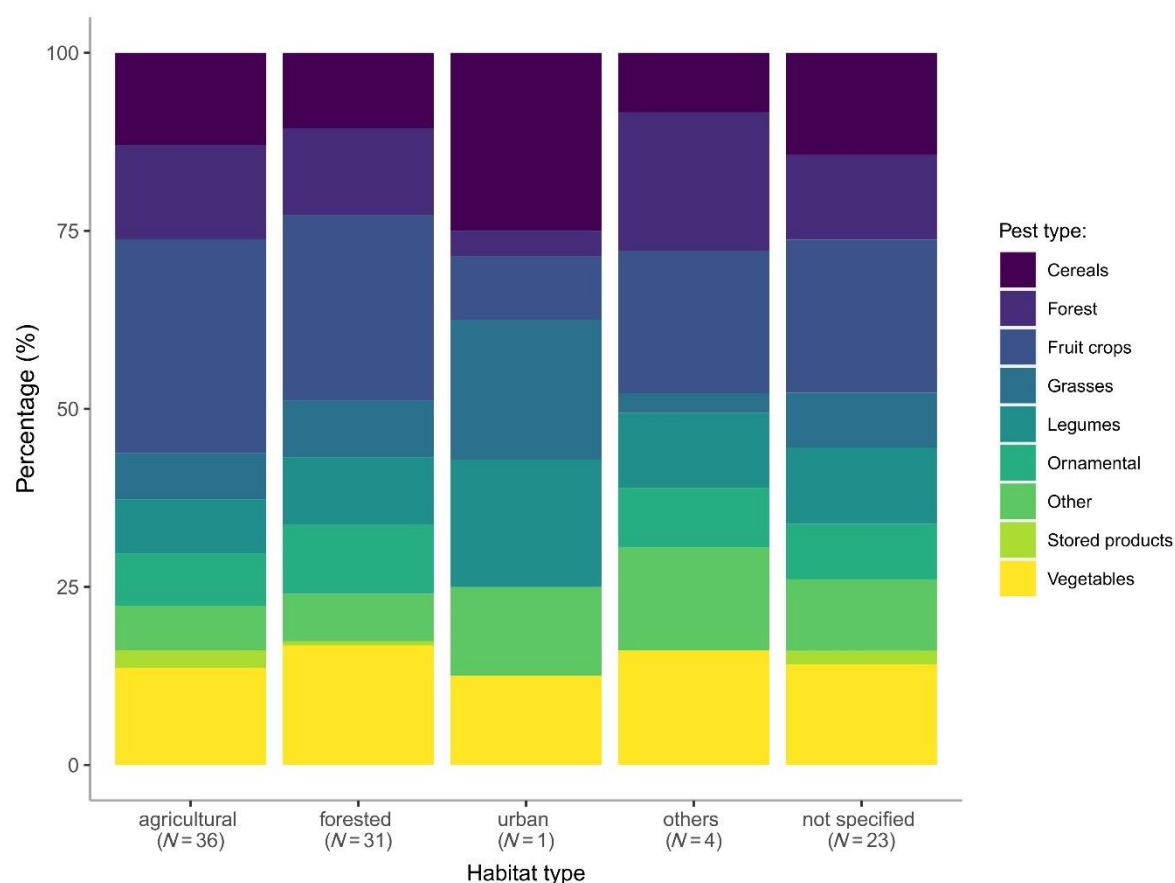


Figure 2.4. The proportion of pest species types (categorised by the crop type they attack) detected in the diet of bats in the different habitats surveyed in the articles reviewed in the second literature search (LS2). Data are expressed as a percentage of pest species types.

2.4. Discussion

2.4.1. Bats as insect pest suppressors in agroecosystems

We detected a bias in the geographical distribution of the studies we examined, identifying knowledge gaps and priority areas for future research in the Global South, particularly in Africa, Central and South America and parts of Asia, where the use of pesticides is currently increasing (Bon et al., 2014; Kunstadter, 2007; Oerke, 2006; Schreinemachers and Tipraqsa, 2012; Schreinemachers et al., 2015; Sharma et al., 2019; Snyder et al., 2015). There may be other studies conducted in these areas that were not accessible to our search (e.g. published

as local reports or in nonindexed formats, or in languages other than English). Many of these areas with scarce or no research on biological pest suppression provided by bats are also those with higher percentages of smallholder farmers dependent on subsistence agriculture (e.g. sub-Saharan Africa and central Asia; Altieri and Koohafkan, 2008; FAO, 2014; Rapsomanikis, 2015), and where yield losses caused by pests tend to be more severe due to relatively inaccessible crop protection methods (Oerke and Dehne, 1997, 2004; Oerke, 2006; Swietlik, 2018). Our results highlight an urgent need to invest research efforts in these regions to enhance food security and rural welfare. There is a clear positive trend in the number of articles published in recent years, identifying this as a topic of increasing interest for the scientific community.

Although half of the studies proved that bats preyed upon pest species, very little evidence exists for a top-down effect of bats directly on crops and few studies directly quantify their economic benefits. We provide a compilation of 2308 recorded interactions between bats and insect pests (Table A1.3, <https://doi.org/10.5281/zenodo.7821119>) to stimulate future work on these interactions.

A wide diversity of crop types has been surveyed in studies assessing the role of bats as insect pest suppressors. Some of the best-studied crop types – cotton, rice, coffee, and corn – are important in terms of food security and/or represent essential economic incomes in developing countries (FAO, 2022; Khan et al., 2020; Muthayya et al., 2014; Shiferaw et al., 2011). The ecosystem services provided by bats as pest consumers have not yet been studied in some important crops such as wheat, a cereal representing 18.3% of the global human caloric intake (Savary et al., 2019). It is also important to note that some crops studied have poor representation in the reviewed articles (e.g. alfalfa, sorghum, sugarcane; Table 2.1) or have only been studied in particular regions (e.g. rice, where nine studies are available but only from Spain, Thailand, the Philippines, India and Madagascar). The average annual rice intake worldwide is 54 kg per person, and represents almost 20% of the daily calorie intake. This value is much higher in regions such as Asia, the major rice producer worldwide, where rice contributes >50% of calorie intake and annual consumption exceeds 100 kg per person (Maclean et al., 2013). This cereal is seen as essential to overcome food insecurity in several African countries such as Madagascar, Sierra Leone, Guinea, Guinea-Bissau, and Senegal. Rice cultivation also is increasing in Latin American and Caribbean countries (Maclean et al., 2013). In these regions there are limited strategies to reduce harvest losses due to pests (Oerke and Dehne, 1997; Oerke, 2006; Swietlik, 2018). Thus, understanding the pest-suppression benefits provided by bats within these regions is a next essential step.

(a) Predation, top-down effect, and economic value assessment

Most studies used DNA metabarcoding to identify predation by bats on agricultural pests. This is the most sensitive and accurate method available to assess bat diet, although it is also the most expensive. A few studies used visual identification of insect parts from faeces, but this approach is limited by poor taxonomic resolution (Russo et al., 2018); identifying the undigested parts of insects to species or even genus level is a challenge. A new technique for predation studies was developed by Denan et al. (2020), who created artificial caterpillars from non-toxic plasticine and deployed them on vegetation surfaces. They could identify different predator groups by the marks left on the caterpillars. Although they could not identify predators to a detailed taxonomic level, their results suggested bat predation of potential insect pests in several crop types.

Several studies assessed directly the top-down effects of bats on crops. In these studies, exclosures were generally deployed in different crop types to prevent access by bats and, in some cases, also by birds and primates. Linden et al. (2019) detected a 27% decrease in total yield (kg/ha) in coffee plantations in South Africa when bats were excluded. Maine and Boyles (2015) reported 56% higher ear infestation in excluded corn plots in the USA. In Chile, Rodríguez-San Pedro et al. (2020) demonstrated that bats prevented a 7% loss of total production in vineyards. Assessing the magnitude of the ecosystem services that bats provide as pest suppressors through exclosures is crucial to understand their true benefit to agriculture. This approach also allows assessment of the economic impact of bats on a crop by comparing the yield obtained in areas patrolled by bats with areas where bats were excluded (Linden et al., 2019; Maas et al., 2013; Maine and Boyles, 2015; Rodríguez-San Pedro et al., 2020). Although bat exclosures are the most appropriate method to measure bat ecosystem services in the field, several disadvantages hinder their application to specific crops or insect species, including: their relatively small sizes compared to the crop area and the insects' flight height; their inability to exclude predation by bats flying near the exclosure; high costs of materials (especially in crops where it is not possible to isolate individual plants) and time (it requires continuous monitoring and maintenance); and potential influences of the exclusion nets on insect behaviour. Recently, Maas et al. (2019) reviewed studies in which bird and bat exclosures were used to assess pest control in agricultural lands across 14 countries and 12 different crops. The authors provided a list of guidelines to improve the performance and validity of this type of research, including common pitfalls associated with experimental design, duration, material choice, and experimental conditions.

Several articles estimated the economic benefits of bats related to pest suppression. For example, Boyles et al. (2011) valued at \$22.9 billion/year the ecosystem services provided by

Tadarida brasiliensis in croplands in the USA. This estimate considered the prevention of crop damage caused by the corn earworm (*Helicoverpa zea*) and also the economic savings related to pesticide applications (Cleveland et al. 2006). The estimated value was even higher for cotton fields in Australia, where the bat *Chalinolobus gouldii* is responsible for saving up to \$63 million each year as a natural controller of the cotton bollworm (*Helicoverpa armigera*) (Kolkert et al., 2021). Wanger et al. (2014) estimated the economic value of bat ecosystem services for rice production at more than \$1.2 million/year. More recently, Linden et al. (2019) estimated the impacts of bats in macadamia orchards of South Africa to be worth \$2421.61/ha/year, with these benefits related to both yield and nut quality. Evaluating the economic importance of bats in agroecosystems might represent a valuable and efficient way to connect farmers with bat biology and conservation.

Most studies used an avoided cost model to estimate the economic value of bats. The costs avoided when foraging bats are present include lower crop damage (due to smaller pest populations) and/or reductions in costs related to the less-frequent use of pesticides. This model does require assumptions to be made, but the model is easy to apply to different crops or regions. By contrast, benefit transfer approaches may provide less-accurate results since this method involves applying ecosystem service values that have been estimated at one location to a new location (Medellin et al., 2017; Wilson and Hoehn, 2006). Interestingly, we found that fewer articles assessed the effect of top-down bat activity on the harvest (19.7%) compared with those that quantified the pest control services provided by these animals (27.3%). This may reflect the difficulties inherent in direct assessment of bat pest suppression on crops compared with making theoretical estimates of the economic value of their ecosystem services. Economically quantifying the pest control services provided requires assumptions to be made, and there are probably many sources of biases and site-to-site variation. For example, the trade-offs between services and disservices also need to be properly assessed to understand the true magnitude of the ecosystem services bats provide and to establish clear guidelines to enhance these (see, e.g. Vansynghel et al., 2022), but this layer of complexity has often been disregarded to date.

Confirmation of bat predation of insect pests, providing evidence for bat ecosystem services and their economic evaluation represents a promising approach to persuade farmers to embrace sustainable practices and to raise awareness about the importance of bats for their crops.

(b) Integrated pest management – guidelines to enhance bat activity in agroecosystems

Most authors of the reviewed articles proposed recommendations and management measures to favour bat communities in agroecosystems and increase the benefits these mammals provide (Fig. 2.2, Table 2.3). However, we found almost no information regarding the effectiveness of the suggested measures. This serious knowledge gap needs to be addressed to recommend bats as part of IPM practices.

- (i) Landscape heterogeneity.** The most popular recommendation in the reviewed articles was to increase landscape heterogeneity (36.3%). An increase in heterogeneity and structural complexity in agroecosystems generally translates into increased biodiversity (Benton et al., 2003; Graham et al., 2018). A more complex landscape provides more niches allowing higher arthropod diversity, in turn favouring predators such as bats through higher food resource availability (Benton et al., 2003; Graham et al., 2018). During recent decades, rapid agricultural intensification has led to homogenisation of farmland landscape structure, argued to be the leading cause of diversity declines in these environments (Benton et al., 2003; Gardner, 1996; Krebs et al., 1999). Promoting heterogeneity by creating and maintaining hedgerows, leaving patches of natural vegetation, planting a higher diversity of cover types, and/or enabling good connectivity of croplands with natural areas will favour arthropod populations and increase foraging habitat for bats (Costa et al., 2020). Landscape-level heterogeneity in agroecosystems can increase biological pest control not only due to enhanced bat activity (Froidevaux et al., 2019; Graham et al., 2018; Monck-Whipp et al., 2018) but also due to larger populations of natural enemies of agricultural pests (Redlich et al., 2018). Many studies provide evidence for the success of these practices (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2017, 2019; Heim et al., 2015; Kahnonitch et al., 2018; Kalda et al., 2015; Lacoëuilhe et al., 2018; Rodríguez-San Pedro et al., 2018, 2019). Froidevaux et al. (2019) detected positive effects on bat populations following a reduction in hedgerow trimming frequency. In the vineyards of Chile, bat activity and diversity were higher in agricultural landscapes with more complex structural configurations (Rodríguez-San Pedro et al., 2019). Smaller and irregular patches, as well as higher edge density, favoured the presence of both bats and insects. Several studies highlight the importance of hedgerows and forested patches in agroecosystems since bats commonly use them as corridors and they can act as shelters for arthropods, thus these structures represent valuable foraging habitats for insectivorous bats (Heim et al., 2015; Rodríguez-San Pedro et al., 2018, 2019).

(ii) Legislation. Nearly one third of the studies argued for improved conservation legislation and measures to protect bat population stability in agroecosystems as well as in other habitats. Implementing effective and well-designed monitoring programs represents a significant challenge that must be met to fill knowledge gaps regarding the status of bat populations and to detect potential threats in different ecosystems (Frick et al., 2020; Jung et al., 2014; Kingston, 2010). Conservation of natural habitats and roost protection initiatives are also essential to ensure the viability of bat communities. This is particularly important for cave-dwelling species, some of which are also important pest suppressors (Aizpurua et al., 2018; Kemp et al., 2019). These underground habitats are susceptible to perturbations and are increasingly under pressure from human recreational activities, vandalism, guano mining, pollution, and other factors (Medellin et al., 2017). The disturbance and disappearance of large colonies can impact bat populations, and the protection and regulation of caves and mines is likely to be fundamental to keeping these populations stable (Medellin et al., 2017; O'Shea et al., 2016). Several countries, such as the USA and Australia, have already applied laws to protect these underground ecosystems and manage tourism appropriately. Medellín (2003) reported evidence of bat population recovery after restoration of a cave environment in Mexico. Other authors highlight the importance of reducing bat mortality at wind farms (Arnett and Baerwald, 2013; Kunz et al., 2007) or integrating light pollution into conservation action plans to maintain biodiversity in anthropogenic habitats (Azam et al., 2016).

(iii) Roost availability. Installation of artificial roosts such as bat boxes was the next most common strategy (28.8%). Intensive logging practices and agricultural expansion are significant drivers of habitat loss, directly threatening tree-dwelling bat species (Lopez-Baucells et al., 2017). Such artificial roosts can be a good alternative for some bat species in areas with low availability of natural refuges such as agroecosystems (Flaquer et al., 2006; Long et al., 2006). New roost opportunities in these habitats may attract bats, increasing the ecosystem services they provide (Boyles et al., 2013; Flaquer et al., 2006; Long et al., 2006). Puig-Montserrat et al. (2015) detected a significant decline in damage due to the striped rice stem borer moth *Chilo suppressalis* in the Ebro Delta (Spain) after the installation of bat boxes and their subsequent occupation by 3500 soprano pipistrelles (*Pipistrellus pygmaeus*). The authors estimated that 9–16 bats/ha were needed to reduce rice borer moth levels below the aerial treatment threshold and 42–67 bats/ha to suppress any need for treatment. Brown et al. (2015) reported high proportions of insect pests in bat faeces collected from artificial roosts distributed in pecan orchards in the southern USA. Weier et al. (2019) also installed artificial roosts in macadamia orchards in South Africa that were occupied by several species. In Australia, bats and other small

vertebrates occupied nesting boxes in farm forestry plantations more frequently than boxes installed in intact forests (Smith and Agnew, 2002). This was probably due to the scarcer natural roost availability in plantations than in the natural forest. Where they are adopted by bats, artificial roosts can enable increases in bat densities in agricultural areas. However, although the use of artificial roosts is popular in regions such as Europe or North America, this practice is still in its infancy in Asian and African countries, and its impact on a variety of agricultural environments and crops has not been tested.

(iv) Agrochemical use. One in five articles highlighted the importance of the appropriate use of agrochemicals. Pesticide use is one of the primary drivers of the mass insect extinction worldwide, threatening insect predators such as bats (Sanchez-Bayo and Wyckhuys, 2019). The European Food Security Agency has recently highlighted the need for a bat-focused pesticide risk assessment (Hernandez-Jerez et al., 2019). Many studies argue that chemical spraying affects bats adversely by reducing their prey resources (Kahnonitch et al., 2018; Park, 2015; Williams-Guillén et al., 2016). For example, Korine et al. (2020) detected a reduction in bat activity after the application of pesticides and these effects lasted for several nights. High levels of biodiversity (e.g. bat richness and activity) are directly related to lower-intensity agricultural practices, which could enhance the efficiency of pest suppression they provide (Kahnonitch et al., 2018; Park, 2015; Williams-Guillén et al., 2016). Bats often exhibit fidelity to foraging sites with predictable resource availability (Hillen et al., 2009; Kapfer et al., 2008; Perry, 2011), a condition that agroecosystems exposed to repeated chemical spraying are not likely to fulfil due to their fluctuating availability of insects. However, we only found two studies describing direct poisoning of bats due to the consumption of insects, flowers or fruits exposed to agrochemicals or roost pollution (Bayat et al., 2014; O'Shea et al., 2016).

(v) Water sources. Many studies have reported a positive influence of water sources on the abundance of bats due to higher concentrations of prey and provision of a drinking resource (Cruz et al., 2016; Froidevaux et al., 2017; Stahlschmidt et al., 2012; Sirami et al., 2013). In this review, 9.1% of studies emphasised the importance of increasing water availability (Kahnonitch et al., 2018; Russo and Jones, 2003; Sirami et al., 2013; Stahlschmidt et al., 2012). In arid or semiarid ecosystems where natural water sources are scarce during some periods of the year, artificial sources may be the only perennial water available during dry periods (Korine et al., 2015; Tuttle et al., 2006). In Germany, Stahlschmidt et al. (2012) showed that both bat activity and insect abundance were significantly higher in vineyards with ponds than in those without them. Sirami et al. (2013) supported this finding in a study in Western Cape (South Africa), where farm dams played

an essential role for all bat species. In both cases, well-managed artificial water sources in agricultural areas contributed to the availability of insect prey, attracting bats and consequently favouring the ecosystem services provided by them (Sirami et al., 2013; Stahlschmidt et al., 2012).

(vi) Education. Integration of social strategies into conservation plans has increased in recent years (Ban et al., 2013; Guerrero and Wilson, 2017; Robinson, 2006). Of the articles reviewed, five proposed education initiatives to enhance and promote bat conservation in agriculture. Suggestions included the implementation of educational activities, citizen science projects, public communication, and other outreach projects to involve local communities in the conservation of wildlife, enhancing their connection with nature (Ardoin and Heimlich, 2013; Braus, 2009; Dietz and Stern, 2002). This is particularly important for bats given their historical negative perceptions (Kingston, 2016). Misconceptions or exaggerated and misinformed news about disease outbreaks have led to an erroneous view of bats worldwide (Lopez-Baucells and Fernandez-Llamazares, 2021b; Lopez-Baucells et al., 2018; Hoffmaster et al., 2016; Rocha et al., 2021a,b). Educating policymakers, farmers and local communities about the benefits of insectivorous bats in agriculture and quantifying the value of the ecosystem services they provide as pest suppressors will be an indispensable tool for promoting more sustainable practices in agroecosystems as well as for mitigating human–bat conflict and enhancing the conservation of bat populations (Aizpurua et al., 2018; Deshpande and Kelkar, 2015; Linden et al., 2019). In urban areas, where intense pressure on wildlife exists, informing people about the benefits of bats as natural controllers of agricultural pests but also as predators of human disease vectors (e.g. those carrying malaria, filariasis, encephalitis, yellow fever, dengue) can also help to promote the use of bats as biological controllers. For example, Hoffmaster et al. (2016) reported that educational programs changed participants' perceptions about bats and their willingness to protect these mammals. However, it remains essential to understand how farmers in different cultures perceive bats to be able to offer biocultural approaches to bat conservation (Deshpande and Kelkar, 2015; Forth, 2021; Lavery et al., 2021; Low et al., 2021; Rocha et al., 2021a,2021b; Shapiro et al., 2021).

(vii) Bat lures. One publication suggested the use of bat lures to enhance bat activity. Several studies have reported the effectiveness of bat lures that broadcast conspecific calls in attracting bat species (Arnold and Wilkinson, 2011; Carter et al., 2015; Gillam, 2007). Indeed, this strategy is used to capture bats in mist nets, especially rare or difficult-to-catch species (Braun De Torrez et al., 2017; Hill and Greenaway, 2005; Lintott et al., 2013;

Loeb and Britzke, 2010). Braun de Torrez et al. (2019) proposed this technique to attract bats to agroecosystems since many species associate conspecific feeding buzzes with high-quality foraging areas (Dechmann et al., 2010; Gillam, 2007; Wright et al., 2011), but further evidence regarding the impact of this recommendation is needed.

2.4.2. Bat–insect pest interactions

In all, 81 bat species belonging to 36 bat genera and eight bat families were listed as consumers of 760 insect pests, in 2308 different bat–insect interactions. Several bat species classified as Vulnerable, Near Threatened, or Endangered by the IUCN were agricultural pest consumers. Our results suggest that bats are important providers of ecosystem services as pest suppressors worldwide. The insect pest taxa consumed most often by bats belong to Lepidoptera, Coleoptera and Hemiptera. Major pests of crops including fruit (e.g. grapevine, apple, strawberry), vegetables (e.g. lettuce, potato, tomato), cereals (e.g. maize, corn, rice) and other economically important products such as cotton, tea and tobacco also belong to these insect orders. Many pest insect species not documented in literature are likely consumed by bat species, and several other bat species are also probably predators of agricultural pests.

The similar proportions of pests found in bat faeces from different study habitats underscore the remarkable mobility of most bat species, the uneven distribution of their roosts across landscapes, and their ability to cover long distances during nocturnal flights. While it is crucial to protect insectivorous bats in agricultural areas, other habitats such as caves, forests, rivers, lakes, and urban areas, as well as heterogeneous landscape mosaics are also critical for the survival of these beneficial arthropod predators.

2.5. Conclusions

This review aimed to provide a practical assessment of current knowledge for researchers and farmers concerning the pest control services provided by bats to agriculture and how to improve IPM. Investigation of the role of bats as pest suppressors has been increasing in recent years. However, studies have not taken place uniformly throughout different regions. Very little research has focused on regions such as the African continent, Central and South America, and most parts of Asia; in these areas food security is highly dependent on subsistence agriculture, and the use of agrochemicals is currently increasing. We recommend that future research directly assesses the top-down effects of bats on crops as well as their

economic benefits as pest suppressors. Providing evidence for bat predation and their ecosystem services represents a promising way to encourage farmers to apply sustainable and ecofriendly strategies to fight pests as well as to raise awareness about the importance of bats in agroecosystems.

We also reviewed conservation recommendations suggested in the literature to promote foraging bats in agroecosystems and to increase their effectiveness in suppressing pests. Actions such as increasing habitat heterogeneity, installing artificial bat roosts, and strict management of pesticide use could attract foraging bats to farmland. Such actions should be combined with conservation legislation and protection measures appropriate to the agricultural market in each region. A transdisciplinary social and ecological approach with broad collaborations between scientists and practitioners should be employed as a more inclusive and integrative way to implement scientific research with land use policy (Maas, Ocampo-Ariza and Whelan, 2021). Finally, we provide a publicly available and updatable list of 2308 registrations of bat–insect pest interactions reported to date (<https://doi.org/10.5281/zenodo.7821119>).

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Chapter 3 – Quantification of bat-mediated rice pest suppression



Bat enclosure installed in rice paddies in Alcolea de Cinca, Spain. © Adrià López-Bosch

Article II:

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Article II – Bats and rice: Quantifying the role of insectivorous bats as agricultural pest suppressors in rice fields

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Abstract

Rice represents the main staple food for more than half of the world's population, playing an essential role in food security and economic growth. One of the major pests affecting this crop is the striped rice stem borer moth (*Chilo suppressalis*), a widespread species found in Australasia, Asia and southern Europe. Bats are paramount insect consumers and their role as natural pest controllers in agriculture has been increasingly acknowledged, including in rice paddies. In this study we quantify, for the first time in Europe, the economic value of the ecosystem services provided by insectivorous bats as suppressors of a rice pest through exclusion experiments in rice plantations in Spain. Our study design included exclosures that prevented bats from hunting over some experimental areas, combined with molecular analyses of bat guano. By assessing the crop damage levels caused by *C. suppressalis* inside and outside the exclosures, we showed that pest impact almost doubled in the absence of bats (94.5% of damage increase). We estimated that bats were preventing crop losses of almost 70 kg of rice per hectare on average, which in economic terms would imply savings of 56€/ha. If we extrapolate our results to the national level, these values could reach up to 7.6 thousand tonnes of rice, or more than 6 million euros saved by bats per year in Spain. Our findings highlight the importance of implementing management measures that favour bat populations in agrosystems as part of the Integrated Pest Management strategies to fight harmful insects, thereby increasing yields and land productivity in a sustainable and environmentally friendly way.

Keywords

Agricultural pest, bat ecosystem services, pest suppression, bat exclusion, economic quantification, rice production

3.1. Introduction

Agriculture is essential for human well-being, ensuring food security and bringing income to rural communities (Gebbers and Adamchuk, 2010). Covering almost 40% of the Earth's surface (Foley et al., 2005; Ramankutty et al., 2008; FAO, 2020), agricultural lands suffer substantial harvest losses, some of which caused by arthropods, weeds, fungi and other organisms (Culliney, 2014; Dhaliwal et al., 2010, 2007; Hall, 1995; Singleton et al., 1999). Losing large amounts of harvest often impedes meeting food demands and hinders economic stability in many regions of the world, generally those less capable of dealing with such difficulties (Flood, 2010; Kumar and Kalita, 2017). Insect pests are considered one of the main causes of crop damage in agriculture worldwide (Dhaliwal et al., 2007; Hall, 1995; Sharma et al., 2017). In fact, yield loss due to pests has been estimated at 18–40% worldwide, primarily due to ecosystem simplification, agricultural intensification, and large-scale production (Oerke, 2006; Sharma et al., 2017). Worryingly, in a global warming climate scenario, the main cereals' yield losses due to insects are expected to increase by 10% – 25% per degree of global mean surface warming (Deutsch et al., 2018).

Rice (*Oryza sativa*) is the main staple food of more than half of the world's population, playing an essential role in food security worldwide (Gnanamanickam, 2009; Maclean et al., 2013; Oerke, 2006). Rice accounts for 43–85% of all cereal crops produced in Asia and supplies 50–80% of the daily caloric intake per person (Papademetriou, 2000; Timmer, 2010). In Africa, rice consumption is growing faster than any other food staple (Saito et al., 2015). This cereal is often severely affected by various organisms, but especially by insects, which are estimated to cause crop losses of about 15% of the world's rice production (Sharma et al., 2017). Other authors estimated that 37% of the global rice production is being lost each year due to different types of pests, including weeds, animals, pathogens, and viruses (Deutsch et al., 2018; Oerke, 2006; Zhao et al., 2016). These crop losses are very likely to increase due to global warming, while the estimated global rice demands are also expected to grow by at least 25% by 2030 (Li et al., 2015). In the light of this, several efforts have been committed worldwide to enhance sustainable rice pest management and improve rice production and human well-being simultaneously.

During the last decades, Integrated Pest Management (IPM) has increasingly gained importance in agriculture as an eco-friendly, efficient, and affordable way to overcome and control pests (Deguine et al., 2021; Orr, 2003; Prokopy, 2003). IPM consists of the coordinated and simultaneous application of multiple strategies to manage agricultural pests through sustainable practices that minimise risks and improve the quality of human health and environment (Deguine et al., 2021; Ehler, 2006; Prokopy, 2003; Vreysen et al., 2007). Amongst multiple strategies used in IPM, biological control is one of the most commonly applied, promoting the role of natural enemies as regulators of pest populations thus minimising the use of pesticides. However, its application in many countries is still far from being widely adopted and exploited (Legg and Gerli, 2003; Yaninek and Cock, 1989).

Amongst potential predators used to control pests in agricultural lands, bats have recently caught the attention of farmers and conservationists. Bats are the second-most diverse group of mammals worldwide, and approximately 70% of all bat species are essential insect predators (Simmons, 2005), being able to eat up to 80–100% of their weight in insects each night (Kunz et al., 2011; Kunz and Stern, 1995; Kurta et al., 1989). For this reason, many authors have supported the role of bats as natural pest controllers, thus providing essential ecosystem services to humans, along with seed dispersal or pollination (Kunz et al., 2011). Although this is a challenging research question, several studies around the world have attempted to quantify the role of bats as pest suppressors (Tuneu-Corral et al., 2023). For instance, the economic value of bats as suppressors of agricultural pests was estimated at \$22.9 billion/year in agrosystems across the USA (Boyles et al., 2011), \$390 million/year in corn fields in Brazil (Aguiar et al., 2021), \$2422/ha in macadamia orchards in South Africa (Linden et al., 2019), or more than \$1.2 million/year in rice paddies in Thailand (Wanger et al., 2014).

A broadly applied method to quantify the effects of wildlife on crop yields in tropical and temperate countries involves using experimental exclosures (Ancillotto et al., 2024; Ferreira et al., 2023; Maas et al., 2013; Maas et al., 2019; Maine and Boyles, 2015; Rodríguez-San Pedro et al., 2020). An exclosure consists of a structure covered with a mesh net that works as an exclusion cage. This cage is installed around the target plants or crop area to isolate it from certain taxa, including both vertebrates (e.g. bats or birds) and invertebrates (e.g. ants or flying insects), while allowing the free passage of other species (Cassano et al., 2016; Maas et al., 2019; Perrot et al., 2019). Therefore, this experimental design allows the assessment of the top-down effect these taxa induce on crops and, consequently, the economic quantification of their benefits. Focusing on vertebrates, exclosures have typically been applied to assess the control services offered by birds (Garfinkel and Johnson, 2015; Kellermann et al., 2008; Martin et al., 2013; Redlich et al., 2018). However, they are also

increasingly being used to study the effect of bats as pest suppressors (Ancillotto et al., 2024; Beilke and O'Keefe, 2023; Ferreira et al., 2023; Maas et al., 2013; Maine and Boyles, 2015; Rodríguez-San Pedro et al., 2019; Williams-Guillén et al., 2008). Several authors have demonstrated this technique's efficiency in assessing the role of insectivorous bats on arthropod population regulation and estimating the value of their ecosystem services. For example, in cacao plantations in Indonesia, Maas et al. (2013) reported an increase in cacao yields by more than 31% where bats were not excluded, saving (along with birds) \$730/ha each year. Another study carried out in vineyards in Chile detected relevant differences in crop yield between control and excluded areas, valuing the suppression services of bats at \$188 - \$248/ha/year (Rodríguez-San Pedro et al., 2019). In corn fields, Maine and Boyles (2015) detected 59% more corn earworm larvae/ear inside exclosures than in control areas where bats were able to exert predation pressure on adult corn earworms.

Regarding rice agriculture, only one study has assessed the effect of bat exclusion on crop damage and productivity (Bhalla et al., 2022). The authors conducted the study in India and reported a significant increase in rice plant damage due to grasshoppers, caseworms, and caterpillars when bats were excluded from rice paddies, although no differences in the final rice yield were detected, probably due to methodological limitations. The study conducted by Wanger et al. (2014) is the first precedent in estimating the economic value of bat ecosystem services as pest suppressors in rice paddies. In this case, authors used data on bat predation on the white-backed planthopper (*Sogatella furcifera*), as well as several types of information on this insect species to estimate the economic value of pest suppression services provided by the Wrinkle-Lipped Bat (*Tadarida plicata*) in rice paddies in Thailand. In Europe, Puig-Montserrat et al. (2015) studied the predation potential of soprano pipistrelle bats (*Pipistrellus pygmaeus*) on the striped rice stem borer moth (*Chilo suppressalis*) and proved the efficiency of bat boxes in attracting foraging bats to rice fields of Ebro Delta region (Spain). After the colonisation of artificial roosts by soprano pipistrelles, pest levels in the area decreased below the pesticide treatment thresholds. In this area, the economic value of the ecosystem services provided by soprano pipistrelles as pest suppressors was estimated at 21 €/ha. This value was calculated as the total avoided costs in pesticides in the presence of bats, to which the avoided yield loss would also need to be added.

With a cultivated extension of 109,411 ha, rice plantations in Spain account for 30% of the EU's rice production, being Europe's second largest rice-producing country (Gómez De Barreda et al., 2021). The main insect affecting this crop is the striped rice stem borer moth (*C. suppressalis*), a widespread pest found in Australasia, Asia, and Europe, affecting a million hectares of rice plantations yearly (Heinrichs and Muniappan, 2017; Maes, 2022). Despite the importance of rice for food security worldwide, studies using exclosures to evaluate and

economically quantify the top-down effect of bats as rice pest suppressors had not yet been conducted in Europe or any other temperate region. Thus, accurate quantification of the pest suppression conducted by bats was still lacking and broadly required by farmers and their agricultural institutions. For this reason, the main objective of this study was to use experimental exclosures in rice paddies to assess the pest-regulating effects of aerial insectivorous bats predated on one of the major rice pests worldwide, the striped rice stem borer moth (*C. suppressalis*) in Spain. Specifically, we aimed to A) compare pest pressure and damaged plants inside and outside the exclosures, B) confirm genetically whether a common bat species (common pipistrelle, *Pipistrellus pipistrellus*) was consuming this pest, C) calculate the amount of rice that would be lost in a potential scenario with no bats suppressing *C. suppressalis*, and D) economically quantify the harvest loss in the sampling location and infer potential economic losses at a regional and national level. By conducting an exclusion experiment, we wanted to provide the first robust economic quantification of the bat ecosystem services as pest suppressors in rice plantations in arid Mediterranean ecosystems.

3.2. Materials and methods

3.2.1. Study area

This study was carried out in rice plantations of Alcolea de Cinca village, located in Huesca province of the community of Aragon, in the northeast of Spain (41.720804, 0.116116, Fig. 3.1). The study area is situated at the edge of the Monegros desert, next to the Cinca River, and has a continental Mediterranean climate. The area presents a wide temperature range with cold winters, hot and dry summers, and annual precipitations of 400–650 mm concentrated especially in spring and autumn. The vegetation in this type of climate is adapted to withstand extreme temperatures and prolonged summer droughts, such as maquis shrubland and garrigue. Local communities in the study area base their economy mainly on agriculture and the paper industry (Alcolea de Cinca Town Council, personal communication). Landscape is dominated by extensive agricultural lands and a few patches of native vegetation (mostly *Pinus* spp.), riparian forest, little hills, and urban/semi-urban areas. Rice is the main cultivated cereal, since it is one of the few crops that can withstand the high salinity levels of the clayey substrate. In Alcolea de Cinca, approximately 40 farmers are growing rice, among other crops (ATRIA n° 226,190 “Arroceros de Huesca”, personal communication). However, fruit tree plantations such as peach, cherry, pear and apple are also common in the area scattered around the riverbanks. The rice variety planted in the paddies where the study took place is called Guadiamar, a medium-grain rice commonly cultivated in the Spanish autonomous communities of Aragon and Navarra. In our study area, rice is sown at the

beginning of June. The flowering and spike formation takes place during August and September, and it is harvested in October, when the grain has reached the appropriate degree of ripeness. The exclosures were built and installed on a private extension of rice fields surrounding an old farmhouse. The building hosted a breeding colony of several hundreds of common pipistrelles (*Pipistrellus pipistrellus*) roosting under the old barn's roof.

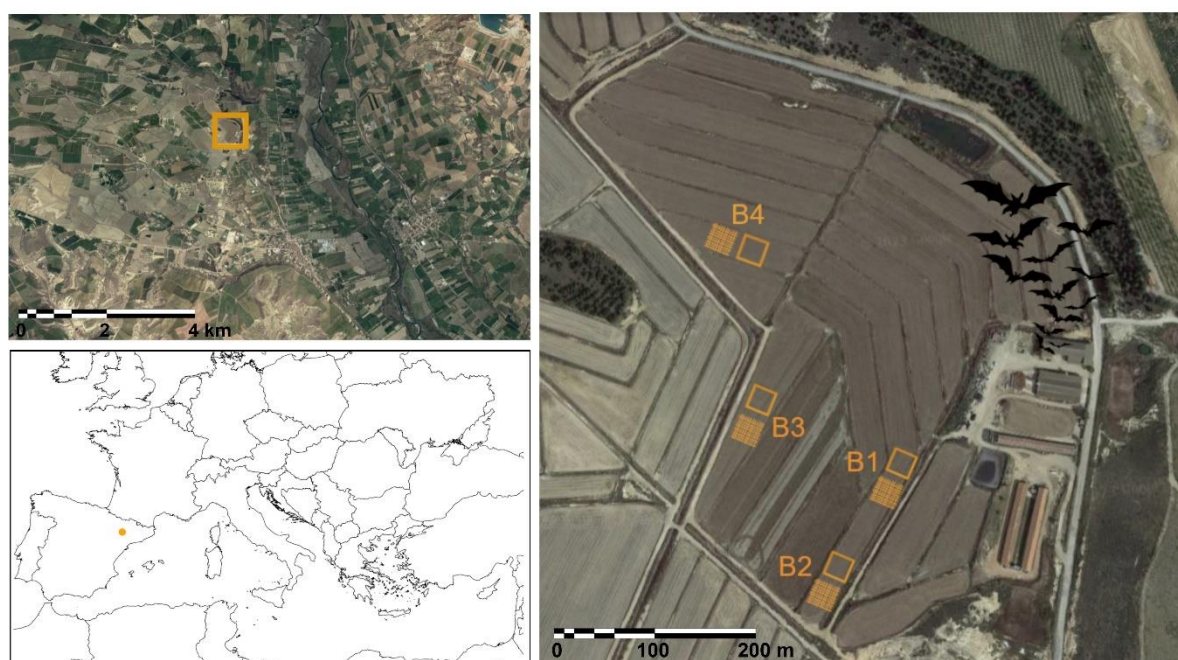


Figure 3.1. Location of the study area (on the left) and configuration of the blocks studied (block 1 'B1', block 2 'B2', block 3 'B3', and block 4 'B4'), consisting of paired 'Control' (orange square) and 'Exclusion' (orange grid) plots (on the right). The bat icons show the old barn where the colony of common pipistrelles (*Pipistrellus pipistrellus*) was found roosting under the roof.

3.2.2. Experimental exclosures installation

A total of four experimental exclosures were established in four zones of the farm from early June to mid-October 2021 (126 days). We established four blocks (one in each zone) consisting of two treatments: the exclusion plot and the control plot (without exclosure) (Fig. 3.1). The exclosures were 20 m × 20 m × 5 m in size and were installed just before the sowing, covering a surface of 400 m² of rice field each (Fig. 3.2). Because of the regular flying behaviour of *C. suppressalis* (0–3 m above the rice plants), we consider that a height of five meters is sufficient to prevent bats from hunting moths flying over the plants located within the exclosure. The structure of each exclosure was built using eight steel tubes, fixed and tensioned using wire cables. The structure's top and all four sides were covered with a net of mesh opening 4 cm x 4 cm, thus allowing a normal flow of flying insects and even small birds inside and outside the exclosures. We adjusted the mesh opening to the wingspan of striped rice stem borer moth adults, which ranged from 20 to 28 mm in outstretched wings (Hill, 1983).

The design, list of materials and instructions to build the exclosures are found in Supplementary Materials (File A2.1).

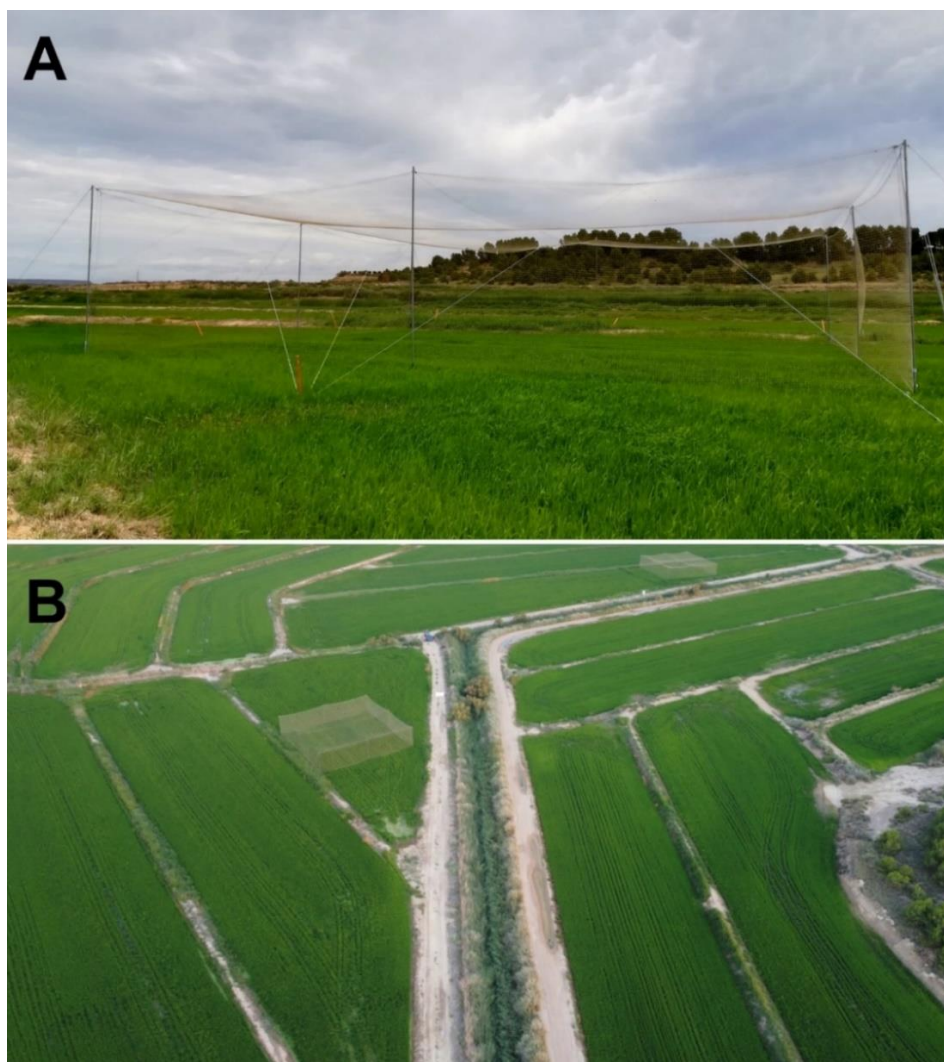


Figure 3.2. Experimental exclosure structures. A) Frontal view of one of the 400m² exclosures installed in the rice paddies of our study area (Alcolea de Cinca, Spain); B) Aerial view of the rice paddies with two of the exclosures installed.

An adjacent surface of the exact same dimensions was selected next to each of the four exclusion areas as a control plot, totalling eight surveying plots (four exclusions and four control plots). In order to minimise the possible edge effects on insect diversity and bat activity, the distance from the exclosure to the edges of the rice paddies was the same in all plots (Rodríguez-San Pedro et al., 2020). Each treatment block (exclusion/control) was separated by ≥ 100 m from the other blocks.

Because the adults of the studied pest are exclusively nocturnal (Gisbert and Eixarch, 2006; Maes, 2022), and almost all the potential nocturnal predators for these moths are insectivorous bats with the exception of a few nocturnal insectivorous bird species such as nightjars, we

decided to keep the enclosure nets closed permanently. During the day the adult moths are not active and hide under the leaves of the rice plants (Pathak and Khan, 1994; Xiang et al., 2023) and, although there may exist potential predation by diurnal birds foraging inside the rice canes, adults of this pest are much vulnerable to predation during dusk and night. Furthermore, the caterpillars of this species remain inside the rice plants' stems during the whole growth period (Gisbert and Eixarch, 2006; Maes, 2022), being rarely predated by any insectivorous vertebrate. Assuming that pest suppression pressure occurs mostly on night-flying adults, and to avoid causing inherent damage to young plants by stepping on them every day to open and close the mesh net of the enclosures during four months, we decided to leave the exclusion structures closed during both day and night throughout the study period, vastly simplifying the logistics of the experiment.

3.2.3. Rice damage assessment

In southern Europe, three moth peaks of *C. suppressalis* are generally detected from May to September, corresponding to three generations of this pest species (Fàbregues et al., 1995; Ramoneda and De Haro Vera, 1988). Adult females lay 100–550 eggs on rice plants' leaves, distributed in clutches of 60–70 eggs on average (although sometimes clutches may exceed 200 eggs) over a period of 3–5 nights (Maes, 2022; Ramoneda and De Haro Vera, 1988). After hatching, larvae enter the stems to feed by drilling them. This leads to poorly formed rice spikes and weakened stems that severely damage rice production (Maes, 2022). In order to quantify the pest suppression role of aerial insectivorous bats, we assessed the number of damaged stems in the exclusion and control plots using a handmade square structure of 1 m² made of PVC tubes. We assessed rice damage in all plots from early September (when the totality of the rice spikes was already formed) till early October (a few days before the harvest). Once per week and for four weeks, we haphazardly threw the square 15 times (thus covering 15 m²) within each plot and counted the number of stems damaged by *C. suppressalis*. Then we estimated the total amount of infested stems within the total plot surface (400 m²) by extrapolating the values obtained in the enclosure subsample (15 m²). We visually identified the infested stems by recognising the white and often vertical spikes (Fig. 3.3A). This is a consequence of the behaviour of the caterpillar of this moth, which penetrates inside the plant's stem after egg-hatching and remains inside for up to 30 days on average, feeding on the content of the rice cane (Fàbregues et al., 1995; Gisbert and Eixarch, 2006; Ramoneda and De Haro Vera, 1988). For this reason, the most visible symptom of rice damage caused by this pest is the appearance of white spikes (often more upright), contrasting a lot with healthy plants with green spikes that bend more due to the weight of the rice grain. Then, we removed each plant identified as possibly infected by *C. suppressalis* to check the exterior

(Fig. 3.3B) and interior (Fig. 3.3C) of the stem and verify whether the cause of the damage was the striped rice stem borer moth (Fig. 3.3D). We ruled out all other infections, such as the one caused by the fungus *Pyricularia* sp. In addition, by removing the plants examined, we ensured that the same spikes were not counted again during the posterior weekly counts. All counts were conducted by the same researcher to avoid biases derived from person to person.

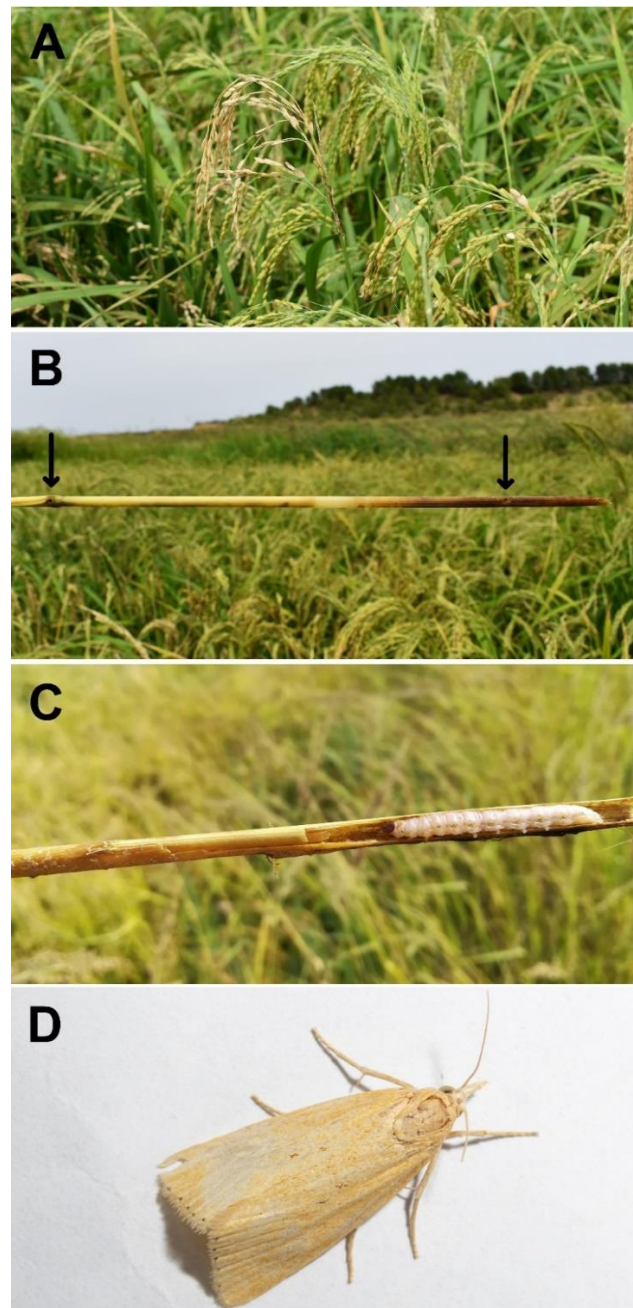


Figure 3.3. Plant affection by the striped rice borer moth. Examples of infested rice plants identified over the course of the experiments: A) Typical white rice spike of a plant infested by *C. suppressalis*; B) Stem of a rice plant collected in the field and infested by *C. suppressalis*. Adult females lay eggs on rice plants' leaves, sometimes with more than 200 eggs per laying (Maes, 2022; Ramoneda and De Haro Vera, 1988). After hatching, larvae enter the stems to feed by drilling them. The arrow on the right points to the entrance hole of the larva(e), and the arrow on the left points to the exit hole; C) Caterpillar of *C. suppressalis* found in a rice plant cane of our study area; D) Adult moth of *C. suppressalis* captured in our study area.

We tested the effect of the exclosure experiments on rice plant damage by applying a generalised linear mixed model (GLMM) with a Poisson distribution using the function *glmer* of the 'lme4' R package (Bates and Maechler, 2009). We developed two GLMMs, considering the number of damaged rice plants (number of infested stems) as the response variable in the first model, and the cumulative mean values of crop damage (cumulative mean values of infested stems) as the response variable in the second model. The treatment (Control or Exclosure) and the date of collection (julian day) were added as fixed variables, and the zone of the farm (zone) as a random variable. The resulting graphics were plotted using 'ggplot2' R package (Wickham and Chang, 2014). All analyses were performed using R software version 4.0.3 (R Core Team, 2022).

3.2.4. Bat predation of the striped rice stem borer moth

Species-specific primers in silico and in vitro testing

Adult specimens of *C. suppressalis* were collected by technicians from ATRIA n° 226,190 “Arroceros de Huesca” (an organisation of agricultural farm holders with the aim of ensuring consumer safety, sustainable use of pesticides and the promotion of integrated pest management of different crops) using pheromone traps installed in the same locality as our study area. These moths were used to test species-specific primers for the mitochondrial COI gene. DNA was extracted from 10 collected specimens using the EasySpin Genomic DNA Microplate Tissue Kit (Citomed, Odivelas, Portugal). DNA barcodes of the Folmer COI region (Folmer et al., 1994) were obtained by amplification of two smaller overlapping regions followed by HTS sequencing, as described in Rosa et al. (2023). Species-specific primers, COI_PPF2a and COI_PPR2b, designed by Puig-Montserrat et al. (2015) were tested in silico using Geneious software R10.2.6 (Kearse et al., 2012) against the produced DNA barcodes to validate complementarity between local *C. suppressalis* specimens and the designed primers. Additionally, primers were tested in vitro with DNA from the collected specimens. For that, 10 µL PCR reactions were performed using 5 µL of NZYTaQ II Master Mix (NZYTech, Lisboa, Portugal), 0.2 µL of each 10 nmol/L primer, 3.6 µL of water, and 2 µL of DNA extract diluted to 0.1 ng/µL. Cycling conditions consisted of an initial denaturing step at 95 °C for 3 min, followed by 45 cycles of denaturation at 94 °C for 45 sec, annealing at 55 °C for 60 sec, and extension at 72 °C for 45 sec, and a final extension at 72 °C for 7 min. PCR products were tested in GelRed (Biotium, San Francisco, USA) stained 2% agarose gel and visualised under UV light to check for amplification success.

Bat droppings collection

In order to determine whether common pipistrelles were consuming the striped rice stem borer moth, we collected bat faecal samples on nine different dates spread between August and September 2021, the period in which the strongest pest peak occurs, corresponding to the third generation of this insect species. To collect them, we placed a clean plastic sheet under the roof openings where bats roost. The plastic sheet was washed and placed again after each collection. We collected 15 faecal pellets individually with sterilised tweezers on each date, gathering a total of 135 samples. The samples were stored in tubes with several grains of silica gel in the freezer at -20°C .

*Molecular detection of *Chilo suppressalis* in bat guano*

DNA extraction of guano pellets followed the protocol described in Mata et al. (2021) that uses a custom lysis buffer combined with the E.Z. N.A. Tissue Kit (Omega Bio-Tek, Norcross, USA). Samples were extracted in batches of 23 plus one negative control, where no sample was added, in a dedicated non-invasive lab. Detection of *C. suppressalis* in samples was done using the primers COI_PPF2a and COI_PPR2b, as described before, except that DNA extracts were not diluted. A positive and negative control was used in every PCR reaction to validate PCR results. Amplified products were tested in GelRed stained 2% agarose gel and visualised under UV light. Samples were scored as positive for *C. suppressalis* when a band of ~ 200 bp was observed.

3.2.5. Economic quantification: Avoided yield loss and economic estimation

The economic quantification of the ecosystem services provided by bats as suppressors of *C. suppressalis* was developed in two steps, based on avoided yield loss estimations in the presence of bats. First, we collected a total of 20 mature rice spikes in order to count the number of rice grains in each spike. Using ready-to-cook rice of the same variety grown in our study area, we weighted the amount of rice grains counted in the aforementioned spike and calculated the average number of rice grains and the average grams of rice per spike. Then, using the pest affectation data obtained in our experiment, we estimated the difference in kilograms of rice harvested between the Control and Exclosure plots, as well as per hectare. Secondly, using the rice market prices in Spain (Ministerio de Agricultura, Pesca y Alimentación, 2023), we estimated the economic value of bats, considering the increase in rice harvest linked to their presence in the fields. This would be, in other words, the final economic value of the ecosystem services provided by bats as rice pest suppressors.

3.3. Results

3.3.1. Top-down effect of bat predation on pest populations

The four exclosures were successfully installed in rice paddies and remained closed during the four months of the rice growth. The baseline plant damage values in our study area (registered in control plots) at the beginning of October (a few days after the end of the third and last peak of adult activity of this pest) was 0.4% of infested stems on average, a remarkably low pest affectation. This value was calculated considering a stem density of 90 rice plants/m² (ATRIA n° 226,190 “Arroceros de Huesca”, personal communication). Bats significantly reduced the rice plant damage caused by the striped rice stem borer moth *C. suppressalis* in all four sampled zones (Fig. A2.1). The pest affectation levels were significantly higher inside the exclosure treatment plots (where bats were excluded) than in control plots (Table 3.1: $z = 34.090$, $p < 0.0001$; Fig. 3.4 and Fig. 3.5A). In fact, we detected an average of 94.5% of damage increase in the exclusion plots, with values ranging from 28.6% to 142.9% of damage increase depending on the block studied (Table 3.2). As shown in Table 3.2, the estimated values of cumulative plant damage (accumulated number of infested stems) over the study period in the exclosure plots (in the absence of bats) at least doubled when compared to control plots (in the presence of bats) in three of the four assessed blocks. The temporal variable Julian day had also a significant effect, suggesting that there were differences in rice plant damage throughout the sampling period.

When we assessed the cumulative mean values of crop damage over time, the effect of the presence of bats was even more evidenced, with pest affectation values consistently higher in exclosure treatment and approximately twice as high as in the control plots (Table A2.1: $z = 11.65$, $p < 0.0001$; Fig. 3.5B).

Table 3.1. Relationship between “infested rice stems” and (i) Treatment (Control/Exclosure) and (ii) Julian day modelled with a GLMM with a Poisson distribution ($N = 32$), assessed in our sampling site in Huesca (Spain).

Fixed effects	Estimate	SE	Z value	P value
Intercept	4.758	0.524	9.076	< 0.0001
Treatment - Exclosure	0.753	0.022	34.090	< 0.0001
JulianDay	0.037	0.011	3.587	0.0003

Random effects:

Zone $\pm$ SD = 1.089 $\pm$ 1.043

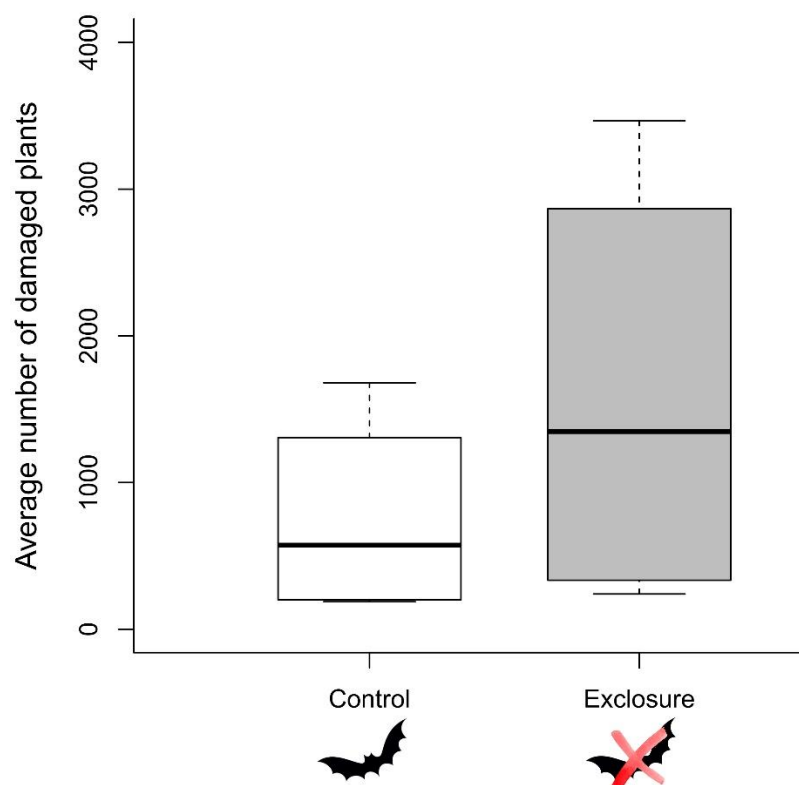


Figure 3.4. Total number of rice plants infested by *C. suppressalis* depending on the two treatments (Control/Exclosure), considering the values recorded in all blocks during the entire study period in Alcolea de Cinca (Spain). ‘Control’ shows the total number of infested plants recorded in the four plots (400 m² each) where bats were not excluded, and ‘Exclosure’ shows the total value of infested plants registered in the four plots (400 m² each) where bats were excluded. In each boxplot, the thick horizontal black bar represents the median of the data, while the lower and upper horizontal thin black bars represent the first and third quartile, respectively. The lower whiskers cover the 25% lowest values and the upper whiskers the highest 25% of the values recorded for each treatment.

Table 3.2. Estimated values of cumulative plant damage (number of infested plants) over the entire study period in the plots (400m²) for each treatment and block. The difference in crop damage as well as the percentage of increased damage between treatments, have also been included in the table.

	Control (C) (n° infested stems)	Exclosure (E) (n° infested stems)	Difference E – C (n° infested stems)	Damage increase E vs C (%)
Block 1	213	427	214	99.9
Block 2	187	240	53	28.6
Block 3	933	2267	1334	142.9
Block 4	1680	3467	1787	106.4
Mean	753	1600	847	94.5

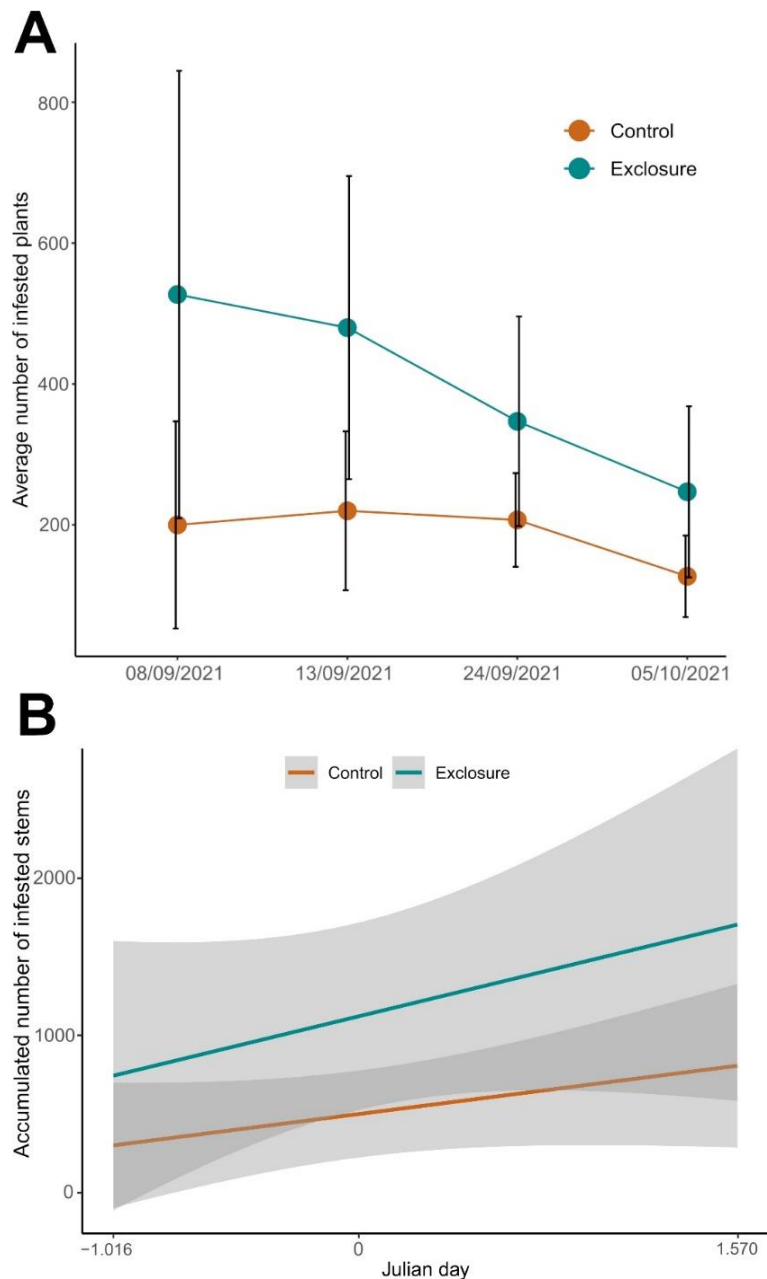


Figure 3.5. Crop damage registered throughout the study period. (A) Mean values of crop damage detected in Control plots (in presence of bats) and Exclosure plots (in absence of bats) on the four dates sampled, (B) Cumulative mean values of damaged rice plants in Control plots (in presence of bats) and Exclosure plots (in absence on bats) over time.

Using molecular analyses and despite the surprisingly low pest affectation levels detected in the region, we found evidence of predation of *C. suppressalis* by common pipistrelles *P. pipistrellus*. One of the samples collected during the study tested positive for the presence of the striped rice stem borer moth *C. suppressalis*, being the percentage of occurrence of this pest in bat guano very low (0.74%; CI: 0.02–4.06%).

3.3.2. Avoided yield loss and economic quantification of bat ecosystem services

The average number of rice grains per spike was 121.45 ± 33 . This means, in terms of ready-to-consume rice, an average amount of 3.28 ± 0.91 g of this cereal per harvested spike. Extrapolating these values to our experiment, bats might save from 200 g to almost six kg of rice in an area of 400 m^2 , which equals to $4.4 - 146.5 \text{ kg/ha}$, being the average 69.4 kg of rice saved per hectare (Table 3.3). According to the Ministry of Agriculture, Fisheries and Food of the Government of Spain (Ministerio de Agricultura, Pesca y Alimentación, 2023), the rice market prices are currently $706 - 923 \text{ €/t}$ ($0.706 - 0.923 \text{ €/kg}$), depending on the rice variety. Considering the four different scenarios that occurred in our experimental blocks, the estimated value of the ecosystem services provided by bats as suppressors of the striped rice stem borer moth ranged from a minimum of 3.11 €/ha/year to a maximum of 135.22 €/ha/year , saving on average 56.55 €/ha/year (Table 3.3).

When we extrapolate these estimates to a national level using a very simple and straightforward mathematical approach, and considering that there are currently 109,411 ha of planted rice in Spain, bats might be able to save from almost 500 tonnes to more than 16 thousand tonnes of rice each year (7.6 thousand tonnes in average). In economic terms, this would mean that bats could be saving an average of more than 6 million euros, with values ranging from 0.3 to 14.8 million euros per year in Spain (Table 3.3).

3.4. Discussion

This research evidences the ecosystem services that bats provide as suppressors of one of the most widespread rice pests in the world: the striped rice stem borer moth. Our results suggest that bat presence in rice paddies can have profound consequences on pest affectation, reducing by half the crop damage caused by this insect pest in our study area. This work also demonstrates that the striped rice stem borer moth is predated by *P. pipistrellus*, one of the most common European bat species. Bats may be preventing mean crop losses estimated of about 70 kg of rice/ha in our study area, which would be valued at 56.55 €/ha . Extrapolating our results to a national level, the value of this ecosystem services could exceed 6 million euros per year only in Spain, corresponding to more than 7 thousand tonnes of rice protected by bats.

The rice production value in Spain has been estimated at more than 250 million euros, representing almost 1% of Spain's vegetable branch production (PRV) (Ministerio de Agricultura, Pesca y Alimentación, 2023). Understanding the role of wildlife in agrosystems or,

Table 3.3. Economic quantification of the ecosystem services provided by bats in the study area (Huesca, Spain) as suppressors of the striped rice stem borer moth. The values have been calculated considering (i) the treatment plot area (400m²), (ii) one hectare (ha) and (iii) the total area of rice plantations in Spain (109,411 ha). The amount of rice and euros saved by bats have been estimated based on the results obtained in each block, including also an average value of all four scenarios. Note that these values are expressed in kilograms (kg) and euros € when considering a surface of 400m² and 1 hectare, and in thousands of tonnes (KT) of rice and millions of euros (M€) when assessing the total area of rice crops in Spain.

	400 m² (plot area)				1 ha		Total area of rice crops (Spain)	
	<i>Control damaged rice (kg)</i>	<i>Exclosure damaged rice (kg)</i>	<i>Rice saved (kg)</i>	<i>Savings (€)</i>	<i>Rice saved (kg)</i>	<i>Savings (€)</i>	<i>Rice saved (KT)</i>	<i>Savings (M€)</i>
<i>Block 1</i>	0.7	1.40	0.7	0.49 – 0.65	17.5	12.36 – 16.15	1.91	1.35– 1.77
<i>Block 2</i>	0.61	0.79	0.2	0.14 – 0.19	4.4	3.11 – 4.06	0.48	0.34 – 0.44
<i>Block 3</i>	3.06	7.44	4.4	3.11 – 4.06	109.3	77.17 – 100.88	11.96	8.45 – 11.04
<i>Block 4</i>	5.51	11.37	5.9	4.17 – 5.45	146.5	103.43 – 135.22	16.03	11.32 – 14.79
<i>Mean</i>	2.47	5.25	2.8	2.28 [1.98 – 2.59]	69.43	56.55 [49.02 – 64.08]	7.6	6.19 [5.36 – 7.01]

in this case, the effect of bats in rice plantations, is vital to help and support rice farmers in protecting their crops by reducing yield losses due to pests in an eco-friendly and sustainable way. After Bhalla et al. (2023), this is the second study worldwide assessing specifically the effect of insectivorous bats on pest populations in rice paddies by using exclusion cages. The results of the present work suggest that bats are probably playing an outstanding role as suppressors of insect pests, reducing significantly the crop damage and, unlike the above mentioned study, also yield losses caused by insect pests, thus favouring rice productivity and decreasing economic losses.

3.4.1. Top-down effect of bat predation on pest populations

In order to comprehend the results of this study, it becomes crucial to understand that in 2021 the pest levels recorded in the region by the technicians from ATRIA nº 226,190 “Arroceros de Huesca” were also very low. In fact, while the crop damage values recorded in our study area at the beginning of October were around 0.4% plants affected by the striped rice stem borer moth, the values registered in another location within the region by ATRIA technicians were even lower (0.01%; ATRIA nº 226,190 “Arroceros de Huesca”, personal communication). The differences in crop damage values registered by our team and by ATRIA technicians may probably be due to the high spatial variation of pest affectation (a relatively common occurrence in the case of *C. suppressalis*, Gisbert and Eixarch, 2006), as both parts were assessing pest incidence in specific locations of the region rather than conducting surveys in different locations throughout the region. In any case, the values of affectation in 2021 were described as “low” since up to damage levels of 3% (considered “very high”) it is not allowed to treat rice crops with pesticides (Martín Gil et al., 2017).

Despite the low regional pest values, we detected an important increase in crop damage caused by this pest in rice areas isolated within the enclosure plots, being the absence of predation by bats one of the most likely explanations, thus evidencing the pest suppression capability of these taxa. In fact, in the areas where bats were not able to hunt and therefore could not exert any predation pressure on this pest, the crop damage levels doubled the values registered in the presence of bats, except in Block 2. The smaller differences detected between the Control and Enclosure plots in this block may be due to the fact that pest incidence was lower at this particular point than elsewhere in the farm. In addition, we also hypothesise that bats may be more likely to forage in other parts of the farm with higher pest densities/affectation and thus, higher prey availability, which would further reduce the differences between the two plots in Block 2. This pattern was also observed over time, although pest incidence levels decreased in both treatments at the end of the sampling period,

coinciding with the end of the period of activity of the striped rice stem borer moth. Our results suggest that bats were playing a crucial role suppressing *C. suppressalis* even when pest population levels are low, providing a preventive protection on crops. Similar results were also found by Puig-Montserrat et al. (2015) in the Ebro Delta, where bats seemed to consume rice borers in rice fields, even when they were found at very low abundances; or by Bhalla et al. (2023), who also reported a significant increase in insect pest damage when bats were excluded in rice paddies in India (although no differences in final rice yield were detected). Our findings also support previous studies that used exclusion structures to assess the effect of insectivorous bats and that also reported a decrease of insect herbivory in the presence of bats in other agrosystems such as corn (Maine and Boyles, 2015), macadamia (Bouarakia et al., 2023; Linden et al., 2019), cacao (Cassano et al., 2016; Ferreira et al., 2023; Maas et al., 2013; Vansynghel et al., 2022) or vineyards (Rodríguez-San Pedro et al., 2020).

The differences in crop damage detected between blocks (not between treatments) were not surprising since the incidence of *C. suppressalis* is usually highly heterogeneous: while in some fields there is almost no affectation, it causes considerable damage in the neighbouring paddies (Gisbert and Eixarch, 2006; Ramoneda and De Haro Vera, 1988). This is generally due to a combination of factors that are difficult to monitor, including the proximity to overwinter reservoirs of this pest, plant vulnerability due to soil composition, water availability or diversity of plant species in the vicinity (Gisbert and Eixarch, 2006). In addition, the limited dispersal capability of the larvae also favours this uneven pest incidence, as they can move to other rice plants but usually attack the closest canes given the caterpillar's low mobility (Ramoneda and De Haro Vera, 1988). All this leads to a fairly typical localisation of the pest in focus of infection, which in this study was detected mostly in the blocks 3 and 4, with significantly higher values of pest incidence than in blocks 1 and 2. All plots were adjacent to a road for easy access to the different sampling points, the rice variety was the same, and the surrounding plant diversity was also the same. However, blocks 3 and 4 were closer to an area of reeds, which are known to be a reservoir for this pest, especially during the winter months (Gisbert and Eixarch, 2006). This fact could have facilitated a greater pest impact at a shorter distance of these reeds, so that blocks 1 and 2 would have been less affected for being at greater distance from these potential reservoirs.

The generalised low pest levels registered in the study region and the high density of bats in the area (the breeding colony located in the farmhouse alone already comprised several hundreds of individuals) can also explain the very low pest occurrence detected in *P. pipistrellus* guano through the molecular analyses (low availability of *C. suppressalis* for the number of bats foraging in the area). However, it is well-known that bats often exploit the most abundant resources, taking advantage of insect emergences and blooms (Gonsalves et al.,

2013; McCracken et al., 2012; Puig-Montserrat et al., 2020). Therefore, we suspect that in potential scenarios with higher pest levels (which usually occurs every 3–5 years; ATRIA technician n° 226,190 “Arroceros de Huesca”, personal communication), the effect of bat predation on *C. suppressalis* populations could easily be magnified, detecting higher percentages of occurrence of this pest in the diet of *P. pipistrellus*, probably leading to greater differences between the two treatments. Our results also showed the preventive protection effect bats may exert on crops, reducing significantly plant damage even when pest levels are very low. Further, our findings also support the increasingly proposed strategy of using bats as natural samplers (Maslo et al., 2017; Montauban et al., 2021). Sampling insect populations by assessing the content of bat guano samples genetically can be a useful and efficient way to detect certain insect species of interest such as agricultural pests, being able to identify them in a specific region even when their populations are still very low and hard to detect using traditional methods.

3.4.2. Avoided yield loss and economic quantification of bat ecosystem services

Regarding the ecosystem services quantification, we estimated that bats avoided mean crop losses of 69.4 (4.37 – 146.5) kg of rice per hectare. In Huesca province, the region where the study was carried out, the average amount of rice harvested per hectare is 6,000 kg (4,000 kg/ha – 8,000 kg/ha), with variations depending on the year (farmer belonging to the rice cooperative “Arrocera del Pirineo”, personal communication). Thus, this would mean that, under our study scenario, bats could prevent losses of 1.2% (0.7% – 2.4%) of the total rice harvest per hectare, saving an average of 56.55 €/ha to farmers. The study led by Puig-Montserrat et al. (2015) estimated the ecosystem services provided by bats in rice fields of Ebro’s Delta (also located in Spain), obtaining a minimum value of 21€/ha, which corresponded to the avoided pesticide costs in the area. It is important to note that our study only addressed the ecosystem services provided by nocturnal predators related to the avoided yield loss and did not consider the avoided pesticide costs. Thus, considering the costs related to these agrochemical treatments would further increase the total amount of savings provided by bats in this agrosystem. Fortunately, the use of pesticides to treat *C. suppressalis* has been reduced over the last few years. The employment of biotechnological techniques of massive capture with pheromone traps and mating disruption by using pheromone diffusors are the most frequently applied strategies in Spain (Martín Gil et al., 2017). Further, bats are also likely to decrease the management costs and the environmental impact related to the use of pesticides in other crops by reducing pest incidence and potentially keeping the insect pest levels under the minimum thresholds established for the application of agrochemical products.

At national level, our estimate indicates that bats could be protecting more than 7 thousand tonnes of rice on average, saving more than 6 million €/year, and potentially reaching 16 thousand tonnes of rice valued at more than 14 million euros annually only in Spain. However, it is important to consider that these estimates have been obtained by simply extrapolating the results from a specific area of the country to the whole territory. While this is an interesting exercise and approximation, these values can vary depending on the spatial scale, rice variety, pest levels, bat population structure, treatment techniques applied to fight this pest or rice market price fluctuation, among other factors. The expertise of other professionals such as economists, agronomists and land-managers would also be needed to obtain more accurate estimates at national level. The study carried out by Wanger et al. (2014) is the only previous reference calculating bat ecosystem services as suppressors of rice pests at national level (in this case in Thailand), using data on the Wrinkle-Lipped Bat (*Tadarida plicata*), pest distribution, and an iterative modelling approach. Authors calculated that bats were preventing crop losses of almost 2,900 tonnes of rice per year, which would mean more than 1.2 million USD. In developing countries such as Thailand where the diet of their citizens is based on rice, the importance of bats on food security becomes more evident. In this study, the authors estimated that bats were ensuring rice meals for almost 26,200 people annually.

3.4.3. Experiment limitations

We also want to point out that, although the use of experimental enclosures represents the best current approach to quantify the ecosystem services in the field, the bat predation effect that we detected might have been greatly underestimated due to several methodological limitations. For instance, although the height of the enclosures was five meters and adults of *C. suppressalis* usually fly close to rice plants (Kondo and Tanaka, 1991; Shaver et al., 1991), individuals found within the excluded area may be able to leave the structures being thus vulnerable to predation. For this reason, we consider our results particularly conservative, which further reinforces the powerful effect of bats suppressing *C. suppressalis* populations.

Another limitation of this experiment was that our exclusion cages were closed permanently, which would also imply the exclusion of other flying insectivorous vertebrates, including birds. As explained in the methods section, small-medium birds were able to get in and out of the enclosures, being regularly observed inside the cages. Although they were not able to fly as freely as outside the structures, insectivorous diurnal birds such as reed warblers, sedge warblers or zitting cisticola, that usually forage among the leaves and canes of rice plants, could have easily accessed the enclosure structures, potentially preying on inactive adult moths hidden inside vegetation. Furthermore, as mentioned previously, larvae of the striped

rice stem borer moth remain inside the stem of the plant, being rarely predated by any flying vertebrate. Taking all this into account, we assume that the suppression pressure of this pest occurs mostly during night and is led mostly by bats. Even so, since we did not monitor birds inside and outside of the exclosures, we cannot rule out the possibility that diurnal birds also contributed to the pest suppression effect observed in rice paddies of our study area, as described by several authors in studies developed in other type of crops such as cacao (Ferreira et al., 2023; Maas et al., 2013), coffee (Karp et al., 2013), or macadamia (Bouarakia et al., 2023; Linden et al., 2019) plantations. For this reason, we would strongly recommend bird monitoring for future research when applying the same methodology as in this study, or by opening and closing exclosures daily.

3.4.4. Implications for farmers and bat conservation

Quantifying the benefits provided by natural enemies of insect pests in agriculture is essential to rise awareness among farmers, and promote their use as an alternative and more sustainable way to fight harmful insects such as the striped rice stem borer moth. Therefore, we highlight the importance of using methodologies like exclusion experiments that allow the economic valuation of the ecosystem services provided by bats and other insectivorous vertebrates, a topic of great interest to farmers, governments, and stakeholders. The implementation of IPM strategies that favour their efficiency as natural suppressors of insect pests would enhance bat conservation and benefit arthropod communities and soil quality (avoiding or reducing the use of agrochemicals), leading to healthier and more biodiverse agrosystems that are more resilient to pest outbreaks (Altieri, 1999; Baweja et al., 2020; Ferraro and Pimentel, 2000; Hoy, 2015; Redlich et al., 2021; Sánchez-Bayo and Wyckhuys, 2019).

Furthermore, we demonstrated that promoting bat conservation is essential not only in natural habitats but also in agricultural matrices that several species use as foraging habitats. As proposed by many authors, high landscape heterogeneity, presence of natural corridors, proximity to water sources, reduction of agrochemical use or availability of natural/artificial roosts are some of the management strategies to be applied to promote and enhance the viability and establishment of bat populations in farmlands (Heim et al., 2017; Kahnonitch et al., 2018; Kalda et al., 2015; Monck-Whipp et al., 2018; Tortosa et al., 2023; Tuneu-Corral et al., 2023). Thus, favouring healthy and diverse bat populations in agrosystems can increase their ecosystem services as well as the resilience of these habitats against pest outbreaks. More research and similar studies in other regions are also necessary to better understand the role of insectivorous bats in agrosystems as predators of herbivorous pests. At the same

time, as we are not able to distinguish between bat services and disservices in this study, it would be important to evaluate the negative impacts that bats might bring to the agrosystems, such as consuming insects that might also act as natural enemies of pests. Molecular analyses can help providing an integral vision of all trophic interactions that are occurring, which is an essential step towards making appropriate decisions and implementing the most suitable measures to promote productive but healthy and sustainable agrosystems.

3.5. Conclusions

This is the first time that experimental exclosures have been used in Europe to assess the top-down predation effect of bats in rice plantations. We quantified the ecosystem services provided by bats as suppressors of one of the most harmful rice pests in the world: the striped rice stem borer moth. Our results evidence bats' important role in agricultural landscapes, specifically in rice paddies, reducing plant damage by more than half. This can have profound economic consequences, preventing crop losses estimated at several thousand tonnes of rice each year, and contributing to bat conservation by farmers and governments. Applying conservation and management measures that favour bat and other insectivorous vertebrate populations in agrosystems is vital to enhance their efficiency in suppressing pests, increasing yield and productivity in a sustainable and eco-friendly way. More research is needed to better understand the trophic interactions occurring in agrosystems and to establish management strategies that favour ecosystem services wildlife provide to human society.

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Chapter 4 – Pest suppression effect of bat ultrasounds



Striped rice stem borer moth (*Chilo suppressalis*) on a rice plant leaf. ©Carme Tuneu-Corral

Article III:

Tuneu-Corral, C., Puig-Montserrat, X., Flaquer, C., Jordà, X., Rebelo, H., Cabeza, M., López-Baucells, A. (*submitted to Pest Management Science*). Landscape of fear in rice paddies: effect of bat ultrasounds on the egg production of a pest insect.

Article III – Landscape of fear in rice paddies: effect of bat ultrasounds on the egg production of a pest insect

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Abstract

Predator-prey interactions are major drivers of species coevolution. Insectivorous bats emit ultrasonic pulses to orientate themselves and to detect and pursue prey in flight. On the other hand, several nocturnal lepidopterans have developed auditory organs that allow them to detect echolocating bats and change their normal behaviour to reduce predation risk, a phenomenon included within the 'landscape of fear' concept or prey's perception of predatory risk. In this study, we assessed whether the presence of bat ultrasounds affects the egg production of the tympante moth species *Chilo suppressalis*, one of the most widespread rice pests in the world. Adults of *C. suppressalis* were captured in rice fields in Spain and kept in captivity in the presence and absence of artificially broadcasted bat ultrasounds. The number of egg clutches laid per female and the size of these clutches were evaluated in both scenarios. While no differences were found regarding the number of clutches laid per female, the clutch size was substantially smaller in the presence of bat ultrasounds, observing a reduction in the number of eggs of up to 46%. This decrease in egg production may be a consequence of delays in adult mating or the inhibition or interruption of oviposition in females, which would alter their normal conduct to minimise their exposure to potential bat predators. Thus, acoustic dimension may have profound implications for farmers, as a reduction of the reproductive success of *C. suppressalis* could also lead to a significant decline in crop damage and yield loss, thereby increasing farmers' economic savings. Promoting stable bat

populations in agrosystems can be very beneficial since, in addition to suppressing harmful insects by predation, they likely reduce pest levels simply by emitting ultrasounds into the environment.

Keywords

Biocontrol, rice production, bat ultrasounds, oviposition, integrated pest management (IPM), pest suppression

4.1. Introduction

Predator-prey interactions are driven by several factors, being predation (also known as the consumptive effect of predators) the most obvious and popular element influencing this interplay. However, there are also non-consumptive effects of predators that have been largely understudied (Weissburg et al., 2014). The ‘landscape of fear’ is a concept encompassed within these effects, which has been increasingly investigated in the last decades (Gallagher et al., 2017; Gaynor et al., 2019; MacKay et al., 2021). The landscape of fear is the prey’s perception of predatory risk and suggests that the landscape use is driven by the fear of being predated or injured, and it has a strong influence on the temporal and spatial dynamics of the predator-prey distribution (Laundré et al., 2010). Prey’s evasive responses to avoid predation as a result of fear perception can alter significantly their normal behaviour and even induce important physiological and morphological changes (Brown and Chivers, 2005; Peckarsky et al., 2008). Therefore, it becomes essential to further study the landscape of fear to broaden our understanding of non-consumptive effects in insect systems to better interpret ecological processes such as bat-prey interactions and coevolution (Hermann and Landis, 2017).

Bats are considered among the most important nocturnal insect predators due to their complex and evolved echolocation system (Boyles et al., 2011; Conner and Corcoran, 2012). Most species use ultrasonic pulses in flight to orientate themselves in the dark as well as to detect and pursue prey in flight. On the other hand, several nocturnal lepidopterans (one of the main insectivorous bat’s prey) have developed tympanic organs or high-frequency ‘ears’ that are sensitive to ultrasounds (Conner and Corcoran, 2012; Ratcliffe et al., 2009). These auditory systems allow them to detect echolocating bats and change their normal behaviour to reduce the chances of being predated, providing a clear survival advantage over non-tympanate species (Ratcliffe et al., 2008; Yack et al., 2007).

In terms of the non-consumptive effects of bats on moth populations, published evidence demonstrates that, in the presence of synthesised ultrasounds, some male moths reduce their activity towards pheromones, and both females and males can cease sexual calling or spermatophore transfer, decreasing mating success (Acharya and Mcneil, 1998; Huang et al., 2003; Huang and Subramanyam, 2004; Skals et al., 2005). Ratcliffe et al. (2008) observed that sound-producing moths do not reduce flight activity to bat-like sounds, while silent moths do, demonstrating the advantages of acoustic aposematism. Some authors have also proved that egg production and larval weight can also be negatively affected by the presence of ultrasounds (Huang et al., 2003; Huang and Subramanyam, 2004). Furthermore, it has also been observed that bat ultrasound emission could delay mating after adult emergence, causing a diminution of egg viability (Akinneye and Ashamo, 2009). These findings suggest that the acoustic environment can profoundly affect agriculture as some of the most damaging agricultural pest insects are nocturnal Lepidoptera (Wagner, 2013).

Several authors have supported the role of bats as insect pest suppressors due to their strong predation power and high insect consumption rates (Tuneu-Corral et al., 2023), providing ecosystem services valued at \$22.9 billion/year in croplands in the USA (Boyles et al., 2011), \$390 million/year in corn fields in Brazil (Aguiar et al., 2021) or more than €6 million/year in rice paddies in Spain (Tuneu-Corral et al., 2024). However, the pest suppression potential of bats has been traditionally attributed to predation, without considering the repercussions of ultrasound emission.

It is only in recent decades that the effect of bat ultrasounds on insect pest populations has been studied and highlighted (Gillam et al., 2011; Huang et al., 2003; Nakano et al., 2022, 2009; Walker, 1996). However, most research has been carried out in laboratory conditions, and some did not use bat-like ultrasound emissions during the experiments. One of the few studies conducted in natural habitat was led by Gillam et al. (2011), who found no effect of bat ultrasound mimicry on the flight activity of *Helicoverpa zea* (a tympanate moth) in cotton fields, suggesting that it seemed more advantageous for the moth to take the risk of being predated in order to increase the chances of mating. More recently, Nakano et al. (2022) reported a drastic reduction in the affectation (in terms of egg numbers and crop damage) of three *Spodoptera* spp., using an ultrasonic playback with bat-like pulses designed artificially in the laboratory. However, due to the limited information available, further research is needed to better understand the role of the acoustic dimension in agricultural pest suppression.

The striped rice stem borer moth, *Chilo suppressalis*, is one of the world's most widespread and harmful rice pest. This lepidopteran species might be able to detect bat echolocation pulses because it belongs to the family Crambidae, characterised by the presence of a paired of tympanic organs in the second abdominal segment (a tympanum supported by two

tympanic chambers). Furthermore, males of *C. suppressalis* can whisper extremely low-intensity ultrasonic courtship songs close to females to increase mating success (Nakano et al., 2009). This fact evidences the hearing ability of this moth species, which further increases the likelihood that they can recognise bat ultrasounds and thus alter their normal behaviour when detecting bats foraging nearby.

In Spain, a study developed in rice paddies in Ebro Delta demonstrated the critical role of the soprano pipistrelle bats (*Pipistrellus pygmaeus*) in suppressing *C. suppressalis*, as well as the efficiency of installing bat boxes to attract bats to rice paddies and further reduce crop damage (Puig-Montserrat et al., 2015). Recently, the ecosystem services provided by common pipistrelles (*Pipistrellus pipistrellus*) as predators of the same pest were quantified for the first time by excluding bats from certain rice field areas. The results suggested that bats might save up to 70 kg of rice per hectare, which in economic terms would be translated into an average of 56€/ha·year (Tuneu-Corral et al., 2024). However, these findings only considered the suppressive potential of bats as pest consumers. So far, no studies have assessed the effect that bats might exert on *C. suppressalis* populations by simply emitting ultrasound into the environment, triggering behavioural changes on this insect.

In this study, we aimed to investigate whether ultrasounds emitted by free-flying bats while foraging induce alterations in the normal behaviour of *C. suppressalis* adults, triggering detrimental effects on the egg production of this pest, thereby enhancing its suppression in rice fields. Specifically, we wanted to assess whether the presence of bat ultrasounds in the environment produced alterations (i) in the average number of egg clutches laid per female and (ii) in the size of the clutches (i.e. number of eggs in each clutch). We hypothesised that, similar to other tympanate moths, *C. suppressalis* could detect bat ultrasounds and alter their normal conduct to reduce predation risk. This behavioural shift is likely to impact reproductive success and potentially reduce egg production.

4.2. Materials and meethods

4.2.1. Study area

This research was conducted in Alcolea de Cinca, Huesca Province, Spain. This rural village is located on the banks of the Ebro River at the edge of the Monegros Desert. The area's continental Mediterranean climate is characterised by a wide temperature range with cold winters and hot, dry summers. Rainfall mainly occurs in spring and autumn, with an annual precipitation of 400-650 mm. The vegetation, such as maquis shrubland and garrigue, is adapted to extreme temperatures and summer droughts. Rice is the main cultivated cereal

due to its tolerance to the high salinity of the clayey substrate. Additionally, fruit tree plantations, including peach, cherry, pear, and apple, are common around the riverbanks.

The study was conducted in two scenarios: fieldwork on a farm with large extensions of rice fields surrounding an old building that hosted a large breeding colony of common pipistrelles (*P. pipistrellus*) (see Tuneu-Corral et al., 2024 for further details) and a captivity experiment inside a traditional house belonging to the same farmer in the nearby rural village.

4.2.2. Experimental enclosures

We built ten handmade 1m³ enclosures, consisting of cubical structures made of PVC pipes and covered with mosquito netting (Fig. 4.1A). These enclosures were used to keep adult *C. suppressalis* individuals alive and allow them to lay eggs during their 3-5 day adult stage. Each enclosure was provided with different materials as potential surfaces for egg laying: brown corrugated cardboard, green corrugated cardboard, wax paper, and living rice plants. To simulate the humidity of rice paddies, we placed a tray filled with water in each enclosure, covered with a grid to prevent the moths from falling in. Additionally, we provided a small bowl of water with sugar for hydration and nutrition. Microclimate conditions and captivity methods were assessed and supervised by entomologist experts. Five enclosures were placed in a room without bat ultrasound presence ('control' room), while the remaining five were placed in a room where we broadcasted the typical nocturnal soundscape of rice fields, including bat ultrasounds ('ultrasound' room). The two rooms were next to each other, had the same size and structure, and were located on the ground floor of a house in a small and quite rural village (Ontiñena, 530 inhabitants). Both rooms had the same orientation and windows of identical dimensions facing outside. Therefore, we confirmed that both rooms experienced the same temperature, humidity, acoustic and lighting conditions, which could vary according to the external climate, but affecting both spaces equally.

4.2.3. Nocturnal soundscape recording and broadcast

At the beginning of the experiment, we recorded the entire soundscape of a typical night in rice paddies of our study area, including the echolocation calls of foraging bats. Recording started 30 minutes before sunset and continued until 30 minutes after sunrise. We used an acoustic ultrasound detector Song Meter SM2Bat+ (frequency range: 256 kHz) recording continuously (with no trigger), with an SMX-US omnidirectional ultrasonic microphone (Wildlife Acoustics, Maynard, Massachusetts, USA), placed 2 meters above the ground to avoid echoes in the recordings. To improve the playback quality, we cleaned up the background noise from the recordings using Audacity software. This recording was subsequently

broadcasted from sunset to sunrise in the 'ultrasound' room using a handmade bat lure, based on the design proposed by Vrignauldt Jean-Do, (<https://framagit.org/PiBatRecorderProjects/bat-player>), and subsequently adapted by Dr. Xavier Jordà, from IMB-CNM institution (CSIC Cerdanyola del Vallès, Spain) (Fig. 4.1B).

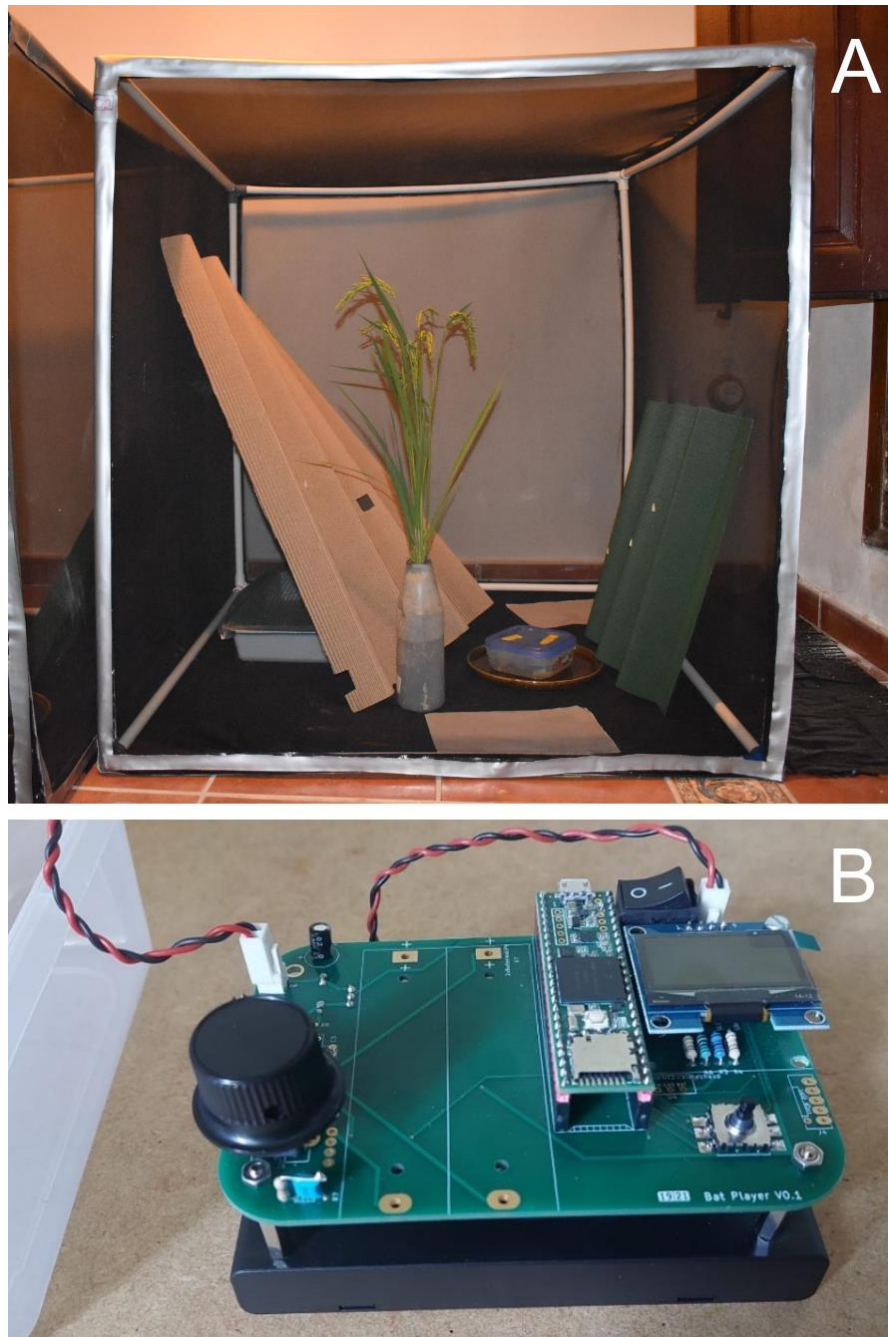


Figure 4.1 Key elements to conduct the captivity experiment to quantify the behavioural responses of *C. suppressalis* towards bat echolocation calls: A) 1m³ enclosure with a living rice plant, corrugated cardboard (green and brown), wax paper, water container (behind the brown corrugated cardboard) and a small bowl with water and sugar (in the middle); and B) one of the lures used to broadcast the nocturnal soundscape (including bat echolocation calls) recorded in rice paddies.

4.2.4. Moth captures

Flying adults of *C. suppressalis* were captured alive in rice paddies for seven nights spread between early August and mid-September 2021. Capture sessions took place from approximately 20:30h to 1:00h, coinciding with the peak activity of this pest species. We used two different methodologies for capturing moths: passive autonomous UV-light-traps (Pachkin et al., 2022) and active manual light traps (Kammar et al., 2020). For the passive method, we placed two autonomous handmade UV-light-traps at different points in the rice paddies for five hours each sampling night. These traps consisted of a bucket, a funnel, a cotton bag, a methacrylate, and UV light LEDs powered by a power bank (Fig. A3.1A). At the end of each nocturnal survey, we collected all *C. suppressalis* individuals in small plastic pots and released all other insects. For the active method, we installed manual light traps at two different points in the rice fields each sampling night. These traps consisted of a 2,5 x 1 m white sheet illuminated with a UV-light torch (Alonefire 395 nm; 128 LED) supported on a tripod (Fig. A3.1B). Two people continuously monitored the sheets and manually captured *C. suppressalis* adults, which were also kept in small plastic pots. All captured individuals were transferred to captivity cages, placing half of them in 'control' enclosures and the other half in 'ultrasound' enclosures, without necessarily filling all captive cages.

4.2.5. Experimental design

Four to six moths were kept in each cage (regardless of sex, which was inspected post-mortem) for 3–5 days, which is the average duration of their adult stage (Fàbregues et al., 1995; Gisbert and Eixarch, 2006; Ramoneda and De Haro Vera, 1988), until all of them had died. We ensured a balanced number of enclosures and moths in each room to evenly expose them to both treatments. After recording the necessary data (see details below), the enclosures were cleaned to host the new *C. suppressalis* individuals. The rice plants and other surfaces were replaced as needed, and the water containers and sugar bowls were refilled. New capture sessions were conducted at the end of each cycle to replenish the enclosures. In both rooms, windows were open, and lights were turned on during the day and off at night to minimise the effects of captivity conditions. In the 'ultrasound' room, two lures broadcasted the nocturnal soundscape in two different directions to ensure that all enclosures received the ultrasounds effectively and equally.

Once all moths in an enclosure had died, we visually inspected all structures to identify and count the total number of egg clutches on the surfaces of corrugated cardboard, wax paper, or rice plants. Scattered eggs found on the mosquito netting were not included in the data. We then counted the number of eggs in each clutch using a binocular loupe with 10X/20X magnification (Motic, China). Finally, we determined the sex of all individuals by identifying the

ovipositor of females (egg-laying organ, Fig. 4.2A) or the claspers of males (genital structures used to grip the female prior to intromission, and, in some species, enhance male control of copulation) located at the end of the abdomen (Fig. 4.2B), allowing to calculate the male/female sex ratio for each enclosure.

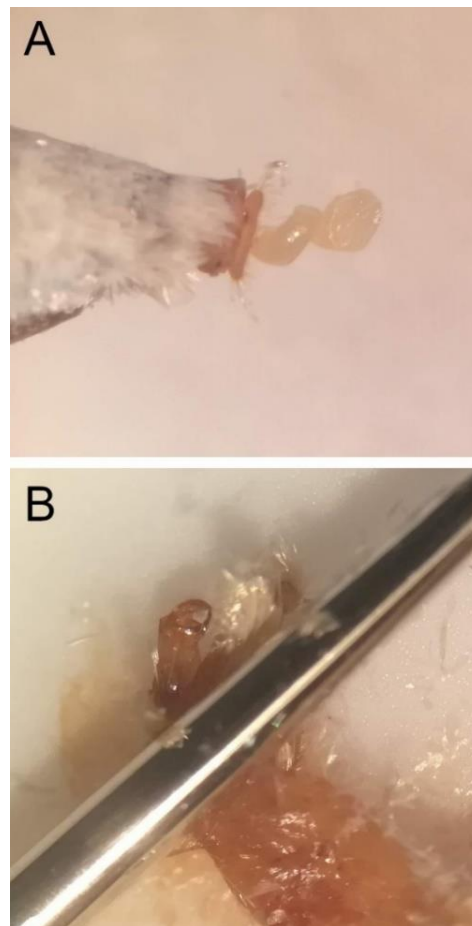


Figure 4.2. Reproductive organs of *C. suppressalis* moths were used to identify the sex of all adults included in the study. The identification features were the ovipositor of the females, and the claspers for the males. A) ovipositor of a female with two eggs still attached; B) male claspers. These images were obtained using a binocular loupe with 10X/20X magnification.

4.2.6. Statistical analyses

In first place, we determined the distribution of the our data by applying the *fitdistr* function from the R package 'MASS', confirming a negative binomial distribution. Then, to test the effects of broadcasting bat ultrasounds on the egg production of *C. suppressalis* we used two different approaches:

First, we conducted Generalised Linear Models (GLMs) using the *glm.nb* function from the R package 'MASS' (Venables and Ripley, 2002). The response variable of these models was 'number of clutches per female', and the explanatory variables were 'treatment' (control/ultrasounds), 'sex ratio,' and 'time' (experimental rounds along the study period). The

variable 'time' was included to account for variations due to the phenology of *C. suppressalis* and external climate conditions during experiments, which would equally affect both rooms. In this model, we considered the captivity enclosures as the experimental units or replicates within seven experimental rounds. We ran seven GLMs to test all combinations of predictor variables, and we chose the model with the lowest corrected Akaike Information Criterion (AICc), which is recommended for small sample sizes (Cayuela and De la Cruz, 2022).

Second, we used Generalised Linear Mixed Models (GLMMs) with negative binomial distribution, applied via the *glmmTMB* function from the R package 'glmmTMB' (Magnusson et al., 2018). Here, the response variable was the clutch size 'number of eggs per clutch,' and the fixed factors, or explanatory variables, were the same as in the previous case: 'treatment,' 'sex ratio,' and 'time.' In these models, the egg clutches were the experimental units. Therefore, we included 'enclosure' as a random effect to account for correlations among observations within the same cage, such as variability due to egg clutches laid by the same female. We ran seven GLMMs to test all combinations of fixed effects, and the model with the lowest corrected Akaike Information Criterion (AICc) was chosen. We plotted significant effects of variables using the *ggboxplot* function from the R package 'ggpubr' (Kassambara, 2020).

Additionally, we evaluated the preference for various materials (brown corrugated cardboard, green corrugated cardboard, wax paper, and rice plant leaves) as surfaces for egg laying by calculating the total percentage of clutches laid on each material recorded in the experiment. All analyses were conducted using R software version 4.4.0 (R Core Team, 2022).

4.3. Results

After seven nights of surveys, we captured a total of 188 adult individuals of *C. suppressalis*. These moths were placed in captivity cages across 17 paired experimental settings: 94 individuals were allocated to 17 enclosures in the 'control' room, and 94 moths were placed in 17 enclosures in the 'ultrasound' room. These paired experiments were conducted over seven different time periods or rounds, corresponding to the seven different nights of captures. After all experimental rounds, we confirmed a total of 60 females and 40 egg clutches in 'control' enclosures, and 76 females and 41 egg clutches in 'ultrasound' enclosures (Fig. 4.3). No significant effects on the number of egg clutches per female were observed among treatments, sex ratio, or time periods. In fact, the model that included only 'treatment' as an explanatory variable showed the lowest AICc value, and indicated that this variable did not significantly influence the number of egg clutches per female either (Table A3.1). The average number of

egg clutches per female, based on values obtained from each enclosure, was 0.79 in the 'control' room and 0.51 in the 'ultrasound' room.

When assessing the impact of predictor variables on clutch size, we found no effect of sex ratio and time. However, substantial differences were detected between the two treatments. The model that included 'treatment' and 'time' as explanatory variables showed the lowest AICc value, and indicated a significant effect of 'treatment' on clutch size: the number of eggs per clutch in the 'control' room was significantly higher than in the 'ultrasound' room (p-value = 0.0454, Table 4.1, Fig. 4.4). The mean number of eggs per clutch was 56.5 in 'control' enclosures and 29 in 'ultrasound' enclosures. Our results suggested a potential reduction in egg production, in terms of clutch size, of up to 46% in the presence of bat ultrasounds.

In both the 'control' and 'ultrasound' rooms, the most frequently used surface for egg-laying was rice plant leaves (48.1% and 48.8%, respectively), followed by brown corrugated cardboard (32.1% and 32.5%, respectively), green corrugated cardboard (12.3% and 15%, respectively), and wax paper (7.4% and 5%, respectively).

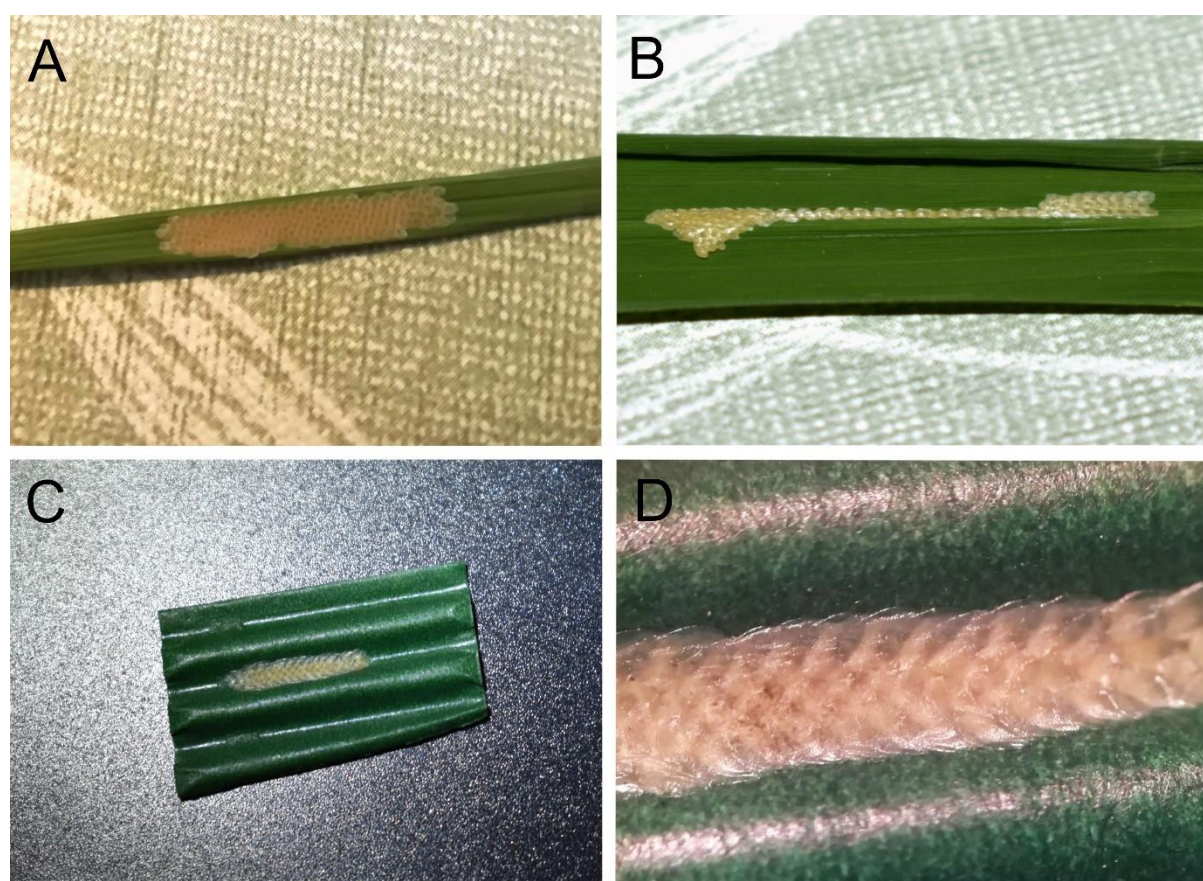


Figure 4.3. Some of the egg clutches found in the captivity enclosures. The first two pictures (A, B) show clutches on rice leaves, and the third (C) is an egg clutch laid on green corrugated cardboard. The last picture (D) was taken through the binocular loupe (10X/20X magnification), showing a zoomed view of the eggs grouped in the previous clutch on the green corrugated cardboard.

Table 4.1. Generalised Linear Mixed Model (glmm.TMB) results for the model with the lowest AICc value assessing the effect of ‘treatment’ (control/ultrasounds) and ‘time’ on ‘clutch size’ (number of eggs in each clutch). Predictors with significant results (p-value < 0.05) are highlighted in bold, which indicates significant effects on the size of the egg clutches.

GLMM				
	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	3.487	0.411	8.491	<2e-16
Treatment (ultrasounds)	-0.708	0.354	-2.001	0.0454
Time	0.141	0.087	1.613	0.1067

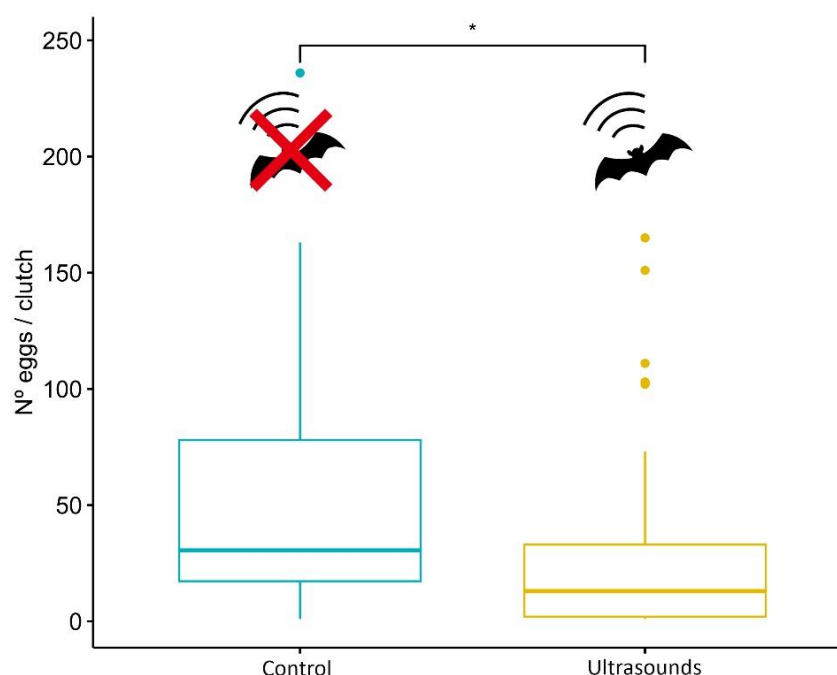


Figure 4.4. Significant differences in clutch size (n° of eggs / clutch) were found between experimental treatments ‘Control’ and ‘Ultrasounds’. Significance was tested using a Generalised Linear Mixed Model (GLMM). In each boxplot, the thick horizontal bar represents the median of the data, while the lower and upper horizontal thin bars represent the first and third quartile, respectively. The lower whiskers cover the 25% lowest values and the upper whiskers the highest 25% of the values recorded for each treatment. * indicates significance with p-value ≤ 0.05.

4.4. Discussion

In this study, we investigated, for the first time to date, the effect of bat ultrasounds on the egg production of the striped rice stem borer moth, *C. suppressalis*, employing experimental designs under captivity conditions. Using adult individuals directly captured in rice paddies, we found no differences regarding the number of egg clutches laid per female in the presence or absence of bat echolocation calls. However, we observed a significant effect in clutch size, with egg clutches laid by females exposed to ultrasounds substantially smaller than those laid by females not exposed to ultrasounds. This finding suggests that this pest insect may have the ability to detect echolocating bats and modify its normal behaviour to reduce predation risk, negatively affecting egg production and therefore also insect reproductive success.

4.4.1. Landscape of fear

The decrease in egg production detected in *C. suppressalis* females exposed to bat ultrasounds can be attributed, on one hand, to potential delays or disruptions in mating behaviour inside the enclosures, as has been reported in other tympanate insects (Huang et al., 2003). This disruption could lead to shorter mating events, causing a decrease in mating success and egg production, observed as smaller egg clutches. Several published studies showed that fecundity and even egg viability of the Indian-meal moth *Plodia interpunctella* (a serious grain-feeding pest spread worldwide) decreased significantly when the mating was delayed due to the presence of ultrasounds produced by a commercial device (Huang et al., 2003; Huang and Subramanyam, 2004). Huang and Subramanyam (2004) reported that each day of delayed mating led to lower egg production and reduced egg viability, underscoring the disruptive effect of ultrasounds on reproductive success of the same moth species. Further, these authors observed that the synthesised ultrasounds altered the intraspecific interactions of this insect, reducing the frequency of female calling and mating, which also caused a decrease in both spermatophore transfer and egg production. Similar results were found by Akinneye and Ashamo (2009), who reported that mating delays after adult emergence resulted in lower egg production and reduced egg viability in the almond moth *Ephestia cautella*, a stored-product pest.

On the other hand, assuming that many of the female moths had already mated before being captured, the decrease in egg production observed as smaller egg clutches could also be explained by a reduction or interruption of oviposition behaviour. This disruption may be triggered by the evasive response of females, which would inhibit their normal activity in the presence of broadcasted bat ultrasounds. This has been documented by many authors, including Belton and Kempster (1962), who reported that sound resembling bat emissions

reduced oviposition and infestation of the European corn borer moth (*Ostrinia nubilalis*) by more than half in sweet corn fields. In field plots of lettuce and broccoli, Payne and Shorey (1968) observed an overall decline in oviposition of the cabbage looper (*Trichoplusia ni*) of 41%, 23%, and 30% when exposed to 20, 30, and 40 kHz sounds, respectively. However, these reductions reached values of up to 66% in some cases. Nakano et al. (2022), reported a drastic reduction of egg masses of *Spodoptera litura* in strawberry greenhouses, suggesting that synthetic bat-like ultrasounds were inhibiting the flight of mated female moths into the cultivation facility. In our study, since *C. suppressalis* moths could not move away from the ultrasound source, they might have spent less time laying eggs to minimise their exposure to potential bat predators.

Our results align well with the concept of the 'landscape of fear'. This sensory landscape, generated by the 'fear' of predation, elicits aversive responses that alter the prey's behaviour, sometimes even leading to physiological and/or morphological changes that may influence the evolutionary trajectory of the species involved (Brönmark and Miner, 1992; Brown and Chivers, 2005; Peckarsky et al., 2008). Our findings suggest the tympanic organs of *C. suppressalis* likely enable adult moths to detect echolocating bats, prompting a shift in their mating activity or oviposition behaviour, resulting in smaller egg clutches (Huang et al., 2003; Huang and Subramanyam, 2004; Payne and Shorey, 1968). This may have important implications for farmers, as a reduction of nearly half the number of eggs could lead to substantial decreases in both crop damage and yield losses.

4.4.2. Integrated Pest Management

The implementation of Integrated Pest Management (IPM) strategies has been growing significantly during the last decades, especially in developed countries (Deguine et al., 2021). IPM consists of the coordinated application of multiple techniques to deal with pests and protect crops in a more respectful and sustainable way towards the environment, favouring human and ecosystem health (Deguine et al., 2021; Ehler, 2006). The use of ultrasonic bat signals for agricultural pest control has been increasingly proposed by many authors. Acoustic devices have been used to monitor, attract and trap harmful insects in agrosystems and also as a repulsion, exclusion or interference strategy (Bhairavi et al., 2020; Mankin et al., 2011; Samarra et al., 2009; Walker, 1996). In the sixties, several studies already proved the efficiency of acoustic devices in tympanate insect pests' management (Agee, 1969a; Agee and Webb, 1969; Belton and Kempster, 1962; Payne and Shorey, 1968). However, the habituation of insects to ultrasonic recordings or sound shadows is one of the multiple problems of using acoustic technology for these purposes (May and Hoy, 1991; Zha et al., 2013). In order to overcome these challenges and enhance the efficiency of acoustic

technology, some authors recommended considering some characteristics of sound broadcasting. For instance, emitting pulses at unpredictable intervals, varying pulse duration, resembling moving signal sources or imparting apparent motion can significantly reduce habituation (Agee, 1969b; Mankin, 2012). A recent study developed by Nakano et al. (2022) designed an ultrasonic pulse using neuroethological screening of *Spodoptera* moths, specifically causing a cessation of wing flapping. When these repellent ultrasounds were broadcasted in different crop types, a drastic reduction of egg numbers and crop damage caused by larvae of these moths was detected, preventing the applications of agrochemical products for insect pest control and thus further impairing larvae production.

However, although acoustic technologies may continue to be refined for more efficient pest control, it is crucial to emphasise that promoting ecologically sustainable pest suppression is best achieved by maintaining healthy agrosystems and stable bat populations that provide these ecosystem services in a cleaner and natural way. In agrosystems such as rice paddies, where natural refugees are often scarce or may even have disappeared, one of the most recommended and successful strategies is to provide artificial roosts to bats (Tuneu-Corral et al., 2023). Considering the results of our study, we would suggest placing bat boxes evenly spread over the cultivation area rather than installing them in a few specific zones. This could enhance the presence of ultrasounds across the rice growing area, potentially reducing the reproductive success of tympanate insects and increasing predation pressure on pest populations. This strategy has already shown success in rice paddies, as reported by Puig-Montserrat et al. (2015). In that study, bat boxes installed in extensive rice fields were successfully occupied by colonies of soprano pipistrelles (*Pipistrellus pygmaeus*), and a substantial decline in pest levels was observed in the area. Although these effects were attributed to predation pressure only, they could probably also be the result of ultrasound emission by echolocating bats.

Furthermore, we want emphasise the importance of conveying accurate information to farmers and land managers, as well as implementing appropriate conservation measures and actions that favour the presence and establishment of not only bat populations, but also other natural enemies of agricultural pests such as birds or insects in agrosystems.

4.4.3. Study limitations

Due to the unique conditions of some agrosystems such as rice fields, as well as the complexity of the acoustic dimension, we want to point out some limitations of this study that should be taken into account in future research. The fact that the moths were captured in rice fields and kept in captivity changing their natural environment, may have stressed them and

altered their normal conduct, irrespective of the presence or absence of bat ultrasounds. In the same way, temperature and humidity conditions to which *C. suppressalis* individuals were kept were slightly different from those in the field, which may have produced a side effect on their natural behaviour. To address this limitation, we ensured that both rooms and enclosures remained under the same environmental conditions, which could vary over time according to weather but affect both rooms equally. We included a temporal factor in our models to account for potential effects due to these variations in weather conditions over time, and also variations associated to the phenology of this insect species. None of the statistical models detected a temporal effect on egg production, reinforcing our assertion that the environmental conditions were consistent across both rooms and enclosures. Therefore, we suggest that the differences detected in this study are robust evidence of the consequences related to the different experimental conditions.

Designing a captivity experiment is the most convenient method to study the effect of bat ultrasounds on the behavioural patterns of *C. suppressalis*, if one aims to separate these effects from direct predation by bats. To facilitate the logistics of the project, we decided to use lures to broadcast bat ultrasounds rather than capturing bats and releasing them into the different treatment rooms. Real echolocating bats may have stronger effects on this insect species that we might be missing using recordings. Even so, instead of emitting bat ultrasounds massively and continuously for hours, we decided to broadcast a single acoustic file that was recorded continuously during an entire night in the rice paddies, creating an artificial acoustic dimension as close to reality as possible.

In this study we have not assessed the effect of bat ultrasounds on egg viability due to logistical limitations in the field. Kirkpatrick and Harein (1965) observed that *P. interpunctella* adults exposed to amplified low-frequency sounds over four days produced 75% fewer larvae compared to those not exposed to the sound. This finding, coupled with other research mentioned previously (Akinneye and Ashamo, 2009; Huang et al., 2003), suggests that a similar effect may occur in *C. suppressalis* moths. Therefore, we highly encourage incorporating this variable in future research, as bat ultrasounds may also reduce *C. suppressalis* populations not only by decreasing egg production, but also by diminishing the fertility of these eggs, negatively affecting larvae production (Hamed et al., 2010; Huang and Subramanyam, 2004).

Finally, we did not test whether the playback (or the bat lure itself) had any effect on the egg production of *C. suppressalis*. To assess this, we would recommend adding a third treatment in future experiments broadcasting only the audible frequencies of the same recordings.

4.5. Conclusions

Our study highlights the important role of bats as pest suppressors in agrosystems. In addition to consume large amounts of insects (Kunz et al., 2011; Kunz and Stern, 1995), bats may reduce populations of tympanate pest species by simply emitting ultrasounds to the environment. Our findings suggest that bat ultrasounds may trigger an alteration of the normal reproductive and/or egg-laying behaviour of adults of the striped rice stem borer moth *C. suppressalis*. As a consequence, females may produce fewer eggs or interrupt oviposition to reduce predation risk, leading to significantly smaller egg clutches. Although predation pressure tends to have a much larger effect on prey populations (Preisser and Bolnick, 2008), this study suggests that the non-consumptive effect of bats may have relevant impacts on plant damage and rice yield.

This study underscores the broader implications for tympanate moth species exposed to natural and synthetic ultrasound sources. However, our aim, far from proposing an efficient acoustic strategy to suppress pests, was to obtain a good picture of the ecological processes occurring between moths (*C. suppressalis*) and bats (*Pipistrellus pipistrellus*) in rice paddies. Although an adequate use of acoustic technology in integrated pest management programmes can be beneficial for croplands and farmers, we emphasise the importance of maintaining healthy and suitable agrosystems for bats. There is no more sustainable and efficient method for controlling insect pests than by favouring their natural enemies. Therefore, establishing appropriate conservation and management measures in agrosystems, such as increasing landscape heterogeneity, creating water sources or providing roost availability, can promote and favour the presence of bats in rice paddies and other crops, enhancing their potential as natural pest suppressors (Tuneu-Corral et al., 2023).

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Chapter 5 – Protected areas and bat pest control in Madagascar



Commerson's leaf-nosed bat (*Macronycteris commersonii*), Madagascar. ©Adrià López-Baucells

Article IV:

Tuneu-Corral, C., Chatain Andrianalijaona, Fabrice Davy Benirina, Steven M. Goodman, Vanessa A. Mata, Michaël Luciano Tantely, Mar Cabeza, Adrià López-Baucells (*submitted to Agriculture, Ecosystems & Environment*). Beyond borders: the role of protected areas in promoting bat-mediated pest suppression in rural areas in Madagascar.

Article IV – Beyond borders: the role of protected areas in promoting bat-mediated pest suppression in rural areas in Madagascar

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Abstract

Protected areas can play a crucial role in enhancing agricultural sustainability by supporting ecosystem services that mitigate key challenges faced by rural farming communities. In Madagascar, subsistence agriculture is a major driver of deforestation and biodiversity loss, worsened by pest-related agricultural and harvest losses. Insectivorous bats are widely known natural enemies of agricultural pests, but the role of protected areas in safeguarding this service in surrounding rural areas is unclear. This study investigates the benefits provided by insectivorous bats roosting within protected areas of northern Madagascar, focusing on their potential to suppress agricultural pests and disease vectors. We used molecular techniques to analyse the diet of bats based on faecal samples from several species and locations. We

found that most bat species consumed agricultural pests affecting rice and other crops, as well as several vectors of pathogens that cause diseases in humans and animals, such as mosquito vectors of *Plasmodium* sp. Given their mobility and home ranges, we suggest that certain bat species roosting in protected areas have the dispersal capacity to forage in nearby agricultural landscapes, contributing to pest suppression and disease risk reduction. Hence, protecting bat roosts within and around protected areas may offer a cost-effective means to enhance agricultural productivity and public health. These findings underscore the need to integrate ecosystem services into conservation and land-use management strategies, fostering sustainability and rural welfare in Madagascar.

Keywords: bats; agriculture; pest suppression; protected areas; ecosystem service flow; rural welfare

5.1. Introduction

Protected areas are the most widely applied strategy for safeguarding ecosystems and conserving biodiversity (Chape et al., 2005; Palomo et al., 2013). Historically, their primary goal was to protect wilderness areas from human disturbance under the ‘fortress conservation model’ (Brockington, 2002; Watson et al., 2014). However, the widespread human impacts have prompted, in some regions of the world, a shift towards a more integrated approach that recognises the interdependence of humans and nature (Guerbois and Fritz, 2017; Kareiva and Marvier, 2012). Long-term biodiversity conservation cannot be achieved without considering the interactions between protected areas and the surrounding landscapes (IUCN, 2004). This paradigm emphasises the role of protected areas in preserving natural habitats and biodiversity but also in maintaining ecosystem services that support human well-being (Palomo et al., 2014; Watson et al., 2014). Highlighting these benefits can foster positive local attitudes and gain political support, which is critical for the viability of protected areas, particularly in the developing world where human pressure on natural resources is often high (Bragagnolo et al., 2016; Ng et al., 2013; Redford and Adams, 2009).

Madagascar is an island nation with over 30 million inhabitants, where more than 80% of the population lives below the poverty line (World Population Review, 2024; World Bank, 2024). Malagasy society is heavily reliant on subsistence agriculture, and the growing population, coupled with limited economic alternatives, has led to widespread deforestation to expand agricultural lands (Scales, 2014; Suzzi-Simmons, 2023). In fact, since 1950, Madagascar has lost 44% of its natural forest cover (Harper et al., 2007; Vieilledent et al., 2018). The island harbours exceptional biodiversity, with endemism rates exceeding 90% for many taxonomic

groups (Goodman, 2023). Around 90% the island's species are forest-dependent, and are at risk of extinction due to habitat loss and degradation (Goodman, 2023; Goodman and Benstead, 2005; Harper et al., 2007; Vieilledent et al., 2018). Conservation efforts have notably focused on expanding the protected area network, currently covering 6.2 million hectares of land (10.8% of the island's surface area) (Antonelli et al., 2022; Gardner et al., 2018; Goodman et al., 2018; Waeber et al., 2020). Nevertheless, deforestation and land conversion remain major drivers of biodiversity loss on the island (Eklund et al., 2019; Ralimanana et al., 2022).

Rice is the main staple food in Madagascar, providing 56% of the population's caloric intake (FAO, 2018). Rural communities and smallholder farmers comprise three-quarters of the island's population, most of them engaged in rice cultivation (Global Rice Science Partnership, 2013). However, 75% of farmers face significant crop losses due to pests, grain storage issues, and extreme weather, which hinders the production of enough rice and other essential foods for their households, making food security an important issue in different portions of the island (Harvey et al., 2014). Madagascar's limited economic resources have hindered the advancement of Integrated Pest Management strategies, including biological control, and crop losses are often compensated by creating new croplands through swidden agriculture (tavy in Malagasy), also known as slash-and-burn (Harvey et al., 2014).

In the field of biodiversity conservation and agricultural sustainability, bats are emerging as key players in maintaining ecosystem health. Most bat species are voracious insect predators, and their role as pest suppressors has been widely recognised, providing essential ecosystem services to humans valued at several millions of dollars worldwide (Aguiar et al., 2021; Boyles et al., 2011; Kolkert et al., 2021; Tuneu-Corral et al., 2023; Tuneu-Corral et al. 2024). Madagascar hosts over 40 species of bats with a high rate of endemism (Goodman, 2023), and many of which have adapted to forage or even roost in anthropogenic environments (López-Baucells et al., 2017).

Kemp et al. (2019) were the first to use molecular techniques to assess the dietary habits of Malagasy bats. They identified several agricultural pest species and disease vectors in the diets of synanthropic bats and a few non-forest dependent cave-dwelling species roosting near villages. Their study provides clear evidence of the benefits and ecosystem services these bat species provide to farmers and human communities. However, little is known about the pest and disease vector suppression potential of bats roosting within protected areas, which may partly forage outside their boundaries. Quantifying this contribution is crucial for understanding the ecological services these bats provide and informing agronomic and land-management practices. By demonstrating the value of bat-mediated pest control,

policymakers and land managers can justify integrating bat conservation into agricultural strategies, aligning biodiversity conservation with sustainable rural development.

The primary objective of this study is to fill this gap by investigating the diet of insectivorous bats roosting in protected areas of northern Madagascar. By using molecular techniques, we aimed to (i) provide a general description of the diet of these species; (ii) evaluate whether they consume crop pests and vectors of human diseases; and if so, (iii) examine seasonality patterns in the consumption of these prey types; (iv) describe consumption variation among bat species and families; and, (v) assess consumption differences between bats roosting inside protected areas and those roosting in rural villages. We hypothesised that certain bat species, probably characterised by medium-high mobility and capable of foraging in open spaces, may leave protected areas to feed in nearby croplands. Thus, we predicted the identification of several rice and other crop pests, and possibly also disease vectors, in the diet of these bat species. Conversely, we also hypothesised that the bats least likely to consume pests or disease vectors would be those with the smallest home ranges or those considered largely forest-dependent, as they would not reach rural areas to forage. Furthermore, given the pronounced seasonality of northern Madagascar, we predicted notable shifts in bat diet composition, with higher pest and disease vector consumption during the wet season, the period of highest insect availability.

5.2. Materials and methods

5.2.1. Study area

Fieldwork was conducted in the DIANA Region of northern Madagascar. In line with the subtropical climate of the island, two pronounced seasons occur: a hot and wet season from December to April, with average temperatures of 25-30°C and rainfall ranging from 180 to 300 mm per month; and a dry and cooler season from May to November, with average temperatures of 20-25°C and notably scarce rainfall, ranging from 15 to 50 mm per month (Unité de Politique de Développement Rural (UPDR), 2003; World Bank Group, 2021). We sampled bats in three protected areas (Montagne d'Ambre National Park, Ankarana Special Reserve and Protected Harmonious Landscape of Ambohitra'Antsingy (widely known as Montagne des Français), complemented with sampling in public buildings located in the nearby rural areas (Fig. 1). These protected areas encompass different habitats and associated vertebrate species.

The upper portion of the volcanic massif of Montagne d'Ambre is characterised by a humid and cool climate, with medium altitude moist evergreen forest, deep crater lakes and

waterfalls, at altitudes of 750 – 1474 m a.s.l. (Gautier et al., 2018; Goodman et al., 2023). Ankarana is composed of large areas of exposed limestone, including karst, deep canyons and caves, at altitudes of 50 – 409 m a.s.l. (Goodman et al., 2023). It has humid semi-deciduous forest, humid deciduous forest and dry deciduous forest (Gautier et al., 2018). Montagne des Français is dominated by dry deciduous forest with exposed calcareous rock and caves, ranging from 100 – 450 m a.s.l. (Gautier et al., 2018). Land use outside these protected areas, and in DIANA Region in general, is primarily comprised of subsistence agriculture, which accounts for more than 70% of the cultivated surface of the region (Unité de Politique de Développement Rural (UPDR), 2003). The main crop is rice, followed by cassava, corn, beans, sweet potatoes, potatoes, legumes, fruit trees and vegetables. There are cash crops such as coffee, pepper, cacao, vanilla, cotton, sugarcane and peanuts, as well as extensive free-ranging livestock (Unité de Politique de Développement Rural (UPDR), 2003).

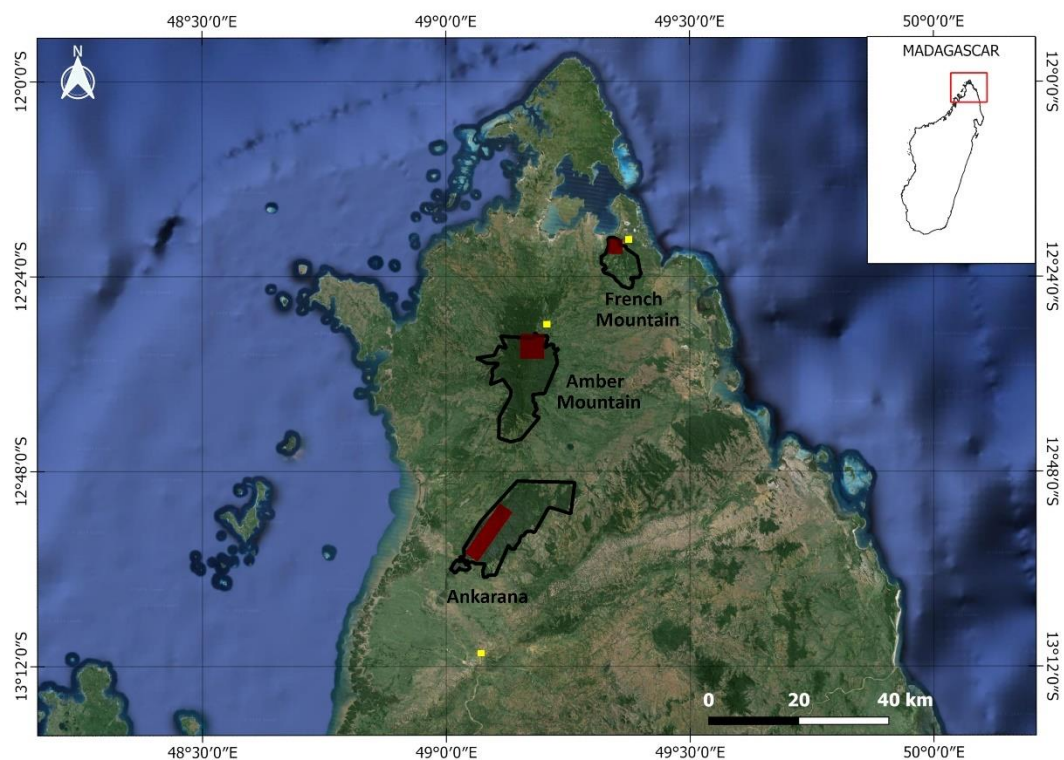


Figure 5.1. Study area and location of the three protected areas sampled in this study: Montagne d'Ambre National Park, Ankarana Special Reserve and Harmonious Protected Landscape of Ambohit'Antsingy – Montagne des Français, all located within the DIANA Region. The black lines represent the perimeter of each protected area, the red-shaded polygons indicate the area where sampling points were concentrated within the protected areas, and the yellow points indicate the location of the rural areas where bats were surveyed.

5.2.2. Bat captures and faecal sample collection

We sampled bats in two periods representing the main climatic seasons for both Montagne d'Ambre and Ankarana. The dry and wet seasons between these two sites vary slightly in timing and extent, and we adjusted the field periods to cover the end of the dry season (October – November 2022), and the end of the wet season (May 2023, as in April Ankarana was inaccessible due to heavy rains). Montagne des Français was visited only in the dry season (October – November 2022) due to logistic limitations.

We used harp traps and mist-nets (Ecotone®, M-14/3, M-14/6, M-14/12, M-14/18) to sample insectivorous bats in protected areas and rural villages. Bat captures were conducted for 7-10 consecutive nights in each protected area, changing sampling points (i.e. different roosts or forest areas) on a nightly basis to cover a wider area. We sampled bats in a total of ten forest points in Montagne d'Ambre (there are no known caves in the visited section of this protected area); six caves and four forest points in Ankarana; and six caves and two forest points in Montagne des Français. Two public buildings were visited within 3 km from the Montagne d'Ambre protected limit, three school buildings 16 km outside the border of Ankarana, and two school buildings 1 km from the limit of Montagne des Français. When sampling forest habitats, mist-nets and harp traps were installed 30 minutes before sunset and remained open for at least four hours. When sampling bats at roost entrances (caves inside protected areas and buildings in rural villages), bats were captured before sunrise when returning to the colony after feeding. In these cases, we used mist-nets and harp traps set up four hours before dawn, which remained in place until 30 minutes after sunrise.

Bat captures and handling were conducted following guidelines approved by the American Society of Mammalogists (Sikes and Gannon, 2011). All captured bats were measured, weighed and identified using different published works (Goodman et al., 2015, 2011, 2010, 2007, 2009a, 2009b; Kofoky et al., 2009; Ramasindrazana et al., 2011a; Russ et al., 2001). Insectivorous bats were kept in clean cloth bags until they defecated, generally for no more than one hour. Faecal samples of each individual were immediately collected and stored individually in 2 ml tubes with 95% ethanol and labelled accordingly. All bats were released at the same site where they were captured. We gathered a total of 500 samples to assess bat diet: 250 collected in the dry season and 250 in the wet season. The number of samples collected per species varied as a function of their capture rates at the different sampling points.

We calculated the minimum distance between our sampling points within protected areas and the nearest croplands using Google Earth images available at the time of sampling. For each sampling point within a protected area, we determined a minimum distance to any agricultural area, and the minimum distance to any paddy rice-growing area. The average minimum

distance to agricultural lands was 1.8 km (ranging from 0.5 – 2.4 km) for Montagne d'Ambre, and 2.4 km (ranging from 1.6 – 3.3 km) for Montagne des Français, corresponding to rice paddies in both cases. For Ankarana, the average minimum distance to the nearest crops (mainly corn and cassava plantations) was 1.2 km (ranging from 0.8 – 1.5 km), and to the nearest rice growing area was 3.3 km (ranging from 2.3 – 3.9 km).

5.2.3. DNA extraction and PCR amplification

We assessed the diet of insectivorous bats through DNA metabarcoding of the faecal samples. DNA extraction was conducted on one random faecal pellet per individual. This sampling technique provides a representative record of its dietary composition at a reduced cost (Mata et al., 2019). Following the technique of Mata et al. (2021), each pellet was homogenised with 650 µL of lysis buffer (0.1 M Tris–HCl, 0.1 M EDTA, 0.01 M NaCl, 1 % N-lauroylsarcosine, pH 7.5–8; Maudet et al., 2002) and incubated at 70°C for 30 min. Afterwards, samples were , and 500 µL was transferred to a new tube containing 25 µL of OB Protease and 200 µL of BL buffer, followed by a second incubation at 70°C for 10 min. Finally, DNA precipitation and washing were conducted following the E.Z.N.A. Tissue Kits guidelines (Omega Bio-Tek, Norcross, Georgia, USA), with the exception that DNA was eluted twice in 50 µL into different tubes. One negative control was processed for every 23 samples (for a total of 22 extraction blanks). DNA extracts were distributed in 96 well plates, with one well left empty in every plate to serve as PCR blank (for a total of 5 PCR blanks). Extracted DNA was stored in a freezer at -20°C until further processing.

PCR amplifications were done using arthropod general cytochrome oxidase subunit 1 (COI) primers fwhF2-R2n (Vamos et al., 2017), modified with Illumina overhangs. PCR reactions were carried out in volumes of 10 µL, comprised of 5 µL of QUIAGEN Multiplex PCR Master Mix, 0.25 µL of forward primer, 0.25 µL of reverse primer, 2.5 µL of ultrapure water and 2 µL of DNA extract. PCR cycling conditions consisted of an initial denaturation at 95°C for 15 min, 42 cycles of 95°C denaturing for 30 s, annealing at 52°C for 30 s, extension at 72 °C for 30 s and a final extension at 60°C for 10 min. Amplification success and quality were checked via gel electrophoresis in 2% agarose gels stained with GelRed. PCR products were diluted 1:4 with water and tagged for individual identification in a second amplification step, this time with P5 and P7 Illumina adaptors along with unique combinations of 7 bp barcodes. The PCR mix consisted of 7 µL KAPA HiFi HotStart ReadyMix (KAPA Biosystems, Roche, Basel, Switzerland), 2.8 µL of ultrapure water, 0.7 µL of each P5 and P7 index and 2.8 µL of diluted PCR product. Cycling conditions of the indexing PCR consisted of denaturation at 95°C for 3 min, followed by 9 cycles of 95°C for 30 s, annealing at 55°C for

30 s, extension at 72°C for 30 s and a final extension at 72°C for 5 min. Afterwards, indexed PCR products were cleaned with Agencourt AMPure XP beads (Beckman Coulter, Brea, California) at a 1:0.8 ratio, following the manufacturer's instructions, to remove remaining nucleotides, primers and primer dimers. Libraries were then quantified using Epoch (dsDNA), pooled equimolarly, and their pool was run in TapeStation (Agilent, Santa Clara, California) using a High Sensitivity D1000 ScreenTape, to validate library quality. DNA concentration was further validated by qPCR (KAPA Library Quant Kit qPCR Mix, Roche, Basel, Switzerland) and diluted to 4 nM. Libraries were sequenced in a MiSeq desktop sequencer (Illumina) using a MiSeq Reagent Kit v3 (2 × 250 bp) along with samples from other projects with a target depth of 30k reads/sample.

5.2.4. Bioinformatic analyses

Raw Illumina sequences were processed using a set of commonly used bioinformatic tools. First, forward and reverse primer sequences were removed using Cutadapt (Martin, 2011), while paired reads were merged using Flash2 (Magoč and Salzberg, 2011). The command '--fastx_filter' from VSEARCH (Rognes et al., 2016) was then used to filter low quality reads (maxEE > 1), followed by '--derep_fulllength' to dereplicate reads into exact sequence variants (ESVs), remove singletons per sample, and tag sequences with sample name. The ESVs of each sample were then pooled into a single file and again dereplicated. To denoise the data, the command '--cluster_unoise' was used, while filtering sequences shorter or longer than 202-208 bp, followed by chimera removal with the command '--uchime3_denovo'. Finally, the remaining sequences were clustered at 99% similarity with the command '--cluster_size', to reduce possible species intra-specific sequence variants. Dereplicated reads without singletons were mapped against the final set of operational taxonomic units (OTUs) to build an OTU table using '--usearch_global' with 99% similarity. This table was further refined using LULU (Frøslev et al., 2017) with default parameters, in order to reduce the number of nuclear mitochondrial DNA segments (NUMTs) and surviving PCR artefacts that can greatly inflate OTU diversity.

Lastly, curated OTUs were taxonomically identified using the 'digger_hit' method of BOLDdigger (Buchner and Leese, 2020). Each OTU identified as Arthropoda were further manually checked and curated, considering their top 20 BOLD hits, and evaluated against the following similarity thresholds: 99% for species, 97% for genus, 95% for family, 90% for order, <90% for class or above. When different OTUs were assigned to the same taxon but at the genus level or above, they were numbered sequentially to differentiate them during statistical analysis (e.g., if OTU1 and OTU2 were both identified at family level to the Noctuidae, they were

classified as “Noctuidae OTU1” and “Noctuidae OTU2”. OTUs identified at order level or below and belonging to one of three classes (Insecta, Arachnida or Diplopoda), were classified as bat dietary items (except for parasites belonging to the Trombidiformes, Mesostigmata, Ixodida and Siphonaptera). OTU reads observed in extraction and PCR negative controls were subtracted from the corresponding samples, while dietary OTUs representing less than 1 % of the total dietary reads of each sample were not included in order to reduce false positives associated with lab and sequencing cross-contamination. Samples with less than 100 dietary reads were considered to have failed and were discarded.

5.2.5. Diet description and statistical analyses

General description of bat diet

General diet composition was described considering all samples, and based on the values obtained for frequency of occurrence (FOO, which is the percentage of samples containing each arthropod order) and percentage of occurrence (POO, which corresponds to the FOO rescaled so that the sum of all food items is 100) of the different arthropod orders. When focusing on the different bat species, we used the weighted percentage of occurrence data (wPOO), which is similar to POO, but it weights each occurrence according to the number of food items in the sample since it may be more biologically realistic than POO or FOO. As discussed by Deagle et al. (2019), POO data is useful because it shows each food taxon's percentage of the total diet (unlike FOO, which does not sum to 100%). However, wPOO may be more accurate because it weights each sample equally, preventing samples with many food taxa from having stronger influence. wPOO values were also calculated for each season (dry/wet) independently, in order to detect changes in prey preferences depending on the season.

To visualise the dietary composition among bat species, we created a barplot using the ggplot function of the R package ‘ggplot2’. We then used the metaMDS function of the R package ‘vegan’ for nonmetric multidimensional scaling (NMDS) on a Bray–Curtis distance matrix to visualise the dietary data at the bat family level. Further, we created a food web using the plotweb function of the R package ‘bipartite’, to show the interactions between different bat species and the arthropod orders they consumed.

Agricultural pest and disease vector consumption by insectivorous bats

To evaluate whether bats were consuming agricultural pests or disease vectors, we only included prey identified at species level. By using published scientific literature, we classified

each arthropod species in one of the following categories: 'non-pest prey', 'known human-disease vector' (species confirmed as human-disease vector on Madagascar), 'known livestock-disease vector' (species confirmed as livestock-disease vector on Madagascar), 'potential human-disease vector' (species not confirmed as human-disease vector on Madagascar, but considered as such in continental Africa), 'potential livestock-disease vector' (species not confirmed as livestock-disease vector on Madagascar, but considered as such in continental Africa), 'known agricultural pest' (species confirmed as agricultural pest on Madagascar), 'potential agricultural pest' (species not confirmed as agricultural pest on Madagascar, but considered as such in continental Africa).

We calculated the percentage of samples containing pests or disease vectors for both seasons, as well as for each type of habitat (caves and forests inside protected areas, and buildings in rural villages). We used ggplot2 function of the R package 'ggplot2' to illustrate the differences in the number of pests consumed per bat species between seasons. For each bat species, we also calculated values of FOO of pests and disease vectors in their samples.

To assess whether 'season' (dry/wet), 'type of area' (forested protected area/rural village) and 'bat species' (predictor variables) had a significant effect on the FOO of the different pest species and disease vectors (response variable), we used PERMANOVA analysis (Ingala et al., 2021; Mata et al., 2019) based on Bray-Curtis distance matrix, tested with 9,999 permutations using the adonis function from the vegan R package (Oksanen, 2018). We used FOO data of each pest and disease vector species in faecal samples. The betadisper function from the R package 'vegan' was used to test for homogeneity of group variance for each predictor variable. The significant PERMANOVA results were excluded when the variance was not homogeneous. Thus, only explanatory variables with significant PERMANOVA results (p value < 0.05) and non-significant betadisper results (p value > 0.05) were considered to influence pest composition in bat diet. For the explanatory variables kept in the model, we plotted a Principal Coordinates Analysis (PCoA) of the betadisper outcomes. The simper function from the R package 'vegan' was used to conduct a similarity percentage analysis between levels of explanatory variables influencing diet composition.

5.3. Results

5.3.1. General description of bat diet

We captured 15 different insectivorous bat species, 11 endemic to Madagascar, and four regional endemics also occurring on the nearby islands of the Comoros Archipelago. Twelve bat species were captured exclusively inside the protected areas and those considered largely

forest dependent are highlighted in bold (*Chaerephon jobimena*, *Laephotis matroka*, *Macronycteris commersoni*, *Miniopterus aelleni*, *M. ambohitrensis*, *M. gleni*, *M. griveaudi*, *Myotis goudoti*, *Otomops madagascariensis*, ***Paratriaenops auritus***, ***Paremballonura tiavato***, *Triaenops menamena*), and two were captured exclusively in villages outside the protected areas (*Chaerephon leucogaster*, *Mops leucostigma*). *Mormopterus jugularis* was the only species found roosting both in caves and buildings, although it was primarily captured in cave roosts in this study. We collected faecal samples for all these species, obtaining dietary information from 454 of the 500 faecal samples analysed (Table A4.1). In the curated dataset, a total of 2,914 OTUs (corresponding to 1,354 distinct prey items) were retained and identified at different taxonomic levels: class (21.8%), order (23.6%), family (20.9%), genus (11.1%) or species (22.6%). Out of the 1,354 distinct dietary items, 97.8% (1,325 OTUs) belonged to the Class Insecta, 2.1% (28 OTUs) to Araneae and 0.1% (1 OTU) to Diplopoda. Overall, taking into consideration the prey identified at order or lower taxonomic levels (78.2% of all OTUs obtained), we detected at least 16 orders, 109 families, 237 genera and 188 species (Table 5.1). The order with the highest FOO and POO with respect to bat diet was, by far, Lepidoptera, followed by Hemiptera, Diptera and Coleoptera (Table 5.1).

Table 5.1. Number of distinct families, genera, and species found in bat faecal samples summarised to arthropod order level. Number of samples in which they occur, frequency of occurrence (FOO), percentage of occurrence (POO) and distinct OTUs detected for each arthropod order are also provided.

Prey order	N° families	N° genus	N° species	N° samples	%FOO	%POO	distinct OTU
Araneae	5	4	1	29	6	2	28
Blattodea	3	2	4	65	14	6	31
Coleoptera	14	19	15	150	33	14	116
Dermaptera	1	1	1	1	0	0	1
Diptera	22	25	27	177	39	16	174
Embioptera	1	0	0	1	0	0	1
Ephemeroptera	1	1	0	3	1	0	2
Hemiptera	18	24	21	180	40	16	123
Hymenoptera	2	11	12	49	11	5	30
Lepidoptera	27	139	100	343	76	31	448
Neuroptera	3	3	1	33	7	3	15
Odonata	0	0	0	1	0	0	1
Orthoptera	6	6	5	60	13	5	31
Psocodea	4	0	0	8	2	1	9
Thysanoptera	1	1	1	1	0	0	1
Trichoptera	1	1	0	7	2	1	5

When assessing the dietary habits of the different bat species using the wPOO estimates (Fig. 5.2A, Table 5.2), Lepidoptera was the most consumed prey by most species, followed by Diptera, Hemiptera and Coleoptera. We created a bipartite network to visualise dietary interactions between bat species and their prey, summarised to arthropod taxonomic order (Fig. 5.3). As illustrated in Fig. 5.2B, we detected many similarities in diet composition based on arthropod orders when examining food preferences at the bat family level, with *Macronycteris commersoni* (one of the two members of the Hipposideridae family on Madagascar) having the most different feeding habits with respect to the rest.

Table 5.2. Weighted percentage of occurrence (wPOO) of each arthropod order in the diet of the different bat species captured in the study. The values in brackets next to each species' name are the total samples collected for that species. The shaded rows show the values for *Chaerephon leucogaster* and *Mops leucostigma*, the two species captured exclusively outside protected areas.

%wPOO	Araneae	Blattodea	Coleoptera	Dermoptera	Diptera	Embioptera	Ephemeroptera	Hemiptera	Hymenoptera	Lepidoptera	Neuroptera	Odonata	Orthoptera	Psocodea	Thysanoptera	Trichoptera
<i>Chaerephon jobimena</i> (25)	0	1	14	0	4	0	0	12	1	57	0	0	11	0	0	0
<i>C. leucogaster</i> (91)	0	0	8	0	17	0	0	22	2	40	3	0	6	0	0	0
<i>Laephotis matroka</i> (4)	0	0	15	0	67	0	0	0	0	19	0	0	0	0	0	0
<i>Macronycteris commersonii</i> (15)	0	51	24	0	7	0	0	14	3	1	0	0	0	0	0	1
<i>Miniopterus aelleni</i> (35)	5	5	12	0	14	0	0	15	1	47	2	0	0	0	0	0
<i>M. ambohitrensis</i> (69)	2	16	4	0	11	0	0	5	0	57	2	0	2	0	0	0
<i>M. gleni</i> (20)	2	1	3	0	0	0	0	3	3	69	1	0	19	0	0	0
<i>M. griveaudi</i> (56)	0	1	10	0	37	0	1	17	5	24	0	0	3	1	0	0
<i>Mops leucostigma</i> (23)	0	3	19	1	9	0	0	26	3	34	2	0	3	0	0	0
<i>Mormopterus jugularis</i> (25)	2	10	27	0	11	0	0	32	10	7	0	0	1	0	0	0
<i>Myotis goudoti</i> (20)	13	1	7	0	19	0	0	6	6	46	1	0	0	1	0	0
<i>Otomops madagascariensis</i> (22)	0	0	1	0	0	0	0	0	0	93	0	0	6	0	0	0
<i>Paremballonura tiavato</i> (10)	0	0	23	0	24	0	0	13	2	36	1	0	0	0	0	0
<i>Paratriaenops aurltus</i> (11)	0	5	21	0	6	0	0	2	3	58	6	0	0	0	0	0
<i>Triaenops menamena</i> (28)	0	4	14	0	2	0	0	4	0	74	1	0	1	0	0	0

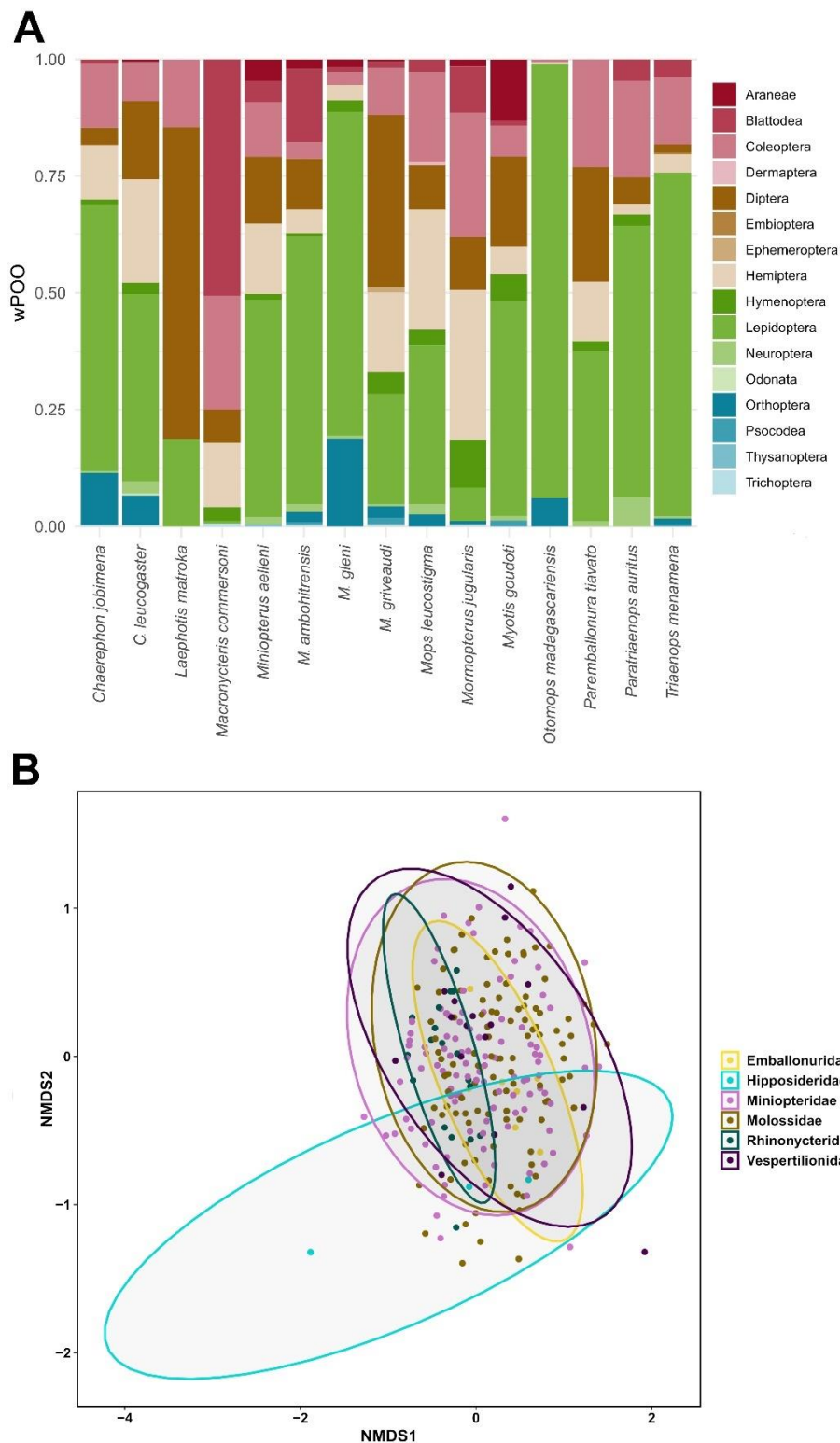


Figure 5.2. A) Illustration of the wPOO for each arthropod order found in the diet the bat species studied; B) Nonmetric multidimensional scaling (NMDS) ordination of the arthropod order composition in the diet of different bat families. Each dot represents an individual faecal sample or a group of faecal samples with very similar or identical NMDS scores, coloured according to the taxonomic family to which it belongs.

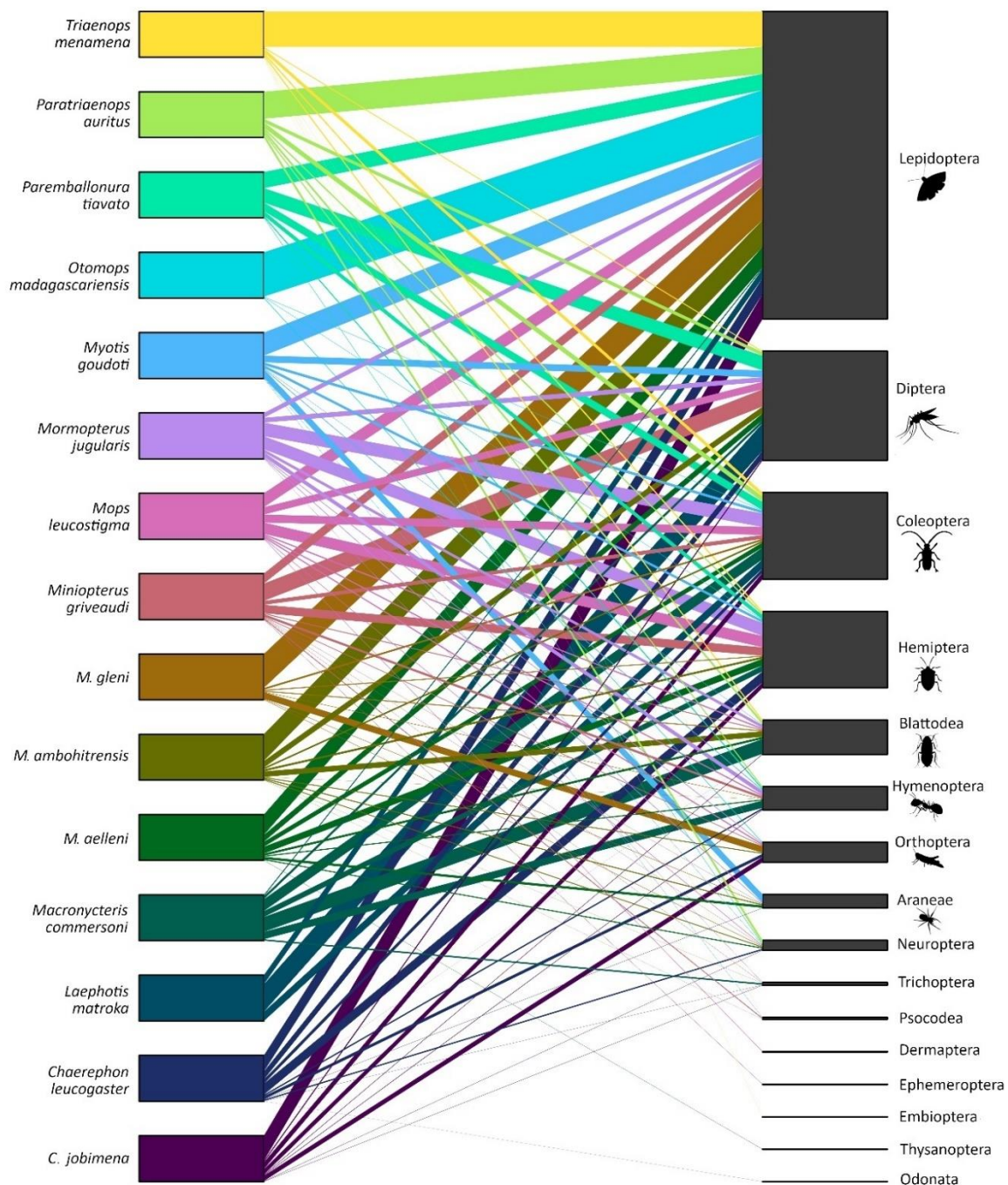


Figure 5.3. Food-web showing associations (wPOO) between insectivorous bat species (left) and prey items summarised at the order level (right). Interactions are illustrated in different colours according to the different bat species. Connecting bar width represents the percentage of interactions between each bat species and each arthropod order.

Our results suggest that bat species shift the composition of prey (at the order level) consumed depending on the time of the year (Table A4.2). There was a dominant prey item order throughout the year (Lepidoptera in most cases), but the proportion of less frequent arthropod orders changed between seasons for some species. Some examples include *Myotis goudoti*, which preyed mostly on Lepidoptera and Araneae during the dry season, but Araneae was

replaced by Coleoptera during the wet season; or *Miniopterus griveaudi*, which consumed mostly Diptera and Lepidoptera during the dry season, but preyed more on Hemiptera and Coleoptera during the wet season (Table A4.2).

5.3.2. Agricultural pest and disease vector consumption by insectivorous bats

Fourteen of the 15 bat species studied consumed pests or disease vectors (Table 5.3). A total of 70 different species identified from bat faecal samples were classified as agricultural pests or disease vectors (55 species and 15 species, respectively; Table A4.3), and were detected in 35.7 % of the samples collected (162 out of the 454, Table A4.4). Accounting for agricultural pests and disease vectors separately, these were found in 29.5% and 9.9% of the samples, respectively. Considering the different pests and disease vectors identified, 59 species (84%) were detected in the diet of bats captured within protected areas and 29 species (41%) in the diet of bats roosting in rural villages. We found a notable difference in pest and disease vector occurrence in bat diet between seasons, more than doubling the incidence in the wet season (FOO % 22.2 vs 48.5, respectively). The average number of pest and disease vector species consumed per bat species also doubled in the wet season, from 3.3 species in the dry season to 6.6 in the wet season (Fig. 5.4A).

Samples with pests or disease vectors were predominantly collected from bats captured inside protected areas (67.3% of the samples: 53.1% from caves and 14.2% from forests). These samples mainly belonged to the genus *Miniopterus* (45.9%), captured mostly in cave day roosts, followed by Molossidae (35.8%), captured exclusively in cave roosts, and *Triaenops menamena* (11.9%), captured almost exclusively in forests (Table A4.5). The remaining one-third of the samples containing pest and disease vectors (32.7%) were collected from bats roosting in buildings, and all belonged to the family Molossidae. The frequency of occurrence of pest and disease vector species varied by habitat type: 44.9% of samples from bats captured in buildings of rural villages contained these type of insects, 50.3% of samples from bats captured in caves and 13.9% of samples from bats captured in forests. Most samples containing pests were collected in Ankarana and nearby rural areas (72.2%), followed by Montagne d'Ambre and nearby rural areas (21.6%) and Montagne des Français and nearby rural areas (6.2%) (Table S5). The species consuming more agricultural pests (known and potential) and disease vectors (known and potential) was *Chaerephon leucogaster* (28 species), followed by *Miniopterus griveaudi* (24), *Otomops madagascariensis* (17), *C. jobimena* (15) and *Triaenops menamena* (14) (Table 5.3). Insect pests were detected in at least half of the samples of *O. madagascariensis* (FOO 82%), *M. gleni* (FOO 60%), *C. jobimena* (FOO 72%), *C. leucogaster* (FOO 55%) and *T. menamena* (FOO 48%) (Table 5.3).

Table 5.3. Summary of the number of distinct pests and disease vectors detected in the dry and wet seasons, along with their frequency of occurrence (%FOO) in the diet of different bat species. Note that species are listed in descending order based on the total number of pests and disease vectors they consume. In the %FOO column, the number of samples collected for each species is shown in parentheses. The shaded rows show the values for *Chaerephon leucogaster* and *Mops leucostigma*, the two only species captured exclusively outside protected areas..

Bat species	N° pests dry season	N° pests wet season	Total n° of distinct pests	N° disease vectors dry season	N° disease vectors wet season	Total n° of distinct disease vectors	Total n° of distinct pests and disease vectors	%FOO
<i>Chaerephon leucogaster</i>	10	15	22	1	5	6	28	0.55 (91)
<i>Miniopterus griveaudi</i>	7	8	14	6	7	10	24	0.43 (56)
<i>Otomops madagascariensis</i>	3	15	17	0	0	0	17	0.82 (22)
<i>C. jobimena</i>	5	11	15	0	0	0	15	0.72 (25)
<i>Triadenops menamena</i>	1	12	13	1	0	1	14	0.48 (28)
<i>M. aelleni</i>	3	8	11	1	2	2	13	0.38 (35)
<i>M. gleni</i>	3	11	12	0	0	0	12	0.60 (20)
<i>Mormopterus jugularis</i>	2	0	2	1	0	1	3	0.13 (24)
<i>Miniopterus ambohitrensis</i>	0	2	2	0	0	0	2	0.03 (69)
<i>Mops leucostigma</i>	0	2	2	0	0	0	2	0.14 (23)
<i>Paremballonura tiavato</i>	2	0	2	0	0	0	2	0.27 (11)
<i>Paratriadenops auritus</i>	2	0	2	0	0	0	2	0.18 (11)
<i>Myotis goudoti</i>	0	1	1	0	0	0	1	0.05 (20)
<i>Macronycteris commersonii</i>	1	0	1	0	0	0	1	0.07 (15)
<i>Laephotis matroka</i>	0	0	0	0	0	0	0	0 (4)
Total n° of distinct species	27	42	55	8	11	15	70	

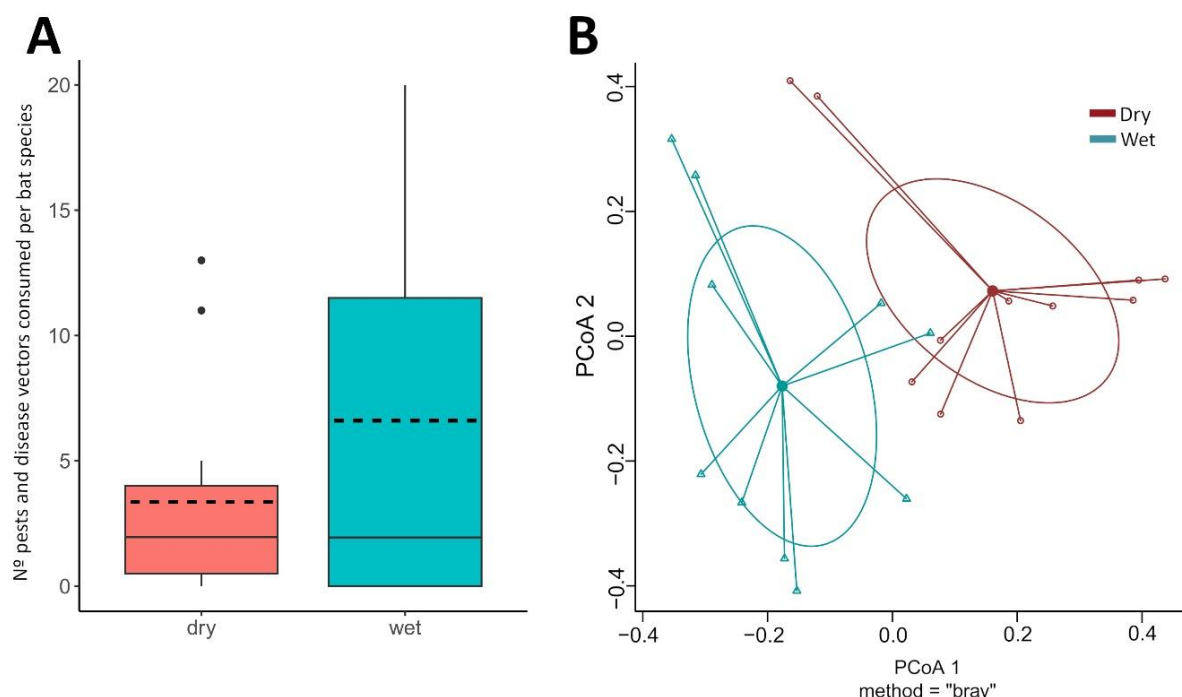


Figure 5.4. Effect of season on pest and disease vector predation. A) Number of pests and disease vectors consumed per bat species in dry and wet seasons. In each boxplot, the dashed horizontal black bar represents the mean of the data, while the continuous horizontal black bars represent, from lower to upper position, the first quartile, the median and the third quartile, respectively. The lower whiskers cover the 25% lowest values and the upper whiskers the highest 25% of the values recorded in each season. B) Principal Coordinates Analysis (PCoA) plot of the pest composition in the diet of bat species during the dry and wet seasons. Each small triangle and circle represents a bat species, coloured according to season.

Out of the 70 prey taxa classified as harmful insects, a total of 55 insect species were identified as potential pests (25 species) or known pests (30 species) of various crops (references in Table A4.3). These include some global major agricultural pests such as *Helicoverpa armigera* (family Noctuidae), *Etiella zinckenella* (family Pyralidae) and *Tuta absoluta* (family Gelechiidae) (Table A4.3, Table A4.4).

Focusing on insects damaging rice, we detected the presence of eight known pest species (*Agrotis ipsilon* [family Noctuidae]; *Herpetogramma licarsialis* [family Crambidae]; *Locusta migratoria* [family Acrididae]; *Maliarpha separatella* [family Erebidae]; *Marasmia poeyalis* [family Crambidae]; *Mythimna loreyi* [family Noctuidae]; *Nezara viridula* [family Pentatomidae]; *Parapoynx fluctuosalis* [family Crambidae]), and three potential pest species (*Eublemma anachoresis* [family Erebidae], *Gryllotalpa africana* [family Gryllotalpidae], *Sitotroga cerealella* [family Gelechiidae]). These prey species were identified in 7.5% of all faecal samples, belonging to eight different bat species (*Chaerephon leucogaster*, *C. jobimena*, *Macronycteris commersoni*, *Miniopterus abbohitrensis*, *M. griveaudi*, *M. gleni*, *Otomops madagascariensis*, *Triaenops menamena*) (Table 5.4).

Other relevant known agricultural pests on Madagascar that were detected in bat faecal samples include *Lobesia vanillana* (family Tortricidae, attacking vanilla and mango trees), *Yanga guttulata* (family Cicadidae, attacking mango trees, banana trees and sugarcane) and *Spodoptera littoralis* (family Noctuidae, attacking cotton plants) (see Table A4.3, Table A4.4). Several bat species consumed more than 10 distinct agricultural pests: *C. leucogaster* consumed the highest number of crop pests (22 distinct pests), followed by *O. madagascariensis* (17), *C. jobimena* (15), *M. griveaudi* (14), *T. menamena* (13), *M. gleni* (12) and *M. aelleni* (11) (Table 4). Most pest species were Lepidoptera (67.9%, belonging mainly to Crambidae, Noctuidae and Pyralidae), followed by Hemiptera (12.3%) and Coleoptera (8.9%).

A total of 15 species identified as food resources for bats were classified as disease vectors (Table 5.5, Table A4.3). Of these, 10 are known human-disease vectors on the island, all them belonging to Culicidae (Table A4.3). We also identified two known livestock-disease vectors on Madagascar (one of which being a human-disease vector mentioned previously, Table A4.3). Additionally, we found two potential human-disease vectors and two potential livestock-disease vectors, with no reported transmission on Madagascar but known from mainland Africa (Table S4). The main species preying on human-disease vectors was *Miniopterus griveaudi* (10 disease vector species), followed by *C. leucogaster* (6) and *M. aelleni* (2) (Table 5.5).

In terms of seasonal consumption of specific pests and disease vectors, our PERMANOVA models suggest that season was the only variable showing a substantial effect on the composition of these insect species in the diet of bats (PERMANOVA, $p = 0.0001$, Table A4.6; Fig. 5.4B). Up to 53 pest and disease vector species were detected in samples collected in the wet season and only 35 species were detected in samples collected during the dry season, with 18 of these species being shared between both seasons. Thus, most insect pest and disease vector species were found exclusively in just one of the two seasons. In fact, the similarity index of insect pest and disease vector species consumption between both seasons was 2.6%.

Table 5.4. Number of samples per bat species and %FOO in brackets for all identified agricultural pests (known and potential). Known and potential rice pest species are highlighted with an asterisk. The shaded columns show the values of pest detection outside protected areas, belonging to *Chaerephon leucogaster* and *Mops leucostigma*.

			<i>Chaerephon jobimena</i>	<i>C. leucogaster</i>	<i>Laephotis matroka</i>	<i>Macronycteris commersonii</i>	<i>Miniopterus aelleni</i>	<i>M. ambohitrensis</i>	<i>M. gleni</i>	<i>M. griveaudi</i>	<i>Mops leucostigma</i>	<i>Mormopterus jugularis</i>	<i>Myotis goudoti</i>	<i>Otomops madagascariensis</i>	<i>Paremballonura tiavato</i>	<i>Paratriaenops auritus</i>	<i>Triaenops menamena</i>	Total n° samples detected
Coleoptera	Curculionidae	<i>Euplatypus parallelus</i>	-	-	-	-	1 (3%)	-	1 (5%)	2 (4%)	-	-	-	-	-	-	1 (4%)	5
		<i>Xyleborus affinis</i>	-	-	-	-	1 (3%)	-	-	-	-	-	-	-	-	-	-	1
		<i>X. ferrugineus</i>	-	-	-	-	1 (3%)	-	-	1 (2%)	-	-	-	-	-	-	-	2
		<i>X. perforans</i>	-	-	-	-	1 (3%)	-	-	1 (2%)	-	-	-	-	-	-	-	2
	Nitidulidae	<i>Aethina tumida</i>	-	-	-	-	-	1 (1%)	-	-	-	-	-	-	-	-	-	1
Diptera	Tephritidae	<i>Bactrocera invadens</i>	-	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	1
		<i>Paraspheniscoides binarius</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Hemiptera	Aleyrodidae	<i>Aleurodicus dispersus</i>	-	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	1
	Cicadellidae	<i>Balclutha rubrostriata</i>	-	1 (1%)	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	2
	Cicadidae	<i>Yanga guttulata</i>	1 (4%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	Delphacidae	<i>Peregrinus maidis</i>	2 (8%)	11 (1.2%)	-	-	4 (12%)	-	-	-	2 (9%)	-	-	-	-	-	-	19
	Miridae	<i>Creontiades pacificus</i>	1 (4%)	8 (9%)	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	10
		<i>Orthops palus</i>	-	3 (3%)	-	-	-	-	-	1 (2%)	-	1 (4%)	-	-	2 (18%)	1 (9%)	-	8
	Pentatomidae	<i>*Nezara viridula</i>	-	2 (2%)	-	1 (7%)	-	-	-	-	-	-	-	-	-	-	-	3
Lepidoptera	Crambidae	<i>Angustalius malacellus</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>Diaphania indica</i>	-	-	-	-	-	-	-	-	-	-	-	1 (5%)	-	-	-	1
		<i>Duponchelia fovealis</i>	2 (8%)	2 (2%)	-	-	-	-	-	-	-	-	-	-	-	-	1 (4%)	5
		<i>Ghesquierellana hirtusalis</i>	-	-	-	-	1 (3%)	-	-	-	-	-	-	-	-	-	-	1
		<i>Hellula undalis</i>	1 (4%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>*Herpetogramma licarsisalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 (4%)	1
		<i>Hymenia perspectalis</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>*Marasmia poeyalis</i>	2 (8%)	1 (1%)	-	-	-	1 (1%)	-	-	-	-	-	1 (5%)	-	-	-	5
		<i>Maruca vitrata</i>	1 (4%)	-	-	-	-	-	3 (15%)	-	-	-	-	1 (5%)	-	-	2 (7%)	7
		<i>Omiodes indicata</i>	1 (4%)	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	1 (4%)	3

		<i>*Parapoynx fluctuosalis</i>	3 (12%)	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	4	
		<i>Spoladea recurvalis</i>	-	-	-	-	-	-	1 (5%)	-	-	-	1 (5%)	-	-	-	2	
Erebidae		<i>Achaea finita</i>	-	-	-	-	1 (3%)	-	3 (15%)	-	-	1 (5%)	7 (32%)	-	-	-	12	
		<i>Anomis flava</i>	-	-	-	-	-	-	-	-	-	-	3 (14%)	-	-	-	3	
		<i>Anticarsia irrorata</i>	-	-	-	-	-	-	-	-	-	-	1 (5%)	-	-	-	1	
		<i>*Eublemma anachoresis</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	1	
Gelechiidae		<i>*Sitotroga cerealella</i>	1 (4%)	1 (1%)	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	3	
		<i>Tuta absoluta</i>	-	2 (2%)	-	-	-	-	2 (4%)	-	-	-	-	-	-	-	4	
Noctuidae		<i>*Agrotis ipsilon</i>	-	1 (1%)	-	-	-	-	-	-	-	-	1 (5%)	-	-	-	2	
		<i>Argyrogramma signata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1 (4%)	1	
		<i>Chrysodeixis chalcites</i>	-	-	-	-	1 (3%)	-	1 (5%)	-	-	-	5 (23%)	-	-	-	7	
		<i>Condica capensis</i>	-	-	-	-	-	-	-	-	-	-	1 (5%)	-	-	-	1	
		<i>Helicoverpa armigera</i>	-	-	-	-	1 (3%)	-	4 (20%)	-	-	-	8 (36%)	-	-	1 (4%)	14	
		<i>*Mythimna loreyi</i>	-	-	-	-	-	-	-	-	-	-	1 (5%)	-	-	-	1	
		<i>M. phaea</i>	-	-	-	-	-	-	2 (10%)	-	-	1 (4%)	4 (18%)	-	-	1 (4%)	8	
		<i>Spodoptera littoralis</i>	-	-	-	-	-	-	2 (10%)	-	-	-	1 (5%)	-	-	-	3	
Nolidae		<i>Earias biplaga</i>	-	-	-	-	-	-	2 (10%)	-	-	-	-	-	-	-	2	
		<i>Pardasena virgulana</i>	-	-	-	-	-	-	-	-	-	-	1 (5%)	-	-	-	1	
Pyralidae		<i>Assara seminivale</i>	4 (16%)	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	1 (4%)	6	
		<i>Cryptoblabes gnidiella</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	1	
		<i>Ectomyelois ceratoniae</i>	-	-	-	-	-	-	-	-	-	-	-	-	1 (9%)	1 (4%)	2	
		<i>Etiella zinckenella</i>	1 (4%)	-	-	-	-	-	1 (5%)	1 (2%)	-	-	-	-	-	1 (4%)	4	
		<i>*Maliarpha separata</i>	2 (8%)	5 (5%)	-	-	-	-	-	1 (2%)	-	-	-	1 (5%)	-	-	8 (30%)	17
		<i>Thylacoptila paurosema</i>	2 (2%)	5 (5%)	-	-	-	-	3 (15%)	-	-	-	-	3 (14%)	-	-	5 (19%)	18
Tortricidae		<i>Dudua aprobola</i>	-	-	-	-	1 (3%)	-	-	2 (4%)	1 (5%)	-	-	-	-	-	4	
		<i>Lobesia aeolopa</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	1	
		<i>L. vanillana</i>	-	3 (3%)	-	-	-	-	-	-	-	-	-	-	1 (9%)	-	4	
		<i>Thaumatotibia leucotreta</i>	-	2 (2%)	-	-	-	-	-	-	-	-	-	-	-	-	2	
Orthoptera	Acrididae	<i>*Locusta migratoria</i>	1 (4%)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
	Gryllotalpidae	<i>*Gryllotalpa africana</i>	-	-	-	-	-	-	2 (10%)	-	-	-	-	-	-	-	2	
Thysanoptera	Thripidae	<i>Frankliniella schultzei</i>	-	-	-	-	1 (3%)	-	-	-	-	-	-	-	-	-	1	
Total n° distinct pests consumed			15	22	0	1	11	2	12	14	2	2	1	17	2	2	13	

Table 5.5. Number of samples per bat species and %FOO in brackets for all identified disease vectors (known and potential). The shaded columns show the values of pest detection outside protected areas, belonging to *Chaerephon leucogaster* and *Mops leucostigma*.

			<i>Chaerephon jobimena</i>	<i>C. leucogaster</i>	<i>Laephotis matroka</i>	<i>Macronycteris commersonii</i>	<i>Miniopterus aelleni</i>	<i>M. ambohitrensis</i>	<i>M. gleni</i>	<i>M. griveaudi</i>	<i>Mops leucostigma</i>	<i>Mormopterus jugularis</i>	<i>Myotis goudoti</i>	<i>Otomops madagascariensis</i>	<i>Pareballonura tiavato</i>	<i>Paratriaenops auritus</i>	<i>Triaenops menamena</i>	Total n° samples detected	
Diptera	Culicidae	<i>Aedeomyia madagascarica</i>	-	2 (2%)	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
		<i>Anopheles gambiae</i>	-	-	-	-	-	-	-	-	8 (15%)	-	-	-	-	-	-	-	8
		<i>A. maculipalpis</i>	-	-	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	1
		<i>A. squamosus</i>	-	-	-	-	-	-	-	-	2 (4%)	-	-	-	-	-	-	-	2
		<i>Culex antennatus</i>	-	-	-	-	-	-	-	-	4 (7%)	-	-	-	-	-	-	-	4
		<i>C. decens</i>	-	-	-	-	1 (3%)	-	-	-	-	-	-	-	-	-	-	-	1
		<i>C. neavei</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>C. perexiguus</i>	-	1 (1%)	-	-	3 (9%)	-	-	-	2 (4%)	-	-	-	-	-	-	-	6
		<i>C. pipiens</i>	-	-	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	1
		<i>C. simpsoni</i>	-	-	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	-	1
		<i>C. tritaeniorhynchus</i>	-	-	-	-	-	-	-	-	3 (6%)	-	-	-	-	-	-	-	3
		<i>Mansonia africana</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>M. uniformis</i>	-	2 (2%)	-	-	-	-	-	-	6 (11%)	-	1 (4%)	-	-	-	-	-	9
	Tabanidae	<i>Atylotus agrestis</i>	-	1 (1%)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>Tabanus taeniola</i>	-	-	-	-	-	-	-	-	1 (2%)	-	-	-	-	-	-	1 (4%)	2
Total n° distinct disease vectors consumed			0	6	0	0	2	0	0	10	0	1	0	0	0	0	1		

5.4. Discussion

This is the first study that uses DNA metabarcoding to assess the diet of insectivorous bats roosting in protected areas of Madagascar. We describe the prey types of 15 bat species occurring in caves, forests and rural villages in the north of the island. Fifty-five prey species detected in the diet of bats were identified as agricultural pests and 15 as human or livestock-disease vectors. Most bat species studied fed upon crop pests or disease vectors, being the members of the families Molossidae and Miniopteridae the main consumers. Given the proximity of our sampling sites within protected areas to agricultural lands and the medium-high mobility typically associated with the two families, we suggest that some of these bat species may move to foraging sites in crop landscapes.

5.4.1. General description of bat diet

Our study confirms that bats in northern Madagascar are feeding on many of the same arthropod groups described in previous research using the morphology of faecal and stomach fragments. However, our molecular approach revealed a wider diversity of prey items (Adrianaivoarivelo et al., 2006; Dammhahn and Goodman, 2014; Rakotoarivelo et al., 2007; Rakotondramanana et al., 2015; Ramasindrazana et al., 2012; Rasoanoro et al., 2015; Razakarivony et al., 2005). For a number of species, *Paremballonura tiavato*, *Miniopterus griveaudi*, *M. aelleni*, *M. gleni*, *M. ambohitrensis*, *Paratriaenops auritus* and *Chaerephon jobimena*, the data presented herein is the first detailed information on their dietary habits.

In several bat species we describe seasonal differences in arthropod consumption at the order level. This can be easily explained by the varying abundance of insects between seasons due to their biological cycles related to climatic conditions. Regardless of season, our results showed that Lepidoptera was the predominant food source for most species, followed by Hemiptera, Diptera and Coleoptera. In fact, there is an important niche overlap in terms of arthropod orders. Although Coleoptera was an important prey order for some bats, their presence in the diet of certain species was less predominant than described in previous studies (Adrianaivoarivelo et al., 2006; Andriafidison et al., 2007; Rakotoarivelo et al., 2007; Rakotondramanana et al., 2015; Rasoanoro et al., 2015; Razakarivony et al., 2005).

Differences in the diet of a given species between this and previous studies can be explained by several factors, such as geographical or seasonal variation in prey consumed, as well as different methodologies to determine diet composition. To date, all previous bat diet studies were conducted in western, eastern and south-eastern Madagascar, and prey availability might differ due to spatial fluctuation of arthropod populations in different habitat types or

latitudinal variation associated with bioclimatic clines. On the other hand, visual identification of faecal or stomach remains under a microscope is a very different approach to describing diets and results in resolutions at broader taxonomic levels than using molecular techniques. The study by Kemp et al. (2019) is the only precedent for Madagascar using DNA metabarcoding to characterise bat feeding habits. However, diet composition of the three shared species between that study and our work also differs slightly, with greater presence of Coleoptera in the earlier study. These differences, apart from geographical aspects, could also be explained by the different molecular primers used in these two projects, which might have an unequal affinity for certain arthropod orders (Browett et al., 2021; Corse et al., 2019; Tournayre et al., 2020).

5.4.2. Agricultural pest and disease vector consumption by insectivorous bats

Insectivorous bats consumed at least 55 agricultural pest species, 11 of which can cause serious damage to rice plantations. For much of the Malagasy population, rice is the critical staple and large quantities of it are grown by smallholder farmers. Even so, domestic production does not meet the national needs, and rice is imported to help ensure national food security (FAO, 2020). Further, up to 10 species confirmed as vectors of several diseases affecting humans in Madagascar (such as malaria, West Nile fever or Rift Valley fever) were also prey items of certain bat species. Malaria remains an important public health issue in this country, with more than 2.8 million cases reported in 2023 (Ihantamalala et al., 2018; Médecins Sans Frontières, 2024). This disease is causing serious problems for the Malagasy population, especially children under five years of age. For this reason, providing evidence that not only synanthropic bat species (Kemp et al., 2019), but also species roosting inside protected areas suppress agricultural pests and reduce important human and livestock disease vectors, has important bearing on aspects of Malagasy public health and economy.

This study provides the first recorded presence of *Culex perexiguus* in Madagascar, a mosquito species that is known for its role in the transmission of arboviruses in other African and Asian countries (Benbetka et al., 2018). However, this remains to be confirmed with mosquito collections in the field, as they belong to the *univittatus* group comprising three species (*Cx. univittatus*, *Cx. neavei* and *Cx. perexiguus*) that are morphologically difficult to distinguish (Harbach, 1988; Jupp, 1971).

The seasonal patterns of bat diet composition revealed a significantly higher predation of pests and disease vectors in the rainy season, likely due to the increased abundance of arthropods and, therefore, proportionately, pests. In tropical and subtropical regions, insect pest

infestations and mosquito densities are generally higher during the wet season, driven by favourable environmental conditions such as higher humidity and abundance of food sources from increased plant growth (Fournet et al., 2010; Gahukar, 1989; Masukujane et al., 2018; Skendžić et al., 2021).

Our molecular analyses revealed that agricultural pests and disease vectors were part of the diet of most bat species studied, regardless of whether these insects were consumed in agricultural areas or not. While many pests are associated with anthropogenic environments, they may spread into surrounding natural habitats, appearing in lower densities (McKone et al., 2001; Tscharncke et al., 2005). Consequently, some of the pests and disease vectors found in bat faecal samples collected in protected areas were likely consumed within these natural zones, possibly at forest edges. To infer whether bats in protected areas are physically capable of foraging in nearby rural landscapes, it is important to consider the distances between roosts and agricultural areas, as well as the bat species' home ranges. The average minimum distance between our sampling sites within the three protected areas and the nearest crops was 2.1 km (ranging from 0.8 to 3.9 km). Such distance could be easily covered within the home ranges of bats with medium-high mobility, such as those belonging to the Miniopteridae and Molossidae families (Fenton et al., 2002; Lehmkuhl-Noer et al., 2012; Pretorius et al., 2020; Van Harten et al., 2022; Vincent et al., 2011). In fact, the highest consumption of crop pests and disease vectors was detected precisely in molossid or miniopterid bats.

Molossid bats, with long, narrow wings and high wing loading and aspect ratios, are adapted for high mobility and fast flight, and for open-space foraging due to poor manoeuvrability (Fenton and Griffin, 1997; Norberg and Rayner, 1987). In this study, *Chaerephon leucogaster* (forearm 33 – 37 mm), the primary pest predator, and *Mops leucostigma* (forearm 41 – 47 mm) were found roosting in rural villages. The other studied members of this family, *Otomops madagascariensis* (forearm 57 – 66 mm), *C. jobimena* (forearm 45 – 48 mm) and *Mormopterus jugularis* (forearm 30 – 39 mm), were captured in caves within protected areas and consumed numerous crop pests and disease vectors. Molossids are specialised in hunting fast-flying insects such as moths and large orthopterans, which could also explain the presence of *Locusta migratoria* in the diet of *C. jobimena*. Medium to large-sized species such as *Otomops madagascariensis*, *C. jobimena* and *M. jugularis*, could fly above the forest canopy easily covering the distances between their sampled natural roosts in protected areas and the closest croplands contributing to pest and disease vector suppression. Nightly movements of larger distances have been reported in other African molossid species such as *O. harrisoni* (forearm 60 – 68 mm), *C. pumilus* (forearm 37 – 42 mm) and *Mops condylurus* (forearm 45 – 50 mm), which usually move around 4 to 5 km from their day-roosts, but are capable of foraging at

longer distances (Fenton et al., 2002; Lehmkuhl-Noer et al., 2012). As well, non-African molossid species such as *Tadarida brasiliensis* (forearm 37 – 41 mm), *T. australis* (forearm 57 – 63 mm) and *T. teniotis* (forearm 54 – 70 mm) were reported to nightly fly 50km, 20km, and 30km, respectively (Krauel et al., 2015; Wilkins, 1989; Marques et al., 2004; Rhodes and Catterall, 2008).

Miniopterid bats also have long, narrow wings with moderate wing loading and moderate-high aspect ratio, enabling both sustained and manoeuvrable flight (Findley et al., 1972; Miller-Butterworth et al., 2003; Pretorius et al., 2020; Van Harten et al., 2022; Wright et al., 2020). These bats can use a wide range of habitats, including open spaces, forests, or anthropogenic landscapes (Goodman and Ramasindrazana, 2013). In this study, the four *Miniopterus* spp. were exclusively captured in caves or inside the forest. Except for *M. ambohitrensis* (forearm 37 – 42 mm, more associated with forest habitats, Goodman et al., 2015), these species consumed several pests and disease vectors. *Miniopterus griveaudi* (forearm 35 – 38 mm) was the main predator of disease vectors (probably due to feeding extensively on small Diptera) and also fed on crop pests, followed by *M. aelleni* (forearm 35 – 41 mm) and *M. gleni* (forearm 47 – 50 mm). These bats likely captured some of these pests in ecotone areas such as forest edges, without reaching nearby rural landscapes. However, extensive movements of *Miniopterus* spp. have been documented, for instance, in *M. schreibersii* (forearm 42 – 48 mm, similar in size to *M. gleni*), which forages up to 30 km from roosts (Némoz and Brisorgueil, 2008; Rainho and Palmeirim, 2011; Vincent et al., 2011). While no data exists for smaller species like *Miniopterus aelleni* and *M. griveaudi*, we assume that they have the flight capacity to easily cover distances of 2 km to adjacent agricultural lands, contributing to pest and disease vector suppression.

Bats from other families (Emballonuridae, Hipposideridae, Rhinonycteridae, Vespertilionidae) were predominantly captured in forests after sunset. It is important to take into account that bats captured in forests shortly after dusk had likely consumed little to no prey (especially those caught right at sunset) for several hours. Prey DNA detectability is much higher right after feeding, and faecal pellets collected shortly after feeding have the highest probability of reflecting a broader spectrum of the bats' diet (Schattaneck et al., 2021; Staliński, 1994). In this case, the last digested prey items, represented in the dusk samples, are likely to be significantly tougher insects that require longer digestion times (usually not the case of Lepidoptera species) (Schattaneck et al., 2021). This could be one of the reasons behind the differences in pest and disease vector occurrence between samples collected in forests and roost entrances. This applies to *Macronycteris commersoni* and *Laephotis matroka*, mostly captured in forests, which consumed one and no pests, respectively. However, *Triaenops*

menamena, almost exclusively captured in forests, consumed at least 12 agricultural pests and one potential disease vector. Amongst all species studied, it is the main consumer of the rice pest *Maliarpha separata* (found in 28.6% of its samples), and also fed on important crop pests such as *Ethiella zinckenella*, *Helicoverpa armigera* or *Herpetogramma licarsialis*. *Triaenops menamena* frequently forages at forest edges (Kofoky et al., 2007; Rakotoarivelo et al., 2007), and Bambini et al. (2011) observed a preference for foraging in agricultural landscapes. Given the short distances from sampling sites to croplands and the foraging behaviour of *T. menamena*, we consider that this species may have easily reached adjacent agricultural lands. In contrast, *Paremballonura tiavato* and *Paratriaenops auritus* (found in caves and forests) are considered strongly associated with forests (Goodman et al., 2006, 2005), and by extrapolation, they probably do not forage in agricultural landscapes. This fits with our results, as they only fed on two crop pests, supporting the possibility that the presence of pests or disease vectors in the bats' diet does not necessarily indicate that their consumption occurred outside forested zones.

Finally, molossid and miniopterid bats are the most abundant species on Madagascar. This further underscores their relevance to agriculture and public health. In this study, many species belonging to these families were found roosting exclusively in caves inside protected areas. This suggests that there may exist an effect of roost distance to agricultural areas on pest suppression, particularly for *Miniopterus* spp. In rural villages farther from natural roosts with large bat concentrations, pest suppression may rely on synanthropic species (mainly molossids) and the availability of roosts in these landscapes. Most bat species providing key pest-suppressing services are currently classified as Least Concern (LC), except for *Paratriaenops auritus* (Vulnerable, VU), *Macronycteris commersoni* (Near Threatened, NT), and *Miniopterus griveaudi* (Data Deficient, DD). Despite this, the populations of most species are suggested to be declining due to the loss of suitable habitats. Forest loss and agricultural expansion might bring some bats closer to rural villages, especially those that may use synanthropic roosts, potentially enhancing bat-driven pest control. However, essential habitat loss often goes hand in hand with increased human disturbances, such as bat hunting for consumption, which is common in Madagascar. This disturbance jeopardises the survival of large bat colonies and frequently forces them to abandon roosts, losing the ecosystem services they provide.

5.5. Conclusions

Our research evidences the role of Malagasy insectivorous bats in suppressing disease vectors and pests insects affecting staple crops like rice. It underscores the importance of protected areas, particularly those with caves, in sustaining bat-driven pest control services that extend beyond their boundaries, yielding tangible benefits for agricultural productivity and rural livelihoods.

Outside Madagascar's protected areas, caves in non-forested regions also harbour bat populations that contribute significantly to pest control in nearby farmlands. However, these caves are increasingly threatened by human disturbances. Urgent interventions, such as community-led cave protection and sustainable land-use planning, are needed to mitigate these threats and preserve bats' contributions to agriculture and rural economies.

Research outcomes directly impacting human communities are critical for promoting conservation approaches for people inhabiting in close proximity to protected areas. Strengthening awareness among farmers and rural communities about the benefits bats provide to agriculture can also encourage sustainable farming practices and improve food security. Thus, integrating ecosystem services into agronomic and land management strategies is key for maximising the benefits bats provide, while linking bat conservation efforts and rural development goals.

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Chapter 6 – General discussion



Cave-dwelling bats returning to their natural refuge before sunrise, Madagascar ©Adrià López-Baucells

6.1. Key findings

In this thesis, I contribute to a better understanding of the ecosystem services provided by bats as natural insect predators in agrosystems. My research presents new evidence of the significant role bats play in suppressing agricultural pests on a global scale, with detailed case studies in Spain and Madagascar. Furthermore, I bring forth reference tools for farmers, land managers, governments and other stakeholders to promote and implement sustainable practices for managing harmful insects through bat conservation. These tools are designed to incorporate bats into Integrated Pest Management (IPM) strategies, encouraging the adoption of more holistic and environmentally friendly pest control methods that reduce reliance on chemical pesticides and enhance agricultural sustainability.

One of the first contributions of this thesis is the critical synthesis of conservation strategies, actions, and recommendations that can be implemented to support and enhance bat pest control in agricultural areas, discussed in Chapter 2. In the same chapter, I gathered up to 1798 arthropod species, creating a list of agricultural pests, a reference resource that was missing in publicly accessible platforms. I also assembled a global network of predation-interactions between bats and insect pests into an open database, comprising over 2300 documented prey-predator dyads from around the world. This comprehensive reference list serves as a valuable tool for researchers exploring bat dietary habits and for land managers, filling a previously existing gap. While, undoubtedly, there are numerous interactions yet to be documented, I hope that more researchers will contribute by supplying new data to this list, which can be regularly updated in the open repository where it is currently stored (<https://doi.org/10.5281/zenodo.7821119>).

The next part of the project focused on the assessment of bat ecosystem services in rice paddies in the Mediterranean region (Chapter 3). This work contributed to the knowledge and understanding of the role of bats as natural enemies of rice pests, and complemented the findings reported by Puig-Montserrat et al. (2015). Rice is a crucial staple food globally, and one of the most harmful insect pests affecting this crop is the striped rice stem borer moth (*Chilo suppressalis*). This widespread Lepidoptera species is found in Australasia, Asia, and Europe, affecting a million hectares of rice plantations yearly (Heinrichs and Muniappan, 2017; Maes, 2022). For the first time in Europe using exclusion experiments, I quantified the pest suppression potential of bats in reducing this insect species in rice paddies and its economical implications. Assigning an economic value to the ecosystem services offered by nature is often essential for raising awareness within society. I estimated that bats might prevent crop losses due to the striped rice stem borer moth of nearly 70 kg [4 – 147 kg] of rice per hectare, translating to an average saving of 56€ [3€ – 135€] per hectare each year. Simple

extrapolations of these estimates suggest a potential annual saving of 7.6 thousand tonnes of rice, or more than 6 million euros in Spain alone. This last step, far from pretending to show a very precise national estimate, was intended to give an idea of the magnitude of the benefits provided by insectivorous bats in rice plantations.

Furthermore, in a novel experimental study, I show that the suppression effects may be much larger than those estimated through exclosures (Chapter 4). Bats may be mitigating pest damage not only through direct predation, but also by indirectly reducing the reproductive success of pest populations through the emission of ultrasounds. This is the first time that a captivity experiment has been conducted with individuals of *C. suppressalis*, a tympanate moth species capable of detecting ultrasounds, using broadcasted bat recordings. The findings of this work highlight that echolocating bats may negatively affect the egg production of this pest merely by emitting ultrasounds into the environment. This moth species seems to alter its behavioural patterns to reduce predation risk, which negatively affects clutch size, substantially reducing the number of eggs laid by females. Although this topic deserves further research to understand the final consequences regarding insect survival, behaviour, and fitness, it may have profound impacts on pest populations, crop damage and economic losses.

The last contribution of this thesis addresses bat ecosystem services in the African continent, specifically in Madagascar (Chapter 5). Malagasy society is heavily reliant on subsistence agriculture (Fig. 6.1), and the increasing population, coupled with limited economic alternatives and harvest losses, has driven to a widespread conversion of forests into arable lands. The work presented here focuses on protected areas and provides evidence that many insectivorous bats, most of them Madagascar endemics, suppress important pests of rice and other crops. Additionally, these bats also prey on vectors of relevant diseases such as malaria, West Nile fever or Rift Valley fever. These findings support previous work developed in the country by Kemp et al. (2019) and, for the first time, underscore that protected areas, sheltering large populations of insectivorous bats in caves and forests, likely play an essential role in provisioning and maintaining these bat ecosystem services beyond their borders. Given their mobility and home ranges, I suggest that some insectivorous bat species roosting in protected areas can move to feeding sites in the nearby rural landscapes, where rice paddies and other agrosystems can offer a stable source of insects for bats. Therefore, protected areas in Madagascar are paramount not only to preserve natural habitats and their largely endemic biodiversity, but also serve as a source of essential ecosystem service flows to anthropogenic landscapes, which rural populations heavily rely on.



Figure 6.1. Malagasy woman cultivating rice, Madagascar. © Adrià López-Baucells

6.2. Integrating scientific research and ecosystem services in applied conservation planning

Scientific research is essential to provide reliable data, tools and advice to plan and implement appropriate conservation actions for addressing complex environmental issues, ensuring that decisions are evidence-based (Mair et al., 2018; Martín-López et al., 2009). During my PhD thesis I have been involved with the European CostAction Climbats project (CA18107), which aimed to investigate how climate change will affect European bat populations and the subsequent consequences on insect consumption by bats in farmlands, forests, and urban areas. Chapter 2 was developed and published within the framework of this large-scale, transboundary project. Participating in such a cooperative effort underscores the importance of international cooperation in addressing complex environmental challenges. This project brought together researchers from several countries, fostering the exchange of knowledge and methodologies, and enhancing the robustness and applicability of the findings. Furthermore, such collaborative projects not only enrich the research outcomes but also build a network of experts committed to the conservation of bat populations and their ecosystems. Through this cooperation, we can develop more comprehensive and effective strategies to

mitigate the impacts of climate change on biodiversity and ecosystem services across Europe and beyond.

However, there are some critical points to bear in mind when, as scientists, we communicate our findings, conclusions or recommendations to conservationists, managers, policy-makers or the general public. In the first instance, the use of scientific papers in decision-making is often limited due to several barriers, such as the complexity of scientific literature, accessibility issues due to payment platforms, or the lack of practical applicability of many research findings (Arlettaz et al., 2010; Pullin and Knight, 2003).

My research directly addresses a real-world conservation challenge: dealing with insect pests in agricultural areas in a more sustainable and eco-friendly way, seeking to prevent the use of agrochemicals and other products harmful to ecosystems and human health. Therefore, synthesising the outcomes of this work in an illustrative and easily accessible format will be one of the most relevant future steps to ensure this thesis' findings are taken into account when planning management strategies to be applied both in agrosystems or natural habitats. Most recommendations provided in Chapter 2 are evidence-based and targeted to be applied by farmers and land managers, as well as to be considered by policy-makers when implementing sustainable management regulations. Thus, it would also become a priority to reshape these recommendations into informative and easily accessible guidelines for both European and Malagasy farmers, bearing in mind that they must be adapted and compatible with each location's socio-economic situation.

Many experts emphasise the importance of incorporating ecosystem services into conservation plans, benefiting biodiversity and human well-being (Egoh et al., 2007; Mair et al., 2018; Palomo et al., 2013; Tallis et al., 2008). Demonstrating the economic value of the benefits nature delivers can enhance community engagement and significantly influence policy decisions (Egoh et al., 2007; Tallis et al., 2008). This thesis provides evidence that integrating bat conservation into action plans is an effective strategy for pest suppression in rice paddies and other agrosystems. Bats also serve as natural enemies of disease vectors in tropical and subtropical regions, which is also becoming a topic of growing interest in temperate regions due to climate change. These findings can raise awareness within society and influence policymakers to implement measures that promote stable bat populations, supporting ecosystems, food production, and human health.

Finally, this thesis supports protected areas as critical hubs for the provisioning of bat ecosystem services. They serve as refuges for many bat species, which, in turn, play essential roles in pest suppression and disease regulation beyond their borders. The findings from Madagascar underscore the importance of protected areas in safeguarding biodiversity that

contribute significantly to crop protection and disease prevention in rural landscapes (Fig. 6.2). Thus, integrating bat conservation into protected area management plans is also crucial for maintaining these ecological services beyond reserve boundaries. Research outcomes directly impacting local communities are crucial for promoting and enhancing community-based conservation approaches, involving people inhabiting close to natural habitats in conservation efforts.



Figure 6.2. Rufous trident bat (*Triaenops menamena*) in Ankarana Special Reserve. In the study described in Chapter 5, this Madagascar endemic species was reported to roost exclusively in protected areas and prey on numerous agricultural pests and disease vectors. ©Adrià López-Baucells

6.3. Engagement of local communities through biocultural approaches

Adaptive management and engagement of local communities are essential components of effective conservation planning, allowing for continuous learning and adjustment of strategies based on the real needs of people at each moment, direct results on the ground or new scientific insights (McCarthy and Possingham, 2007; Wali et al., 2017; Williams and Brown, 2016). Furthermore, robust retrospective evaluations of the implemented conservation measures allow demonstrating the positive outcomes of interventions, which would give local

communities and decision-makers more confidence in scientific proposals and facilitate better communication and collaboration among stakeholders (Maas et al., 2019; Pressey et al., 2017). The approach I advocate in this thesis enhances the resilience and effectiveness of conservation efforts, encouraging continued close interaction between researchers, farmers, and land managers, and ensuring that any changes or modifications are approved through the agreements of all stakeholders. Furthermore, incorporating socio-political dimensions and biocultural approaches in conservation planning is crucial for this engagement and for ensuring the acceptance and success of conservation measures (Mair et al., 2018).

Before and throughout the development of this doctoral project I have been in close contact with rice growers in Spain and Madagascar. As a researcher and conservationist promoting sustainable pest suppression through bat conservation, I have witnessed the effect and acceptance or rejection of various recommendations, such as installing bat boxes to attract bats to agricultural lands. In the Ebro Delta, as explained by Puig-Montserrat et al. (2015), the installation of bat boxes was one of the most successful strategies in reducing pest levels in rice paddies and raising awareness among local communities in Spain. Farmers experienced first-hand the significant rice damage reduction, encouraging widespread adoption of this strategy in the area.

Inspired by this success, I initiated a similar project in Madagascar, a country known for its large extensions of rice fields covering all the island. Collaborating with local carpenters and landowners around the Ranomafana National Park, where the study led by Kemp et al. (2019) already demonstrated bat predation on agricultural pests, I installed 75 boxes near rice paddies (Fig. 6.3). Throughout the whole process of construction and installation of the artificial roosts I always adopted a respectful approach to the local culture and involved local people at every stage. To ensure effective communication with rural communities, Matthieu (a Malagasy expert in social sciences and communication) and I explained to farmers the benefits of bats in reducing crop damage caused by insect pests, as well as the purpose and potential effect of installing bat boxes. We also conducted educational visits to local schools to inform younger generations about the importance of bats in agriculture (Fig. 6.4). Additionally, as radio is one of the most used media in rural areas of Madagascar due to the very limited access to electricity, we recorded a program in Malagasy which was broadcasted in all villages in the district.

While the installation of bat boxes has been successful in most locations and involved people generally satisfied with the project, some mistrust or resistance has been raised in a very specific location. After two years, bat boxes have not been occupied yet, which is normally expected, as it can take months or years for bats to detect and use them (Rueegger, 2016). However, there has been a lack of follow-up efforts, a missing local leader, and continuous

monitoring with the farmers, probably favouring the disconnection between researchers and local communities. These obstacles highlight and evidence the need for consistent community engagement, especially when implementing actions that do not yield quick results, as it is easier to lose people's interest. This is especially true in developing countries with different cultural and economic contexts.



Figure 6.3. Bat box installed next to rice paddies in Ambatolahy village, Madagascar. © Adrià López-Baucells

Effective and efficient conservation requires substantial effort in establishing quality, trust-based relationships with local communities, as well as appropriate outreach and communication approaches with the general public. According to community-based conservation theories, success depends on identifying genuine needs and developing strategies that are respectful and equitable to local populations, their realities, and their traditions (Berkes, 2004; Brooks et al., 2013; Galvin et al., 2018; Waylen et al., 2010). These strategies must be tailored specifically to each region to ensure relevance and acceptance. Conservation efforts should aim to foster awareness and a sense of responsibility within communities, planting the seeds for long-term sustainability. This approach aligns with the principles of participatory conservation, which emphasise the importance of community involvement, empowerment and ownership for long-term success (Twyman, 2000; Wali et al., 2017).



Figure 6.4. Matthieu (one of the main collaborators of the project) leading the environmental talks in the schools of Ranomafana (Madagascar), and I, showing one of the bat boxes that were installed in the village. © Adrià López-Baucells

6.4. Empowering bat conservation through general public involvement and national leadership.

Political will and governance structures significantly influence decision-making processes. However, public concern and engagement can also exert pressure on policymakers to prioritise biodiversity conservation. Therefore, it is crucial to underscore the integration of disciplines such as social sciences, humanities, and economics as essential components of conservation science. This integration enables the development of conservation strategies and actions that involve the general public, and that are more efficient, realistic and reliable. As Maas et al. (2019) highlight, transforming research findings from usable to actionable is essential, with citizen science and international cooperation playing key roles in shaping the future of conservation.

During the last stage of this project, I launched a Facebook group in Madagascar named “Bat Conservation Madagascar - Conservation des Chauve-souris à Madagascar”. The aim behind the creation of this group was to establish a network of scientists and enthusiasts interested in bat conservation in this country. Facebook is, by far, the main social media platform used in

Madagascar, accessible to many even without mobile data through partnerships with local telecom companies. My goal was to link people studying bats or working in conservation, as well as Malagasy farmers interested in using bat boxes in croplands, people who have bats roosting in their homes or naturalists, acting as a bridge between scientists and the general public (Fig. 6.5). I also wanted this group to serve as a tool for Malagasy students, early-career researchers or enthusiasts interested in engaging in bat research and conservation projects, promoting and facilitating the sharing of collaboration opportunities, grants, training courses, workshops or environmental education activities by national and international group members. The group already has 419 participants, including Malagasy members and people from other countries. The next step I wish to foresee would be for a Malagasy researcher or conservationist to take leadership of this platform and make it their own.

There is a need to empower national scientists and conservationists, in Europe and developing countries such as Madagascar, to lead conservation initiatives like this, especially community-based projects and citizen science programs. National researchers possess invaluable local knowledge and cultural insights crucial for effective conservation strategies tailored to their regions. During the development of this thesis, I have trained a Spanish student and three Malagasy students in the field of bat research and conservation, with the intention of guiding



Figure 6.5. Researchers from the GCC lab (University of Helsinki, Finland) exchanging knowledge and experiences with farmers from Ranomafana village (Madagascar), regarding rice damage, pests and insectivorous bats in 2018. © Adrià López-Baucells.

and motivating them to take charge of their own research and projects. By fostering leadership among national scientists, we can ensure that conservation efforts are not only scientifically coherent but also socially and culturally relevant. This approach promotes ownership and sustainability within the general public, enhancing the long-term success and impact of conservation initiatives. Furthermore, empowering national scientists strengthens the scientific capacity of the country and encourages international cooperation, contributing to a global effort to address environmental challenges in a more holistic and integrative approach.

6.5. Eco-labelling strategies for sustainable agriculture: local realities and global perspectives

A widely used strategy to encourage and involve the general public in supporting sustainable agricultural practices in the market is the use of eco-labels or green stickers, which have emerged to help consumers identify products that meet different standards of environmental friendliness and sustainable development. Numerous studies have consistently shown that consumers generally hold favourable views towards sustainability, being more inclined to buy products and services from companies that engage in eco-friendly practices (Hughner et al., 2007; Young et al., 2010). For this reason, many industries are adopting these standards to highlight their commitment to sustainable practices in a global market. These eco-labels guarantee that the whole or part of the production process has been carried out in a way that respects the environment and the people involved in this production process.

The 80% of the global vanilla production occurs in Madagascar, being the world's largest exporter of this product, renowned for producing high-quality, organic vanilla beans (Andriamparany et al., 2021; Campbell, 2018; Symrise, 2023) (Fig. 6.6). The vanilla sector is a significant part of the country's economy, with the bulk of the production being organic to meet international demand for organically certified vanilla (Andriamparany et al., 2021; Symrise, 2023). However, in terms of rice production, using eco-labels involving bat pest suppression would not make sense in countries like Madagascar, where critical food security issues occur in several regions, and population economy is based on subsistence agriculture. Despite significant domestic rice production, which reached 4.6 million tonnes in 2022, the country still relies on imports (mainly from India and Pakistan) to cover shortfalls (Famine Early Warning Systems Network, 2024; FAO, 2022).



Figure 6.6. Farmer and owner of a small vanilla plantation in southern Madagascar. © Adrià López-Baucells

In contrast, in European Union countries, eco-label use in organic products is a widely extended practice, and rice is no exception. However, there is no specific eco-labelling scheme for bat-friendly practices yet. The study led by Gatti et al. (2022) evaluated consumer preferences for various sustainability attributes in coffee in the US, including a bird-friendly coffee certification. The authors highlighted the success of eco-labels in effectively capturing consumer interest, but the specific attributes underscored by these labels significantly influenced their market success. Labels focusing on agrochemical-free products were more appealing to consumers compared to those emphasising biodiversity conservation.

To apply the findings of my thesis for the benefit of local livelihoods and biodiversity, fostering collaborations between researchers, local farmers and other stakeholders (including governments) to develop a new eco-labelling scheme for rice could be a strategic approach. This scheme would certify agrochemical-free practices based on bat-mediated pest suppression (Fig. 6.7). Accompanied by a targeted marketing campaign, this eco-label would rise consumer awareness and encourage the general public to pay premium prices to support farmers growing rice through bat-friendly, sustainable and agrochemical-free practices.



Figure 6.7. Photomontage created by combining multiple photos of a Soprano pipistrelle bat (*Pipistrellus pygmaeus*) chasing a striped rice stem borer moth (*Chilo suppressalis*) in rice paddies in Spain. © Oriol Massana Valeriano & Adrià López-Baucells

6.6. Concluding remarks

This thesis underscores the indispensable role of bats as natural allies in the global effort towards sustainable agriculture and biodiversity conservation. By documenting their effectiveness as insect predators across diverse agrosystems globally, including European rice paddies and Malagasy croplands, this research highlights the relevant implications of bat-mediated pest suppression within the Integrated Pest Management strategy.

As we face the urgent challenges of rapid human population growth and climate change, and with agriculture being a major driver of deforestation and biodiversity loss worldwide, the transition towards environmentally sustainable and socially equitable agricultural practices becomes imperative. Sustainable agriculture not only mitigates the detrimental impacts of intensive farming in our ecosystems but also fosters biodiversity, enriches soil health and productivity, and supports the delicate balance of our planet's complex ecological networks. This approach is vital for long-term food security, requiring policies that promote these practices at national and global levels (Duroy, 2011).

The findings of this research highlight that integrating natural pest control agents, such as bats, into agrosystems is not merely a conservation strategy but a vital component of a resilient and productive farming future. In our society, it has become critical to emphasise and demonstrate that, although organic systems might be less productive in the short term

compared to intensive agriculture, they ensure greater long-term productivity and resilience (Altieri, 2000; Gurr et al., 2003; Isbell et al., 2015; Oliver et al., 2015). By adopting and promoting these nature-based solutions, we can achieve a harmonious coexistence between agricultural yield and environmental protection, with agrosystems that are more adaptable to changing climatic conditions, ultimately securing the well-being of future generations.

In the current context of global change, collective responsibility for ecosystems' health is essential (Amel et al., 2017; Hoppe et al., 2023). To implement effective management strategies that are ecologically robust and also socially and economically viable, it is crucial to enhance communication efforts and appropriately adapt scientific findings. There is a need to establish conservation actions through a holistic approach that integrates biocultural perspectives and community engagement. Therefore, by involving local stakeholders and fostering a sense of shared responsibility, we can build sustainable practices that are rooted in local knowledge and cultural values. Awareness and support for these practices, achieved through education and trust-building among scientists, farmers, governments, and the general public, is fundamental for bridging the gap between science and society and enhancing successful conservation efforts.

The time for transformative action is now, and our society needs to find a way to cultivate a world where both humanity and nature thrive together.



Figure 6.8. Peters' wrinkle-lipped bat (*Mormopterus jugularis*) flying over rice paddies in Madagascar.
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Appendix A – Supplementary Information

7.1. Supplementary information for Article I

Article I – Pest suppression by bats and management strategies to favour it: a global review

Carme Tuneu-Corral, Xavier Puig-Montserrat, Daniel Riba-Bertolín, Danilo Russo, Hugo Rebelo, Mar Cabeza and Adrià Lopez-Baucells

List of supplementary Figures and Tables:

Figure A1.1. PRISMA flow diagram illustrating the systematic review process for studies assessing bats as insect pest suppressors in agroecosystems.

Figure A1.2. PRISMA flow diagram illustrating the systematic review process for studies reporting evidence of bat predation of insect pests.

Figure A1.3. Publication year of the 66 articles focused on bats as natural pest controllers identified in the first literature search (LS1).

Figure A1.4. Food web illustrating the relationships between insect pest orders consumed by bats and the crops that those pests damage.

Table A1.1. Articles located by the first literature search (LS1) and the main information extracted. (*embedded link*)

Table A1.2. List of agricultural insect pests used in the second literature search (LS2) (*embedded link*)

Table A1.3. Bat–pest insect interactions identified in the second literature search (LS2) (*embedded link*)

Table A1.4. Pest species preyed upon by bats and the crop types affected by them. (*embedded link*)

Table A1.5. Bat species, IUCN conservation status and the number of agricultural insect pests they consumed.

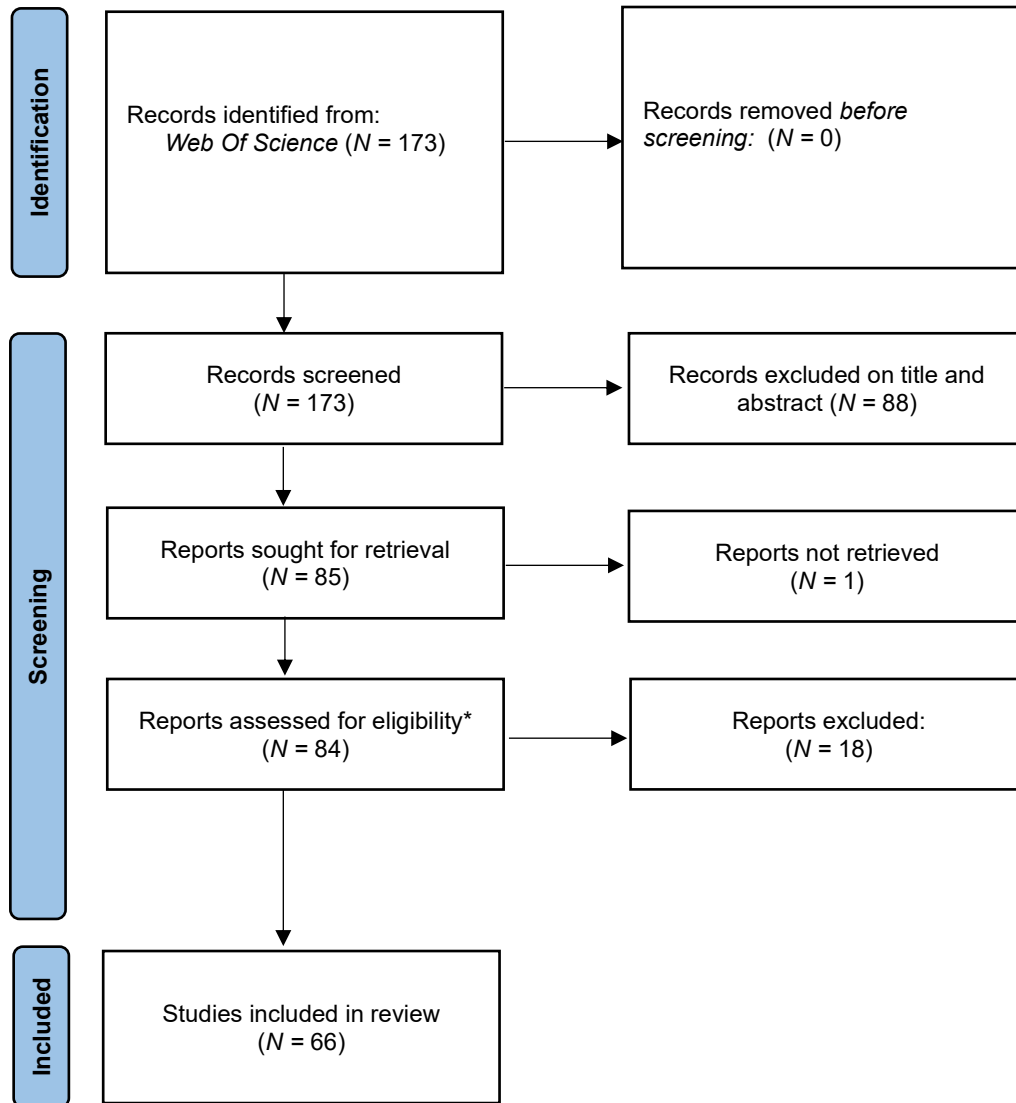


Figure A1.1. PRISMA flow diagram illustrating the systematic review process for studies assessing bats as insect pest suppressors in agroecosystems. *Inclusion criteria: (1) paper studies the potential of bats as pest suppressors, focusing on their role as consumers of certain agricultural pests and the correlation between them; (2) paper reports evidence of the top-down effect of bats in agroecosystems using, for example, experimental exclosures; (3) paper reports quantitative estimations of the ecosystems services provided by bats as suppressors of agricultural pests and/or provides an economic value of their benefits.

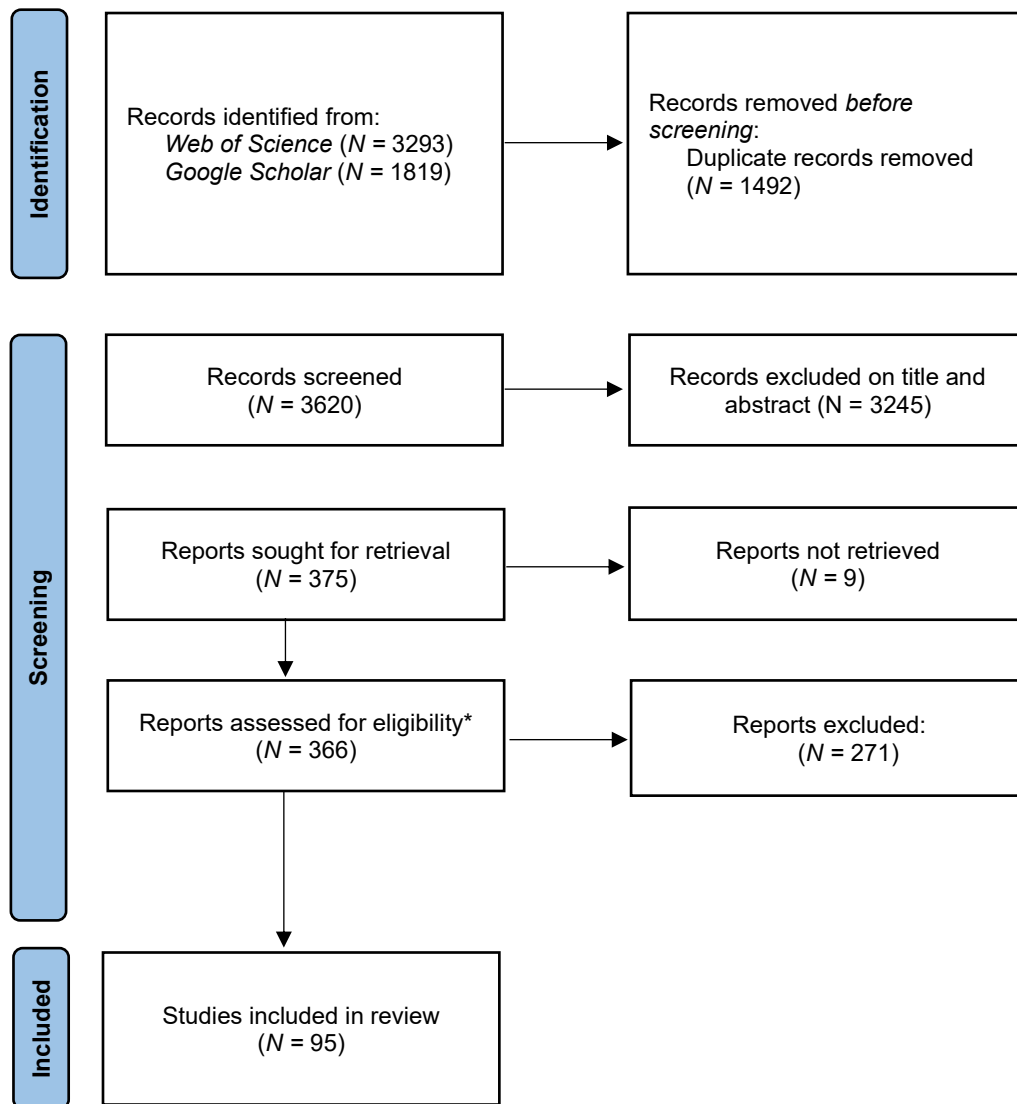


Figure A1.2. PRISMA flow diagram illustrating the systematic review process for studies reporting evidence of bat predation of insect pests. *Inclusion criteria: paper reports evidence of consumption of agricultural insect pests by the determined bat species, by identifying prey at species or genus level either through (i) identification of insect remains on the ground (sometimes complemented with acoustics or visual observations), (ii) visual identification from faeces dissection, (iii) DNA extraction from faeces or stomach contents.

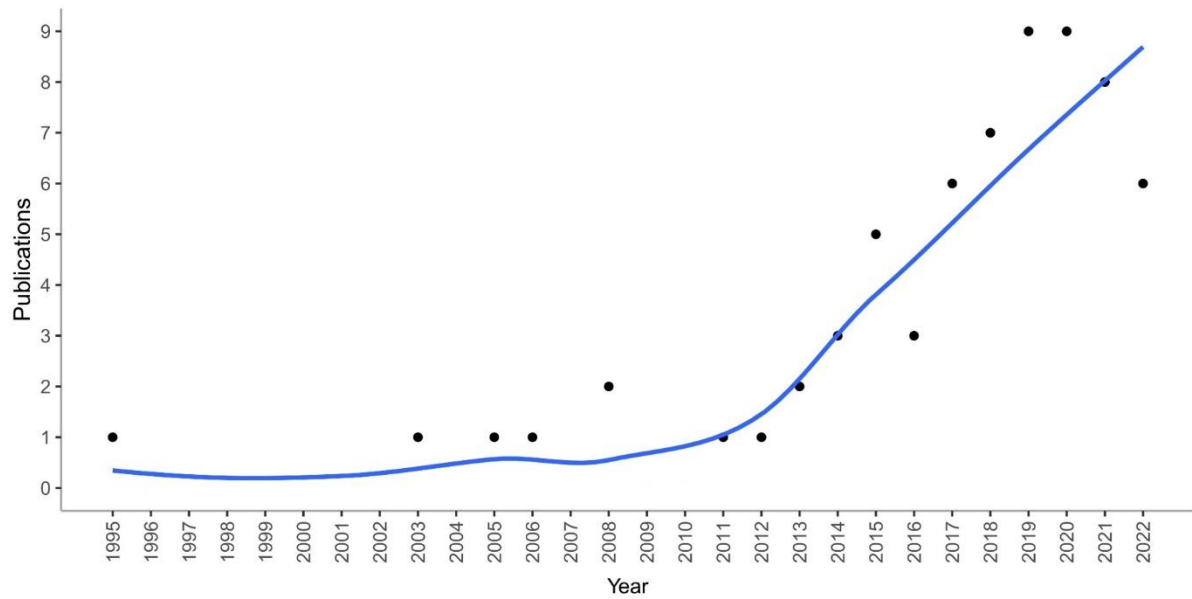


Figure A1.3. Publication year of the 66 articles focused on bats as natural pest controllers identified in the first literature search (LS1).

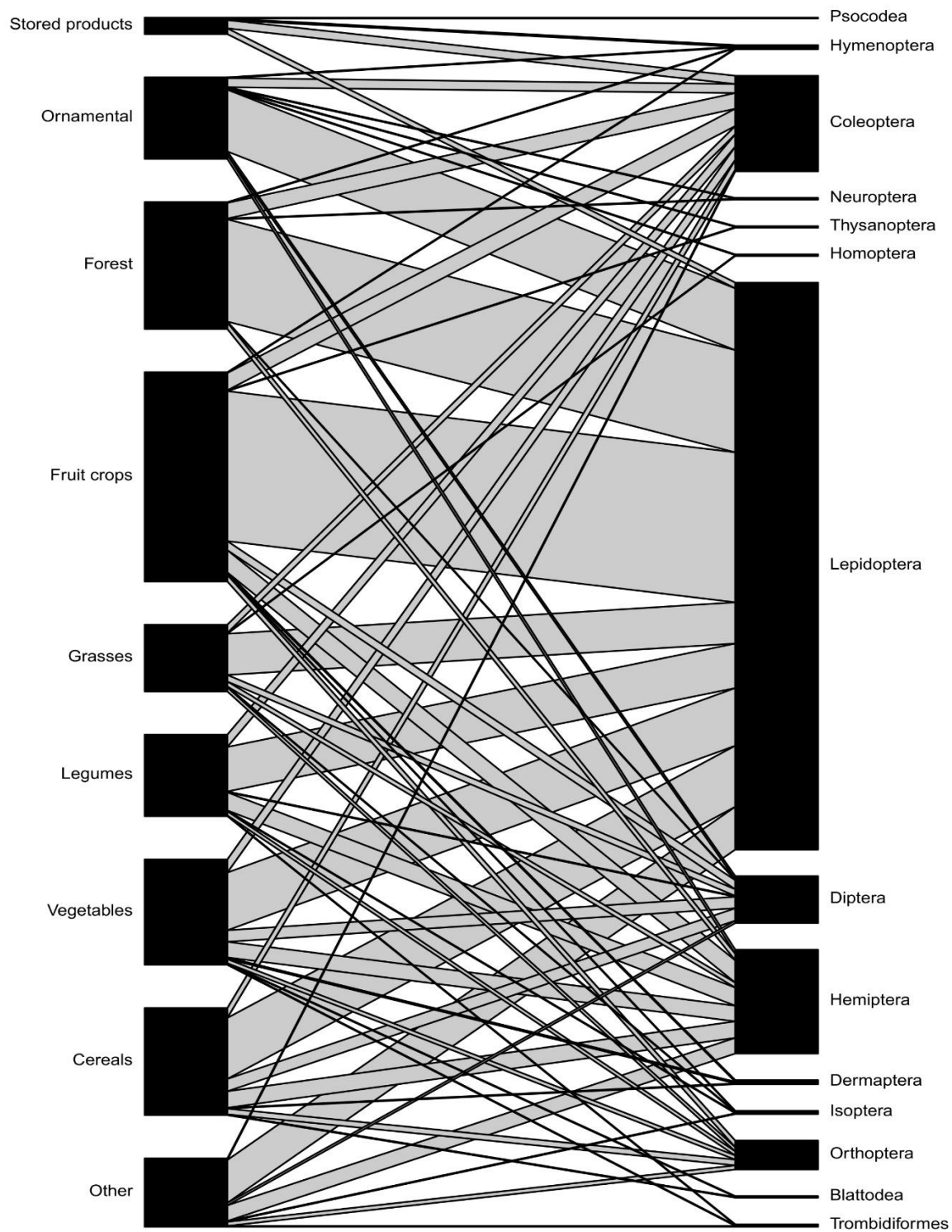


Figure A1.4. Food web illustrating the relationships between insect pest orders consumed by bats and the crops that those pests damage.

Table A1.5. Bat species, IUCN conservation status and the number of agricultural insect pests they consumed.

Bat species	IUCN Category	Number of pest species consumed
<i>Myotis lucifugus</i>	EN	201
<i>Eptesicus fuscus</i>	LC	180
<i>Myotis escalerae</i>	LC	139
<i>Rhinolophus hipposideros</i>	LC	113
<i>Myotis crypticus</i>	DD	111
<i>Pipistrellus pipistrellus</i>	LC	102
<i>Rhinolophus euryale</i>	NT	97
<i>Pipistrellus kuhlii</i>	LC	78
<i>Eptesicus serotinus</i>	LC	67
<i>Miniopterus schreibersii</i>	VU	62
<i>Myotis daubentonii</i>	LC	56
<i>Plecotus auritus</i>	LC	54
<i>Rhinolophus ferrumequinum</i>	LC	49
<i>Tadarida teniotis</i>	LC	47
<i>Plecotus austriacus</i>	NT	39
<i>Tadarida brasiliensis</i>	LC	38
<i>Barbastella barbastellus</i>	NT	35
<i>Lasiurus borealis</i>	LC	30
<i>Myotis mystacinus</i>	LC	29
<i>Nycticeius humeralis</i>	LC	26
<i>Lasiurus seminolus</i>	LC	20
<i>Myotis austroriparius</i>	LC	20
<i>Myotis brandtii</i>	LC	19
<i>Taphozous mauritanus</i>	LC	19
<i>Eptesicus nilssonii</i>	LC	18
<i>Myotis emarginatus</i>	LC	18
<i>Antrozous pallidus</i>	LC	17
<i>Rhinolophus mehelyi</i>	VU	16
<i>Eptesicus isabellinus</i>	LC	15
<i>Pipistrellus pygmaeus</i>	LC	15
<i>Myotis bechsteinii</i>	NT	12
<i>Myotis myotis/blythii</i>	LC	12
<i>Myotis nattereri</i>	LC	12
<i>Murina ussuriensis</i>	LC	11
<i>Corynorhinus townsendii ingens</i>	LC	10
<i>Hypsugo savii</i>	LC	9
<i>Myotis ikonnikovi</i>	LC	9
<i>Mops midas</i>	LC	8
<i>Nyctinomops laticaudatus</i>	LC	7
<i>Eumops perotis</i>	LC	6
<i>Histiotus diaphanopterus</i>	LC	6

<i>Myotis chiloensis</i>	LC	6
<i>Pipistrellus nathusii</i>	LC	6
<i>Miniopterus majori</i>	LC	5
<i>Pipistrellus hesperidus</i>	LC	5
<i>Plecotus macrobullaris</i>	LC	5
<i>Scotophilus dinganii</i>	LC	5
<i>Corynorhinus rafinesquii</i>	LC	4
<i>Mormoops blainvillei</i>	LC	4
<i>Myotis myotis</i>	LC	4
<i>Neoromicia nana</i>	LC	4
<i>Vespadelus regulu</i>	LC	4
<i>Lasiurus cinereus</i>	LC	3
<i>Molossus molossus</i>	LC	3
<i>Myotis sodalis</i>	NT	3
<i>Nycteris thebaica</i>	LC	3
<i>Perimyotis subflavus</i>	VU	3
<i>Vespertilio murinus</i>	LC	3
<i>Chaerephon atsinanana</i>	LC	2
<i>Chaerephon pumilus</i>	LC	2
<i>Cynomops planirostris</i>	LC	2
<i>Mops leucostigma</i>	LC	2
<i>Mormopterus jugularis</i>	LC	2
<i>Myotis velifer</i>	LC	2
<i>Brachyphylla cavernarum</i>	LC	1
<i>Chaerephon plicatus</i>	LC	1
<i>Chalinolobus gouldii</i>	LC	1
<i>Lasionycteris noctivagans</i>	LC	1
<i>Myotis bocagii</i>	LC	1
<i>Myotis dasycneme</i>	NT	1
<i>Myotis evotis</i>	LC	1
<i>Myotis goudoti</i>	LC	1
<i>Myotis septentrionalis</i>	NT	1
<i>Myotis volans</i>	LC	1
<i>Nyctalus lasiopterus</i>	VU	1
<i>Nyctalus noctula</i>	LC	1
<i>Nyctophilus gouldi</i>	LC	1
<i>Pteronotus quadridens</i>	LC	1
<i>Rhinolophus simulator</i>	LC	1
<i>Tadarida plicata</i>	LC	1
<i>Vespadelus pumilus</i>	LC	1

7.2. Supplementary information for Article II

Article II – Bats and rice: Quantifying the role of insectivorous bats as agricultural pest suppressors in rice fields

Carme Tuneu-Corral, Xavier Puig-Montserrat, Carles Flaquer, Vanessa A. Mata, Hugo Rebelo, Mar Cabeza and Adrià López-Baucells

List of supplementary Figures and Tables:

Figure A2.1. Crop damage over time. Amount of damaged rice spikes counted in each treatment (Control/Exclosure) and during the four surveying dates, considering only the area of 15m² sampled. (A) Block 1, (B) Block 2, (C) Block 3, (D) Block 4.

Table A2.1. Relationship between “Cumulative mean values of infested stems” and (i) Treatment (Control/Exclosure) and (ii) Julian day modelled with a GLMM with a Poisson distribution (N = 32).

File A2.1. Instructions for using exclosures: Preinstallation, Material preparation and Exclosure installation

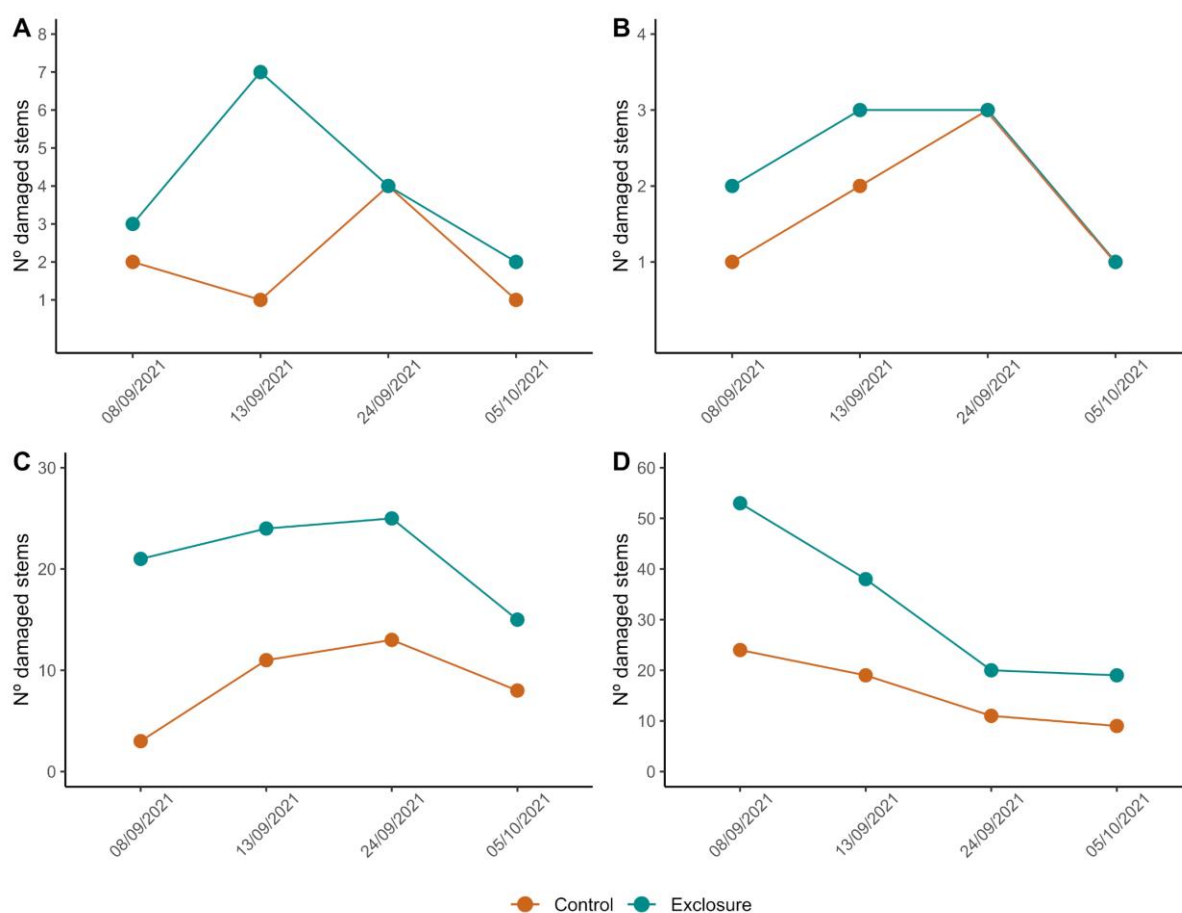


Figure A2.1. Crop damage over time. Amount of damaged rice spikes counted in each treatment (Control/Exclosure) and during the four surveying dates, considering only the area of 15m² sampled. (A) Block 1, (B) Block 2, (C) Block 3, (D) Block 4.

Table A2.1. Relationship between “Cumulative mean values of infested stems” and (i) Treatment (Control/Exclosure) and (ii) Julian day modelled with a GLMM with a Poisson distribution (N = 32).

Fixed effects	Estimate	SE	Z value	P value
Intercept	2.362	0.545	4.331	< 0.0001
Treatment - Exclosure	0.808	0.069	11.650	< 0.0001
JulianDay	0.323	0.031	10.595	0.0003

File A2.1. Instructions for using exclosures: Preinstallation, Material preparation and Exclosure installation

Experimental exclosures in rice fields



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Preinstallation - Material preparation

POLES:

1. Base poles

- **8 metal tubes (Ø35mm) Length: 1.5m.** They will be used as the base of the structure, which will be driven into the substrate.

Note: Before the installation, drill it crosswise at different distances from both sides to allow a corrugated rod (Ø6mm) to pass through (See illustration in point 2 of 'Exclosure installation' section below).

- **8 corrugated rods (Ø6mm) Length: 20-25cm.** They will be used to prevent the structure from sinking into the mud.
- **16 wooden strips.** They will be used to prevent the structure from sinking into the mud (2 for each basis tube).

2. Paired poles

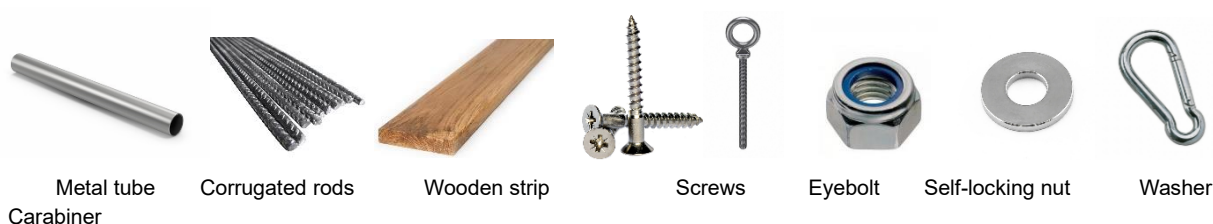
- **16 metal tubes (Ø40mm) Length: 2.5m.** Main elements of the structure. In pairs, they will form vertical tubes of 5m.
- **8 metal tubes (Ø35mm) Length: 1m.** These junction tubes will splice the pairs of 2.5 m tubes.
- **16 screws.** They will affix the junction tubes of 1m length to the 2.5m tube (2 for each pair of 2.5-metre tubes).

Note: Place each 1m-tube of Ø35mm inside a 2.5m-tube of Ø40mm, with the first one protruding 50 cm outwards. Using a drill, place the screws perpendicularly and crosswise through the two tubes, so that they are spliced to each other.

- **8 eyebolts with washer and self-locking nut.** They will be used to attach the carabiniers.

Note: Nail one eyebolt to the upper end of the remaining 2.5m-long tubes, with a washer and a self-locking ring. The emerging part of the eyebolt should be removed.

- **8 carabiniers.** They will be used to tighten the cables and mesh nets. Each carabiner will be attached to each eyebolt.



TENSIONERS:

- **12 units of 8-m long wire cables (Ø5mm).** They will act as tensioner cables.
- **24 cable clamps.**

Note: A handle needs to be made (big enough to be passed through the upper 2.5m-tube of Ø40mm) in one end of the 8 m cable (Ø5mm) and affixed with 2 cable clamps.

- **12 corrugated rods (Ø60mm) of 1.5m.** They will act as anchor points of the tensioners.
- **12 wire tensioners with galvanised ratchet.** They will tighten the tensioner cables.
- **12 galvanised shackles.** They will be used to attach the 12 tensioner cables.
- **12 metal clamps.** They will be used to prevent the galvanised shackle from coming out of the corrugated rods.
- **12 reflective orange PVC tubes.** They will be used for signalling the location of the corrugated rods.



PERIMETRAL CABLE:

- **4 units of 21m-long wire cables (Ø 3mm).** Cut in 4 segments of 21m.
- **20 cable clamps.**

Note: 3 loops need to be made in each segment: A first loop at one end of the cable, then another at 10 metres, and the last one at 10 metres from the second. They all need to be fastened with two cable clamps per loop at the edges (just one for the middle loop). You will finally obtain 4 units of 20m each. If necessary, you can cut off the excess of the cable.



Wire cable



Cable clamp

PERPENDICULAR CABLES AND DIAGONAL ROPES

- **2 units of 20.5m-long wire cables (Ø 3mm).** They will act as internal perpendicular cables.
- **8 cable clamps.**

Note: You should make a loop at each end of the 20.5m wire cable, fastened with two cable clamps per loop.

- **2 units of 50m-long ropes.** These two ropes will act as diagonals of each enclosure at the beginning of the construction.

Note: A loop needs to be made at both ends of each cable, so that they end up being 28.3 metres long.



Wire cable



Cable clamp



Rope

MESH NET (laterals: 2 fixed and 2 mobile)

- **4 units of mesh net of 20m x 5m.** They will cover the four laterals of the enclosure.
- **4 units of 20.5m-long wire cable (Ø 3mm).** They will be used to hang the four lateral mesh nets.
- **8 cable clamps.**

Note: A loop should be done at one end of each cable, fastened with two cable clamps. Take two mesh net pieces and sew one of the 20m edges with a 20.5m wire cable by using its free end. These two pieces will be the fixed laterals of the enclosure.

- **4 cable clamps.**

Note: A new loop should be made at the remaining free end of the wire cable already woven, fastened with two cable clamps. The length of each wire cable woven to a mesh net piece will end up being 20 meters long.

- **2 units of 21m-long ropes (Ø 6mm).**

Note: Take the other two pieces of mesh net. Sew one of the 20m sides using one of the rope segments cut in the previous step. Repeat the same action for the other mesh net piece. Then, make a loop at each rope end, obtaining two segments of 20m each.

- **160 keyrings.**

Note: Thread 80 keyrings with one of the remaining 20.5m wire cables using its free end. Repeat it with the other 20.5m-long cable.

- **4 cable clamps.**

Note: Make a loop at the free end of the cables with the keyrings, fastened with two cable clamps in each end, obtaining two cables of 20m. Take the two wire cables with the keyrings. Join each 20m wire cable to one of the mesh net pieces sewn with a rope by using the keyrings. One keyring must be attached to the rope every 25 cm.

- **4 units of 20m-long ropes (Ø 6mm).**

Note: make a loop in one of the ends of each segment.

- **4 carabiniers.**

Note: Use a carabinier to attach one of the 20m ropes (using the loop) to the keyring located at one end of the 20m side of the mobile lateral. Attach another 20m rope to the keyring at the other end of the 20m side. Repeat it for the other mobile lateral.

- **8 carabiniers.**

Note: Place a carabinier at each end of the 20m wire cable attached to the mesh net.

- **8 units of 6 m-long ropes (Ø 6mm).**

Note: Sew one rope to each 5m edge of the mesh net pieces and attach the upper ends of the rope with the carabiniers.

- **4 units of 22m-long ropes (Ø 6mm).**

Note: Sew each rope to the remaining 20m edge of the mesh net pieces.

- **8 stainless steel carabiniers.**

Note: Use a stainless steel carabiniers to attach the rope ends at the lower vertices of the mesh net pieces. stainless steel carabiniers.



Mesh net



Wire cable



Cable clamp



Rope



Keyring



Carabiner

MESH NET (Roof)

- **4 units of 21m-long wire cables (Ø 3mm).**

- **8 cable clamps.**

Note: Make a loop in just one end of each 21m segment, fastened with two cable clamps.

- **1 unit of mesh net of 20m x 20m**

Note: Sew a 21m-long wire cable in each mesh net edge using the free ends of the cable.

- **8 cable clamps.**

Note: Make a loop in the free end of the woven end of the wire cable, fastened with two cable clamps. The final length will be 20m.

- **4 carabiniers.**

Note: Use a carabinier to attach the two loops coinciding at each vertex



Wire cable



Cable clamp



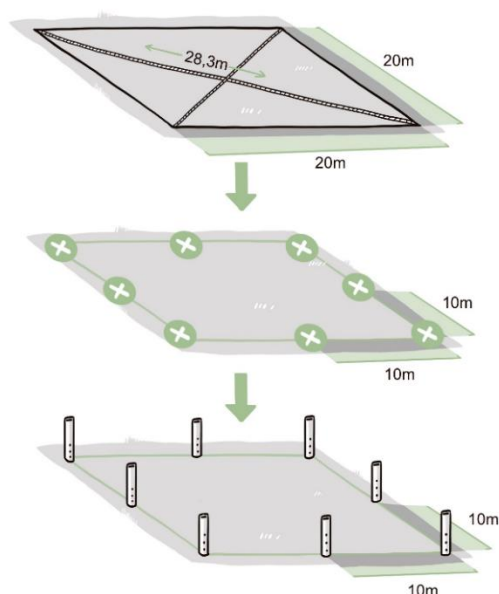
Mesh net



Carabiner

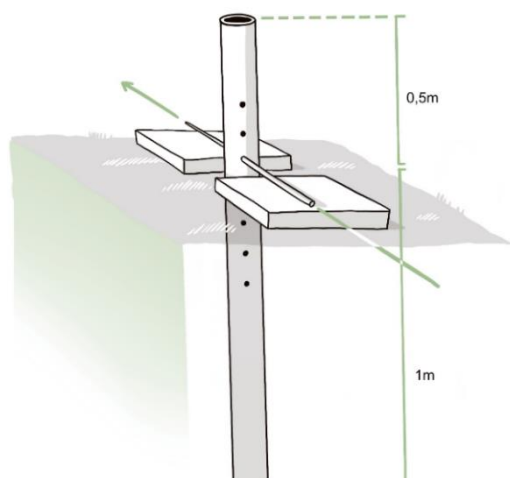
Exclosure installation

Setting up the exclosure structure:

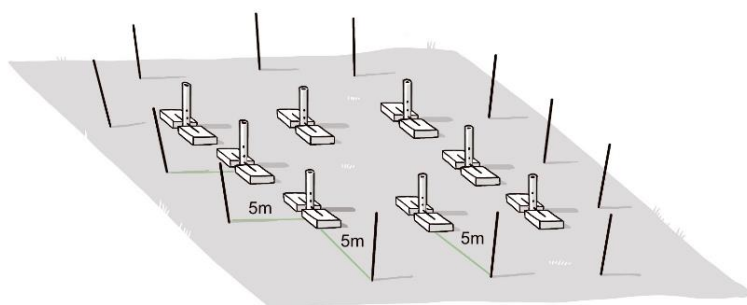


1. Extend the perimetral cables together with the diagonal ropes attached between them using carabiniers until they are fully extended, in order to make a perfect square (it is not necessary to use the internal perpendicular cables in this step). This will allow finding the exact position where to drive the 8 basis tubes of 1.5m into the ground. The tubes will be placed at the four vertices as well as at the midpoint of each side (10m from the vertices).

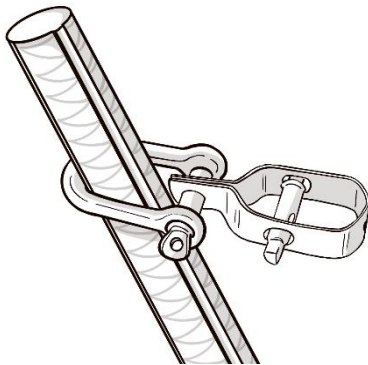
Each basis tube will be driven into the ground until it protrudes by approximately 0.5-0.75m.



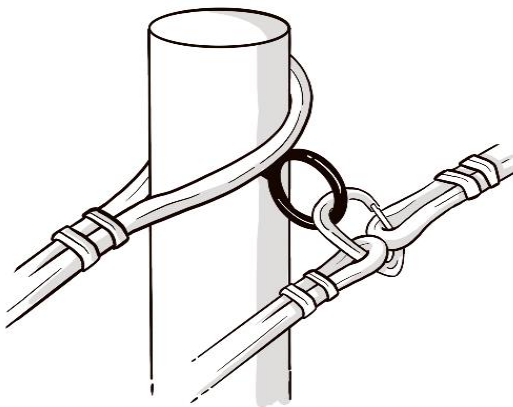
2. Place the small corrugated rods in the basis tubes so that they pass through the hole closest to the ground surface. Place a wooden strip under either side of the rod, just below the ends of the rod exiting from each side of the tube. This will prevent the first segment of each vertical tube from sinking into the mud.



3. Hammer the 12 corrugated rods (Ø16mm) at 5m in a straight line from the 8 basis tubes. The tubes placed at the corners will have 2 corrugated rods aligned in opposite directions.

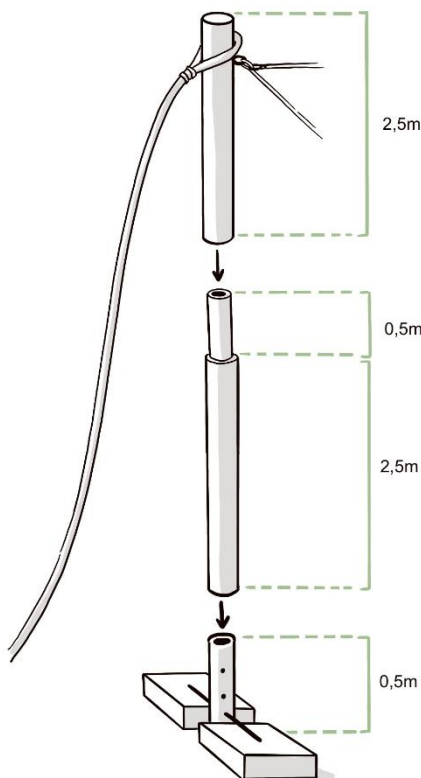


4. Place 1 wire tensioner with galvanised ratchet + 1 galvanised shackle in each corrugated rod (Ø 16mm).

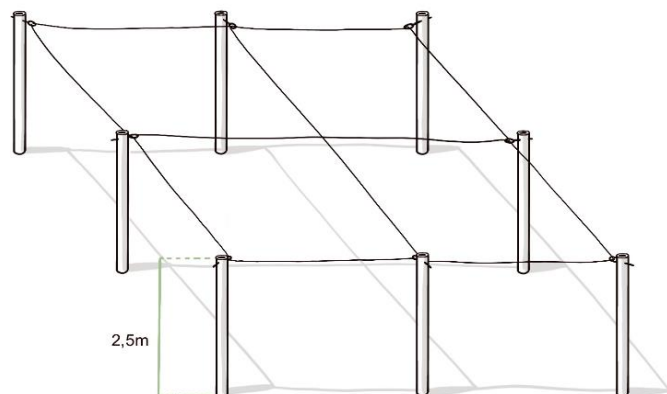


5. Attach both the perimetral and perpendicular wire cables to the eyebolts of the upper vertical tubes by using the carabiniers of the cables.

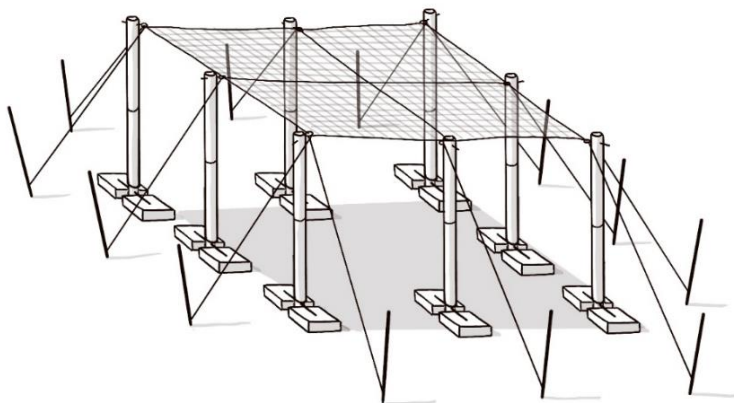
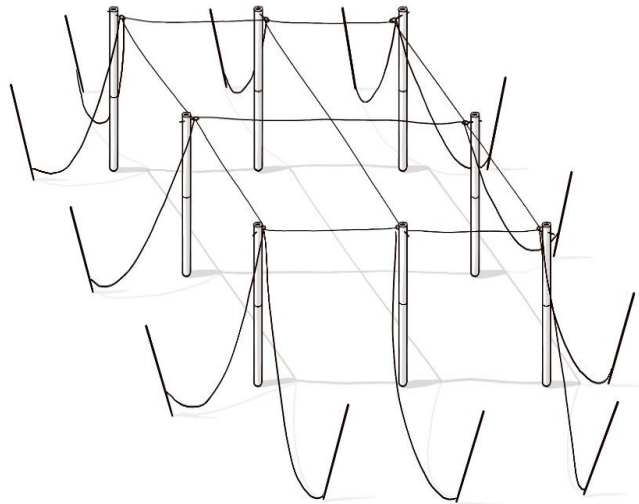
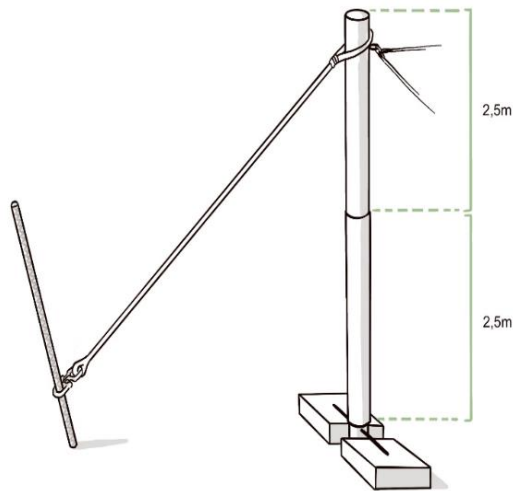
6. Place the handle of the tensioner cables at the highest part of the vertical tubes. Two tensioner cables will be attached at four corner tubes.



7. Pair and raise the vertical tubes and fit them with their corresponding basis tube, starting at the corners and making sure that the tensioner cables are attached at the top of the upper tubes.



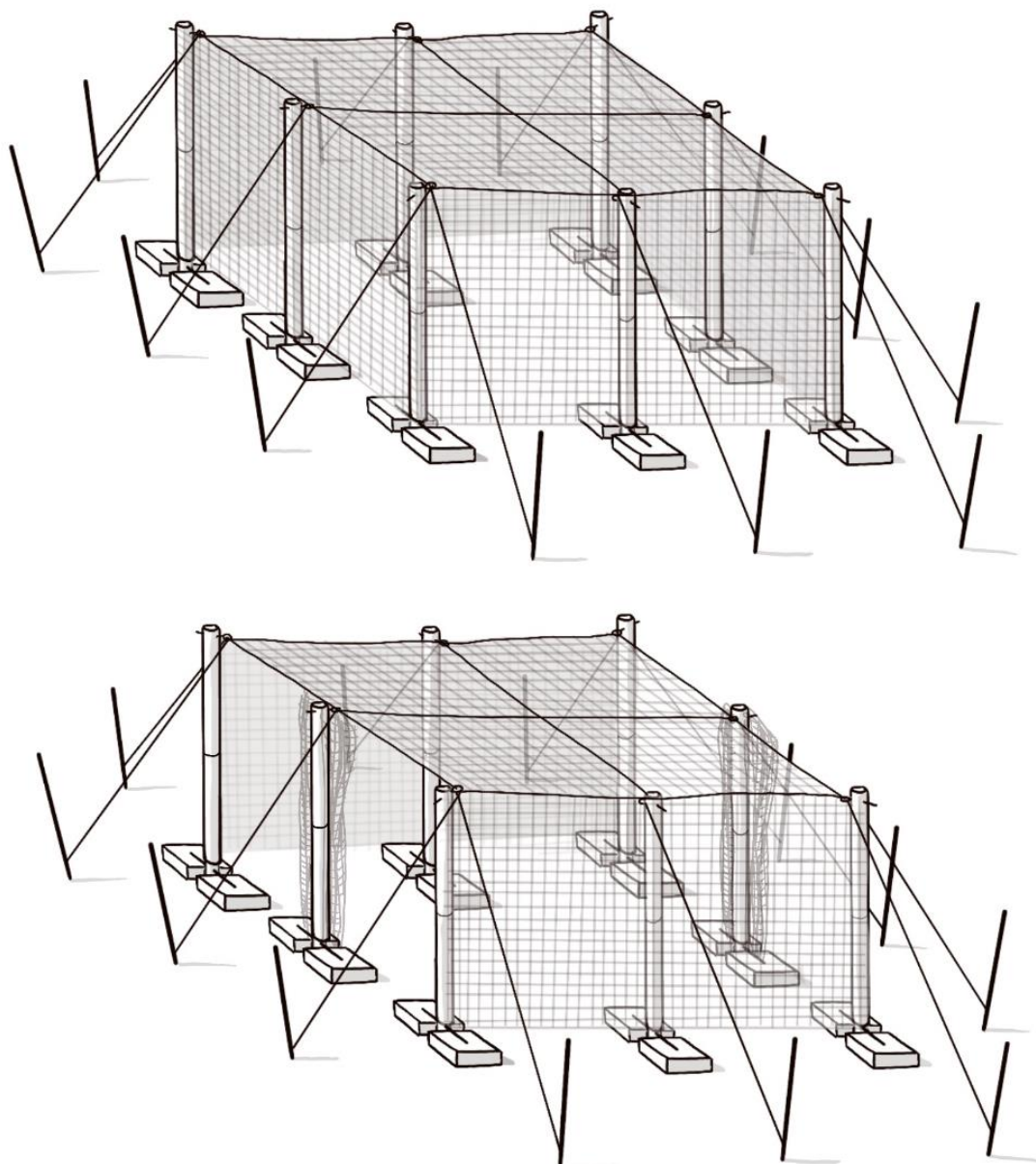
8. Tighten the cables with the wire tensioner with galvanised ratchet to the corrugated rods ($\varnothing$ 16mm). The galvanised shackle will block the ratchets on the corrugated rods.



9. Using a ladder, hand the net of 20m x 20m (roof) on the vertical tubes by attaching the carabiniers of the net corners to the eyebolts of the upper part of the vertical tubes.

Use the carabiniers of the eyebolts of the central vertical tubes or use new carabiniers to attach the cables of the roof net.

10. Hang the four lateral nets on the eyebolts of the upper part of the vertical tubes by using the carabiniers. Attach the carabiniers of the lower vertices of the lateral nets in the small corrugated rods of the basis tubes. Place the lateral nets which can be opened and closed on opposite sides of the structure.



Opening and closing of the enclosure

Fasten and unfasten the stainless steel carabiniers that attach the mesh to the underside of the structure depending on whether you want to open or close the enclosure.

Opening: Tight the ropes that are attached to the keyrings when you want the mesh net to be extended (and therefore the enclosure to be closed). The ropes can be tied to the corrugated rods that hold the tensioner cables on the corresponding side.

Closing: To open the enclosure, loosen the ropes until you can fold the mesh net into the centre tube. Use the ropes at the top of the side central tube to fold the mesh net tightly.

7.3. Supplementary information for Article III

Article III – Landscape of fear in rice paddies: effect of bat ultrasounds on the egg production of a pest insect

Carme Tuneu-Corral, Xavier Puig-Montserrat, Carles Flaquer, Xavier Jordà, Hugo Rebelo, Mar Cabeza and Adrià López-Baucells

List of supplementary Figures and Tables:

Figure A3.1. Light traps used to capture alive individuals of *Chilo suppressalis* in rice paddies in Alcolea de Cinca (Spain). a) Hand-made autonomous UV-light-trap. It consisted of a bucket, a funnel, a cotton bag, a methacrylate, and a UV light LEDs powered by a power bank (20000 mAh Redmi Fast Charge). b) Manual UV-light-trap. It consisted of a 2,5 x 1 m white sheet illuminated with a UV-light torch (Alonefire 395 nm; 128 LED) supported on a tripod. In this picture, the UV-light torch was placed behind the white sheet.

Table A3.1. Generalised Linear Model (glm.nb) results for the model (negative binomial distribution) with lowest AICc value assessing the effect of the explanatory variable ‘treatment’ (control/ultrasounds) on the number of egg clutches per female (response variable) of *Chilo suppressalis*. The variables ‘sex ratio’ and ‘time’ were discarded from the model.

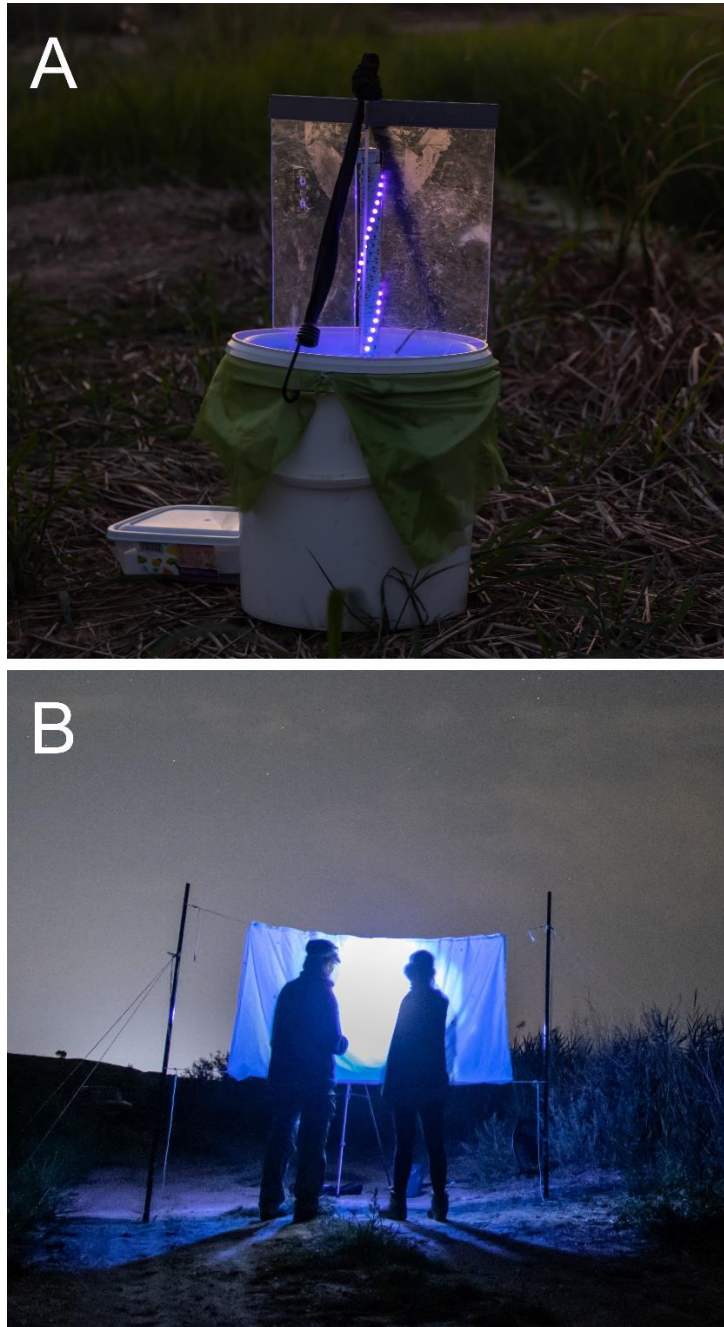


Figure A3.1. Light traps used to capture alive individuals of *Chilo suppressalis* in rice paddies in Alcolea de Cinca (Spain). a) Hand-made autonomous UV-light-trap. It consisted of a bucket, a funnel, a cotton bag, a methacrylate, and a UV light LEDs powered by a power bank (20000 mAh Redmi Fast Charge). b) Manual UV-light-trap. It consisted of a 2,5 x 1 m white sheet illuminated with a UV-light torch (Alonefire 395 nm; 128 LED) supported on a tripod. In this picture, the UV-light torch was placed behind the white sheet.

Table A3.1. Generalised Linear Model (glm.nb) results for the model (negative binomial distribution) with lowest AICc value assessing the effect of the explanatory variable 'treatment' (control/ultrasounds) on the number of egg clutches per female (response variable) of *Chilo suppressalis*. The variables 'sex ratio' and 'time' were discarded from the model.

	GLM			
	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.231	0.272	-0.849	0.396
Treatment (ultrasounds)	-0.443	0.435	-1.018	0.304

7.4. Supplementary information for Article IV

Article IV – Beyond borders: the role of protected areas in promoting bat-mediated pest suppression in rural areas in Madagascar

Carme Tuneu-Corral^{1,4}, Chatain Andrianalijaona⁵, Fabrice Davy Benirina⁶, Steven M. Goodman^{7,8}, Vanessa A. Mata^{2,3}, Michaël Luciano Tantely⁹, Mar Cabeza⁴, Adrià López-Baucells¹

List of supplementary Figures and Tables:

Table A4.1. Number of samples analysed per bat species in each location, season and habitat type. Buildings were all located in rural villages outside protected areas, and caves and forests were all located inside protected areas. (*embedded link*)

Table A4.2. Weighted percentage of occurrence (wPOO) of each arthropod order in the diet of the different bat species for each season (dry and wet). The values in brackets next to each species name are the total samples collected for that species. (*embedded link*)

Table A4.3. List of agricultural pests (known and potential) and disease vectors detected in the diet of insectivorous bats, BOLD ID percentage (similarity), and information on the type of crops attacked or disease transmitted by them in Madagascar and/or continental Africa. (*embedded link*)

Table A4.4. Arthropod species detected in bat faecal samples and classified as insect pests or disease vectors, and their interactions with bat species. Information on the bold percentage of similarity, study site, habitat type and pest type. (*embedded link*)

Table A4.5. Number and percentage of samples containing pest insects or disease vectors in each type of habitat, organised by bat family and species.

Table A4.6. Permutational multivariate analysis of variance (adonis) and betadisper results for the model on the pest composition on the diet of insectivorous bats for frequency of occurrence (FOO) data. Predictors with significant PERMANOVA results (p-value < 0.05) and non-significant betadisper results (p-value > 0.05) are highlighted in bold, which indicates significant differences on the composition of pests in the diet

Table A4.5. Number and percentage of samples containing pest insects or disease vectors in each type of habitat, organised by bat family and species.

Type of habitat	N° of samples	% of samples
Building (rural village)	53	32.7
- Molossidae	53	32.7
<i>Chaerephon leucogaster</i>	50	
<i>Mops leucostigma</i>	3	
Cave (protected area)	86	53.1
- Emballonuridae	3	1.9
<i>Paremballonura tiavato</i>	3	
- Hipposideridae	1	0.6
<i>Macronycteris commersonii</i>	1	
- Miniopteridae	41	25.3
<i>Miniopterus aelleni</i>	10	
<i>Miniopterus gleni</i>	11	
<i>Miniopterus griveaudi</i>	20	
- Molossidae	39	24.1
<i>Chaerephon jobimena</i>	18	
<i>Mormopterus jugularis</i>	3	
<i>Otomops madagascariensis</i>	18	
- Rhinonycteridae	2	1.2
<i>Paratriaenops auritus</i>	1	
<i>Triaenops menamena</i>	1	
Forest (protected area)	23	14.2
- Miniopteridae	9	5.6
<i>Miniopterus aelleni</i>	3	
<i>Miniopterus ambohitrensis</i>	2	
<i>Miniopterus gleni</i>	1	
<i>Miniopterus griveaudi</i>	3	
- Rhinonycteridae	13	8
<i>Paratriaenops auritus</i>	1	
<i>Triaenops menamena</i>	12	
- Vespertilionidae	1	0.6
<i>Myotis goudoti</i>	1	
Total n° samples with pest or disease vectors	162	

Table A4.6. Permutational multivariate analysis of variance (adonis) and betadisper results for the model on the pest composition on the diet of insectivorous bats for frequency of occurrence (FOO) data. Predictors with significant PERMANOVA results (p-value < 0.05) and non-significant betadisper results (p-value > 0.05) are highlighted in bold, which indicates significant differences on the composition of pests in the diet.

		PERMANOVA					BETADISPER			
		df	SS	R2	F	Pr(>F)	SS	MS	F.value	Pr(>F)
For pest data only	Season	1	0.8453	0.03191	1.7761	0.0001	0.011913	0.011913	3.5686	0.096
	Type of area	1	0.5317	0.02007	1.1171	0.0287	0.057196	0.057196	30.626	0.001
	Bat species	12	5.6004	0.2114	0.9806	0.0015	0.92576	0.071212	609123	0.001
	Residual	41	19.5138	0.73661						
	Total	55	26.4912	1						

Appendix B – Other publications during the PhD

Article V – Bats actively prey on mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture

Xavier Puig-Montserrat^{1,2}, Carles Flaquer¹, Noelia Gómez-Aguilera², Albert Burgas², Maria Mas¹, **Carme Tuneu-Corral¹**, Eduard Marquès³, Adrià López-Baucells¹

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² Galanthus Association, Celrà, 17460 Catalonia, Spain

³ Servei de Control de Mosquits de la Badia de Roses i del Baix Ter, 17486 Castelló d'Empúries, Catalonia, Spain

Abstract

The fact that bats suppress agricultural pests has been measured for some particular dyads of predator and prey species both in economic and food security terms. The recent emergence of new molecular techniques allows for wide screenings of bat diet and provide a further evidence that bats consume an ample array of agricultural pest species. The main focus about the regulatory services that bats provide in agroecosystems has been on crop pests that cause yield losses. Rice paddies constitute a particular agronomic system with specific challenges, not only related to crop productivity but also to human health. Dipteran density in such ecosystems poses a serious threat to human wellbeing and hinders crop production. Mosquitoes cause direct harm to human populations transmitting a number of infectious diseases. Non-biting midges (Chironomidae) can consume and weaken rice seedlings and can cause major yield losses. Mosquito populations and bat activity were assessed in rice paddies of Montgrí, Medes i Baix Ter Natural Park (NE Iberian Peninsula). Molecular analyses of bats faeces (6 weekly samples of 15 faeces each between mid-August and September) proved the presence of both mosquitoes and non-biting midges in all of the diet samples. Furthermore, bat activity at the sampling locations was related to adult mosquito density. This article is protected by copyright. All rights reserved. Our results suggest that bats actively exploit the emergence of adult mosquitoes and further prove that they prey on mosquitoes, non-biting midges and other deleterious insects. Promoting the presence of bats next to human settlements in such agroecosystems may constitute a biological control system with direct impact on both human health and crop yield.

Keywords

Chiroptera, bats, biological pest control, Chironomidae, Culicidae, mosquito-borne disease, rice, DNA metabarcoding

Citation

Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, M., López-Baucells, A. 2020. Bats actively prey on mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture. *Pest Management Science*, 76(11), 3759-3769. <https://doi.org/10.1002/ps.5925>

Article VI – Bat echolocation plasticity in allopatry: a call for caution in acoustic identification of *Pipistrellus* sp.

Cecilia Montauban^{1,2}, Maria Mas¹, **Carne Tuneu-Corral¹**, Owen S. Wangenstein³, Ivana Budinski^{1,4}, Joan Martí-Carreras⁵, Carles Flaquer¹, Xavier Puig-Montserrat^{1,6}, Adrià López-Baucells¹

¹ Natural Sciences Museum of Granollers, Granollers, Spain

² Department of Life Sciences, Imperial College London, London, UK

³ Norwegian College of Fishery Science, UiT the Arctic University of Norway, Tromsø, Norway

⁴ Department of Genetic Research, Institute for Biological Research “Siniša Stanković” - National Institute of Republic of Serbia, University of Belgrade, Belgrade, Serbia

⁵ Department of Microbiology, Immunology and Transplantation, Clinical and Epidemiological Virology Division, Rega Institute, KU Leuven, Leuven, Belgium

⁶ Galanthus Association, Celrà, Catalonia, Spain

Abstract

Animals modify their behaviours and interactions in response to changing environments. In bats, environmental adaptations are reflected in echolocation signalling that is used for navigation, foraging and communication. However, the extent and drivers of echolocation plasticity are not fully understood, hindering our identification of bat species with ultrasonic detectors, particularly for cryptic species with similar echolocation calls. We used a combination of DNA barcoding, intensive trapping, roost and emergence surveys and acoustic recording to study a widespread European cryptic species complex (*Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*) to investigate whether sibling bat species could exhibit extreme echolocation plasticity in response to certain environmental conditions or behaviours. We found that *P. pygmaeus* occupied the acoustic niche of their absent congeneric species,

producing calls with *P. pipistrellus*' characteristic structure and peak frequencies and resulting in false positive acoustic records of that species. Echolocation frequency was significantly affected by the density of bats and by maternity rearing stage, with lower frequency calls emitted when there was a high density of flying bats, and by mothers while juveniles were nonvolant. During roost emergence, 29% of calls had peak frequencies typical of *P. pipistrellus*, with calls as low as 44 kHz, lower than ever documented. We show that automatic and manual call classifiers fail to account for echolocation plasticity, misidentifying *P. pygmaeus* as *P. pipistrellus*. Our study raises a vital limitation of using only acoustic sampling in areas with high densities of a single species of a cryptic species pair, with important implications for bat monitoring.

Keywords

Bioacoustics, automatic classifiers, metabarcoding, call variability, conspecifics, *Pipistrellus*

Citation

Montauban, C., Mas, M., Tuneu-Corral, C., Wangenstein, O. S., Budinski, I., Martí-Carreras, J., Flaquer, C., Puig-Montserrat, X., López-Baucells, A. 2021. Bat echolocation plasticity in allopatry: a call for caution in acoustic identification of *Pipistrellus* sp. *Behavioral Ecology and Sociobiology*, 75(4), 1-15. <https://doi.org/10.1007/s00265-021-03002-7>

Article VII – Benefits of organic olive farming for the conservation of gleaned bats

Xavier Puig-Montserrat^{1,2,*}, Maria Mas¹, Carles Flaquer¹, **Carme Tuneu-Corral¹**, Adrià López-Baucells¹

¹ Natural Sciences Museum of Granollers, Granollers, Catalonia, Spain

² Galanthus Association, Celrà, Catalonia, Spain

Abstract

Current intensification and expansion of agricultural lands are some of the main anthropogenic processes driving the global decline of biodiversity. Organic farming is generally regarded as a better compromise between production and ecosystems and biodiversity preservation.

However, while this practice is gaining popularity worldwide, conventional agriculture is still the main approach, hindering the conservation of many taxa. Bats are poorly studied and generally negatively affected by conventional farming. Their high mobility and long lifespan make them excellent ecological indicators in agroecosystems. We assessed the effect of different crop treatments (conventional and organic olive groves, and sparse coniferous forest as a control) on bat activity, at both guild and species level. In addition, we evaluated whether bat activity was influenced by the abundance of the olive fruit fly *Bactrocera oleae*, the major insect pest of olive groves worldwide. Bats were surveyed acoustically during autumn 2014 in all treatments using passive ultrasound detectors. In parallel, pheromone traps for *B. oleae* were used to monitor pest insect abundance. Our results show that aerial hunting bats were significantly more active in sparse coniferous forests compared to the other treatment areas. On the contrary, gleaning bats (those generally more threatened and vulnerable to habitat degradation) showed higher activity rates in organic olive groves. Due to their higher manoeuvrability and slow flight, gleaning species are generally well-adapted to forage in structurally complex and cluttered habitats such as olive groves. A significant negative relation was found between the density of the olive fruit fly and the gleaning bats activity, which were expected to prey on the pest and hence show some positive relation with its density. The reasons are unclear and further research with molecular techniques would be needed to better understand the ecological interaction, if any, between bats and the pest. Organic olive groves, usually more stratified than the conventional ones, are characterised by the presence of spontaneous herbaceous cover and higher diversity of arthropods (either beneficial or deleterious), which favours bat activity. Organic practices should be further prioritised in the agri-environment schemes of the European Union and those of its individual members. If organic farming is not widely implemented, agriculture intensification and the expansion of monocultures may put bat populations at stake, as well as compromise ecosystem quality and the conservation of biodiversity.

Keywords

Ecosystem services, bioacoustics, conventional agriculture, organic olive groves, bat conservation, pest management

Citation

Puig-Montserrat, X., Mas, M., Flaquer, C., Tuneu-Corral, C., López-Baucells, A. 2021. Benefits of organic olive farming for the conservation of gleaning bats. *Agric Ecosyst Environ*, 313, 107361. <https://doi.org/10.1016/j.agee.2021.107361>

Article VIII – Concurrent Butterfly, Bat and Small Mammal Monitoring Programmes Using Citizen Science in Catalonia (NE Spain): A Historical Review and Future Directions

Ignasi Torre¹, Adrià López-Baucells¹, Constantí Stefanescu¹, Lúdia Freixas¹, Carles Flaquer¹, Carme Bartrina¹, Alba Coronado¹, David López-Bosch¹, Maria Mas¹, Sílvia Míguez¹, Joaquim Muñoz¹, Ferran Páramo¹, Xavier Puig-Montserrat¹, **Carme Tuneu-Corral¹**, Andreu Ubach¹, Antoni Arrizabalaga¹

1. BiBio Research Group, Natural Sciences Museum of Granollers, c/Francesc Macià 51, 08402 Granollers, Spain

Abstract

The Biodiversity and Bioindicators research group (BiBIO), based at the Natural Sciences Museum of Granollers, has coordinated four long-term faunal monitoring programmes based on citizen science over more than two decades in Catalonia (NE Spain). We summarise the historical progress of these programmes, describing their main conservation outputs, the challenges overcome, and future directions. The Catalan Butterfly Monitoring Scheme (CBMS) consists of a network of nearly 200 recording sites where butterfly populations have been monitored through visual censuses along transects for nearly three decades. This programme provides accurate temporal and spatial changes in the abundance of butterflies and relates them to different environmental factors (e.g., habitat and weather conditions). The Bat Monitoring Programme has progressively evolved to include passive acoustic monitoring protocols, as well as bat box-, underground- and river-bat surveys, and community ecological indices have been developed to monitor bat responses at assemblage level to both landscape and climatic changes. The Monitoring of common small mammals in Spain (SEMICE), a common small mammal monitoring programme with almost 80 active live-trapping stations, provides information to estimate population trends and has underlined the relevance of small mammals as both prey (of several predators) and predators (of insect forest pests). The Dormouse Monitoring Programme represents the first monitoring programme in Europe using specific nest boxes for the edible dormouse, providing information about biological and demographic data of the species at the southern limit of its distribution range. The combination and complementarity of these monitoring programmes provide crucial data to land managers to improve the understanding of conservation needs and develop efficient protection laws.

Keywords

Bioindicators, volunteers, sampling protocols, species diversity, conservation, population trends

Citation

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