



Quantifying ecological and economic value of pest control services provided by bats in a vineyard landscape of central Chile



Annia Rodríguez-San Pedro^{a,b,c,*}, Juan Luis Allendes^{b,c}, Clemente A. Beltrán^{a,c},
Pascal N. Chaperon^{a,c}, Mónica M. Saldarriaga-Córdoba^d, Andrea X. Silva^e, Audrey A. Grez^a

^a Laboratorio de Ecología de Ambientes Fragmentados (LEAF), Departamento de Ciencias Biológicas Animales, Facultad Ciencias Veterinarias y Pecuarias, Universidad de Chile, Chile

^b Servicios de Consultoría Ecológica, Bioacústica y Conservación - BIOECOS E.I.R.L., Chile

^c Programa para la Conservación de Murciélagos de Chile (PCMCh), Santiago, Chile

^d Centro de Investigación en Recursos Naturales y Sustentabilidad, Universidad Bernardo O'Higgins, Santiago, Chile

^e Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile

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ABSTRACT

The top-down suppression of pest insects by their natural enemies, such as insectivorous bats, represents an important ecosystem service in agricultural systems. Recognizing the importance of bats to suppress pest populations and further conserve their populations near agricultural systems could reduce damage to crops thereby potentially increasing the monetary gain of farmers. Viticulture represents one of the most extensive and economically important agricultural crops in the Mediterranean biome. While pest consumption by bats has been recently revealed in vineyards, direct evidence of the reduction of grapevine pests by bats in vineyards is lacking, and their benefits to winegrape production remains to be quantified. Using large nocturnal enclosures in vineyards, we examined the top-down effects of aerial insectivorous bats in suppressing insect populations by assessing leaf and grape cluster damage; we also examined the benefit of these natural pest predators by quantifying resulting increases in potential vineyard yield. Grapevine plants excluded from bats had significantly higher leaf herbivory and greater grape cluster damage than control plots. Grape cluster damage was 7% lower on control plots, yielding an average economic benefit of US\$188-\$248/ha/year due to bat predation. These results provide the first experimental evidence that bats reduce grapevine pest insect infections and thus increase vineyard yield and winegrowers' income. Therefore, bats should be included in future biodiversity conservation plans in vineyards and be considered within agricultural management strategies based on natural pest suppression.

1. Introduction

Insect pests are a major problem affecting the farming industry by reducing crop production worldwide. The top-down suppression of pest insects by their natural enemies represents an important ecosystem service in agricultural systems by increasing the monetary gain of farmers and supporting food security (de Groot et al., 2012; Naylor and Ehrlich, 1997; Tscharntke et al., 2012). Bats are major predators of arthropods, and thus provide valuable ecosystem services as natural pest suppressors in agricultural landscapes (Kunz et al., 2011). Insectivorous bats may eat up to 75%–100% of their body mass in insects per night, most of which are economically important crop pests (Brown et al., 2015; Kemp et al., 2019; McCracken et al., 2012; Puig-Montserrat

et al., 2015; Taylor et al., 2017). The economic value of pest suppression services provided by Brazilian free-tailed bats (*Tadarida brasiliensis*) to the production of cotton in southern Texas, United States, ranges from about \$30 to \$427/ha, which amounts to between 12%–29% of the value of the cotton crop in that region (Cleveland et al., 2006). By extrapolating these figures to the total area of harvested cropland across the United States, Boyles et al. (2011) estimated bats' economic value to the US agricultural industry as \$22.9 billion/year (range \$3.7-\$53 billion/year). This benefit can go beyond the monetary value of pest suppression services if the affected crop is a staple, such as rice production in Thailand (Wanger et al., 2014), macadamia in South Africa (Taylor et al., 2018) or maize in the United States (Maine and Boyles, 2015). Nevertheless, to date, few studies have

* Corresponding author. Present address: Centro de Investigación e Innovación para el Cambio Climático (CiCC), Facultad de Ciencias, Universidad Santo Tomás, Chile.

E-mail address: arodriguezs@santotomas.cl (A. Rodríguez-San Pedro).

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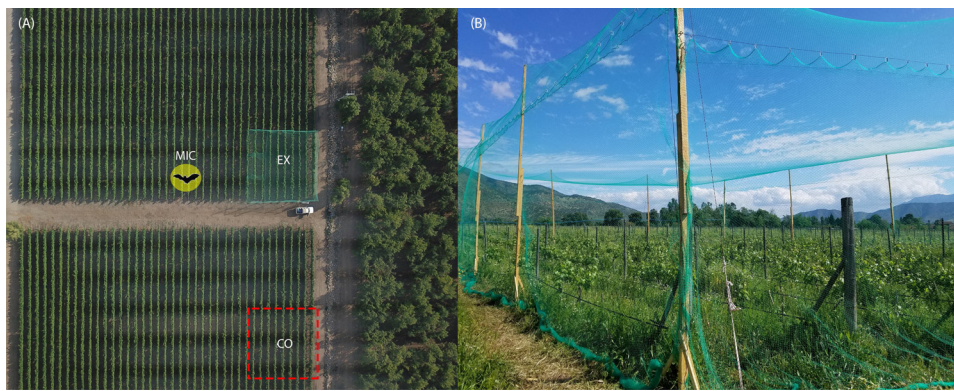


Fig. 1. (A) Aerial photography of one vineyard site in Paine, central Chile, illustrating: bat enclosure (EX), control plot with no enclosure (CO) and the position of the automatic recording bat-detector (MIC) near the experimental plots. (B) A close view of a bat enclosure. Photos by Darío De la Fuente and Annia Rodríguez-San Pedro.

experimentally tested the effectiveness of bats as pest suppressors in agro-ecosystems, of which most have only focused on tropical and subtropical agroforestry and natural systems (Kalka et al., 2008; Karp and Daily, 2014; Maas et al., 2013; Maine and Boyles, 2015; Morrison and Lindell, 2012; Williams-Guillén et al., 2008). Consequently, the extent to which these results can be generalized to other regions or agro-ecosystems remains unknown.

Vineyard plantings cover over 7.5 million hectares, mostly in the Mediterranean Basin and the New World Mediterranean zones (Australia, Chile, South Africa and California), and account for 15 % of agricultural lands worldwide (OIV, 2018). As a monoculture, vineyard crops pose a threat to the regional biodiversity by replacing native vegetation and simplifying the surrounding landscapes (Underwood et al., 2009). However, vineyards may retain some biodiversity, especially those under organic management and with native vegetation remnants around and within the crop, which increases the diversity and abundance of natural enemies (Bruggisser et al., 2010; Nicholls and Altieri, 2011). The European grapevine moth *Lobesia botrana* (Lepidoptera, Tortricidae) is the major pest of grapes in the Mediterranean Basin (Ioriatti et al., 2012; Moschos, 2006). It was found over a decade ago in California, Argentina and Chile, where it is widespread in all wine-growing areas (González, 2015). Damage by this moth is caused by larval feeding on grapevine clusters, which renders them susceptible to fungal infections, such as *Botrytis cinerea*, resulting in grape cluster rot which are the main cause of berry loss. In addition, three other moth species (*Chileulia stalactitis*, *Proeulia auraria*, *Agrotis ipsilon*) and two coleopterans (*Tomarus villosus*, *Athlia rustica*) have been recognized as grapevine pests in Chile affecting both leaves and grape berries (González, 2015).

In Chile, most bats are insectivorous (Canals and Cattán, 2008; Rodríguez-San Pedro et al., 2016), and at least five species are known to use vineyards for both commuting and foraging (Rodríguez-San Pedro et al., 2018, 2019). Insect pest consumption by insectivorous bats in vineyards has been recently reported in vineyards located in Southwestern Europe by Baroja et al. (2019), however direct evidence of a reduction in grapevine pest infections by bats is lacking and their benefits to winegrape production remains to be quantified. Linking increases of winegrape yield with suppression in grapevine pests by insectivorous bats could provide a strong economic incentive to winegrape producers to promote bat conservation in these production landscapes, resulting in a win-win solution for biodiversity and farmers.

We conducted a bat-exclosure experiment on vineyards in central Chile, to examine the top-down effects of aerial insectivorous bats on leaf and grape cluster damage due to insect herbivory. The main goals of our study were to: i) evaluate reductions by insectivorous bats of leaf herbivory and grape damage, ii) determine whether greater damage reductions in grapes are associated with greater bat activity, iii) determine the consumption of major insect pests by bats in vineyards and, iv) quantify the economic value of any observed reduction in grape damage due to bats. We assessed the hypothesis that bats suppress

herbivorous insects, which in turn reduces leaf herbivory and cluster damage in vineyards. Specifically, we predicted that leaf herbivory and grape berry damage would be lowest on grapevines exposed to bat predation and highest on grapevines where bats were experimentally excluded from foraging. We also expected greater damage reductions as bat activity increases.

2. Methods

2.1. Study site

The study was conducted in three vineyards located in the town of Huelquén, in the Maipo valley (33° 48.412'S, 70° 39.086'W to 33° 51.960'S, 70° 35.352'W), one of the most important wine-growing areas in central Chile. Vineyards chosen were located ≥ 3.0 km from each other. Two of the three vineyards were managed organically for 15 years and were certified by official national certifying bodies, while the other one is in transition to be certified and no applications of synthetic agro-chemicals have been conducted over the past five years prior to the study. This area is characterized by agricultural landscapes composed of a variety of crops, including vineyards, in addition to small patches of native vegetation (scrub and sclerophyllous forest), exotic tree plantation lots (*Pinus* sp. or *Eucalyptus* spp.), and urban or semi-urban areas. The remnants of native vegetation mainly contained *Acacia caven*, *Quillaja saponaria*, *Lithraea caustica*, and *Baccharis linearis*, among other trees and shrub species, while almond (*Prunus dulcis*) and walnut (*Juglans regia*) trees dominated the fruit crops (Rodríguez-San Pedro et al., 2019).

2.2. Enclosure experiment and data collection

In each selected vineyard, two experimental treatments were established: nocturnal exclusion of bats, and control treatment (without cage exclusion) (Fig. 1A). Enclosure plots (20m \times 20m \times 5 m) consisted of rectangular wire cables connected by wooden poles, covered on all sides -except the bottom- with agricultural netting (mesh opening 2 \times 2 cm). The four sides of the net were attached to metal clips, which slid over the cable located at the top of each side (Fig. 1B). This allowed us to open and close the netting like curtains daily, at sunrise and sunset, to allow access of diurnal birds and avoid access of bats at nights. The enclosures restricted access of all bat species but allowed access of nocturnal flying insects including large Lepidoptera. A plot of equal dimensions, 25 m from the enclosure, was selected as the control. In each vineyard, both enclosures and control plots were placed adjacent and equidistant from the edge of the vineyard where higher bat activity and diversity had been reported (Rodríguez-San Pedro et al., 2018, 2019). The exclusion experiments took place for a period of 12 weeks, beginning December 2017 and finishing March 2018, corresponding to the austral summer, when bats and insects are more active and the grapevines have leaves and fruits.

In both the enclosure and control plots, we recorded: leaf herbivory, cluster damage and the abundance of larvae/pupae of arthropods. At each plot, we marked 15 grapevine plants, homogeneously distributed from the center to the edges of the plot. In each grapevine plant, we selected five different leaves every 12–18 days, over six sampling periods, to measure herbivory by visual inspection and look for insect larvae or pupae. A total of 450 leaves were sampled for each plot by the end of the experiment. We determined herbivory levels as the percentage of leaf area eaten, assigning each leaf to an herbivory category by visual inspection: 0: not eaten; 1: 1–6% damage; 2: 7–12%; 3: 13–25%; 4: 26–50%; 5: 51–100%. This score was used to calculate an index of herbivory (IH) per plant as: $IH = \sum n_i(C_i)/N$, where i is the herbivory category, n_i is the number of leaves in the i th category herbivory, C_i is the midpoint of each category (i.e. $C_1 = 3.5\%$, $C_2 = 9.0\%$, $C_3 = 18.5\%$, $C_4 = 37.5\%$ and $C_5 = 75.0\%$) and N is the total number of leaves sampled on the grape plant at each plot (Benítez-Malvido et al., 1999).

To evaluate grape berry damage, we visually inspected one cluster from each of the 15 selected grapevine plants in each plot (enclosure and control) every 12–18 days, over five sampling periods, and recorded the number of damaged berries per cluster. A total of 75 clusters were sampled from each plot by the end of the experiment. We estimated an index of damage reduction in grapes at each vineyard by expressing the proportional change in the number of damaged grapes per cluster in the enclosure versus control treatments during each sampling period: $(d_{ex}-d_{co})/d_{ex}$, where d_{ex} is the number of damaged grapes per cluster on the excluded plants and d_{co} is the number of damaged grapes per cluster on the control plants. The resulting index varies from 0 to 1, with values increasing as the level of damage reduces. Larvae/pupae of arthropods were surveyed at each of the 15 grapevine plants by visual inspection, looking at both leaves and clusters. All surveys were performed simultaneously, on the same sampling days, excepting the first sampling date, as berries had not yet formed at the beginning of the experiment.

2.3. Bat survey

Bat activity was recorded using an automatic bat-detector Song Meter SM4BAT FS with an external omnidirectional SMM-U1 ultrasonic microphone (Wildlife Acoustics, Inc., Maynard, MA, USA), placed within 25 m of the enclosure and control plots. The detector was set at a height of 4.5 m from ground level, and was operative from sunset to sunrise, resulting in a 10-h recording period per night. Each vineyard was sampled for four to five consecutive nights before the detector was moved to the next one. After sampling all three, this process was repeated until reaching a minimum of 18 nights of bat monitoring per vineyard. Acoustic sampling was conducted from December 2017 to March 2018, simultaneously with the herbivory and grape cluster damage surveys.

Bat calls were displayed and analyzed using BatSound 2.1 (Pettersson Elektronik AB, Uppsala, Sweden). Each echolocation call was manually identified and assigned to a species by comparing the structure and frequency parameters of the recorded calls with a reference library of bat echolocation recorded in central Chile (Rodríguez-San Pedro et al., 2016; Rodríguez-San Pedro and Simonetti, 2013a). Bat activity was quantified as the number of bat passes per sampling point per night and used to describe changes in bat activity over time, throughout the experiment. A bat pass was considered to be any recording with a maximum duration of 15 s where two or more pulses emitted by a bat were identified. Further, an index of feeding activity was quantified by counting the number of recordings that contained a distinct feeding buzz followed by a pause (sequence of very short duration signals emitted at high repetition rates, which indicate prey capture attempts; Griffin et al., 1960).

2.4. Molecular diet analysis

2.4.1. Faecal sample collection

We collected bat faecal pellets in roosts for *Myotis chiloensis* (two roosts) and *Tadarida brasiliensis* (one roost), the most common bat species in vineyards of central Chile (Rodríguez-San Pedro et al., 2018, 2019). The two colonies of *M. chiloensis* roosted in buildings and consisted of 40–100 individuals on average, respectively. The colony of *T. brasiliensis*, roosted under a bridge and consisted of 200 individuals on average. All roosts were located in vineyard landscapes at ≤ 5.0 km from our study vineyards. Each roost was sampled two times, in November 2016 and March 2017. We analyzed three samples per roost with an average of 20 pellets per sample.

2.4.2. Identification of prey-DNA in faecal samples

DNA was extracted using the PowerFecal®DNA Isolation Kit (MoBio Laboratories, USA) following the indications of the manufacturer, with the exception that DNA was eluted in 25 μ L of water MiliQ. By faeces sample, the mitochondrial COI region was sequenced by Next-generation sequencing. To amplify COI regions, the primer combinations mlCOIintF with jgHCO2198, published by Leray et al., (2013) were used. Libraries were constructed following the Illumina protocol 16S Metagenomic Sequencing. In addition to the specific primers, the sequence was complemented with the design described in Fadrosch et al. (2014), containing a linker sequence optimized for sequencing on the Illumina, an index sequence and a heterogeneity spacer. DNA extraction, libraries and next-generation sequencing were performed in the core research facilities AUSTRAL-omics of the Universidad Austral de Chile (Valdivia, Chile). Amplicon sequencing was performed using 600-cycle kits with paired technology in an Illumina MiSeq sequencer (Illumina, San Diego, CA).

2.4.3. Insect collection and sequencing

Insect samples for genetic analysis were obtained from specimens collected with light traps in the studied vineyards during the spring of 2016 (November) and the late summer of 2017 (March). Collected insects were identified by Dr. Rodrigo Barahona of the University of Los Lagos, Chile, and MSc. Francisco Urrea of the Chilean National Museum of Natural History. This list included one known grapevine pest species, the Chilean fruit leaf roller *Proeulia auraria* (Tortricidae) and an additional thirteen species which are not known to be grapevine pests: Lepidoptera (*Leucoptera sinuella* (Lepidoptera: Lyonetiidae) *Agrotis lutescens* (Lepidoptera: Noctuidae) *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae), *Pyralis farinalis* (Lepidoptera: Pyralidae), and *Plutella xylostella* (Lepidoptera: Plutellidae), Neuroptera *Gerstaeckerella chilensis* (Neuroptera: Mantispidae), *Drosophila simulans* (Diptera: Drosophilidae), *Archytas* sp. (Diptera: Tachinidae), *Maculants hirtipes* (Diptera: Sphaeroceridae), *Delia* sp. (Diptera: Anthomyiidae), *Neoterius mystax* (Coleoptera: Bostrichidae), and *Polistes dominula* (Hymenoptera: Vespidae) and *Neotermes chilensis* (Isoptera: Kalotermitidae). DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA). Extracts were amplified using the primers LCO1490 and HCO2198 (Folmer et al., 1994) amplifying the ca. 648 bp of the COI barcode region. Purification and Sanger bi-directional sequencing of the products was undertaken by the commercial facility offered by AUSTRAL-omics of the Universidad Austral de Chile (Valdivia, Chile). Chromatograms of insect sequences (forward and reverse) were aligned and examined in Geneious Pro v 2020.1.2 (<http://www.geneious.com/>).

2.4.4. Bioinformatics analysis

Raw sequences were quality filtered for a q-value higher than 30, using software PRINSEQ (Schmieder and Edwards, 2011) and paired-end reads were assembled using PANDASeq. We used Geneious prime algorithm (Geneious software package; (Kearse et al., 2012) to cluster reads into operational taxonomic units (OTUs) using the novo

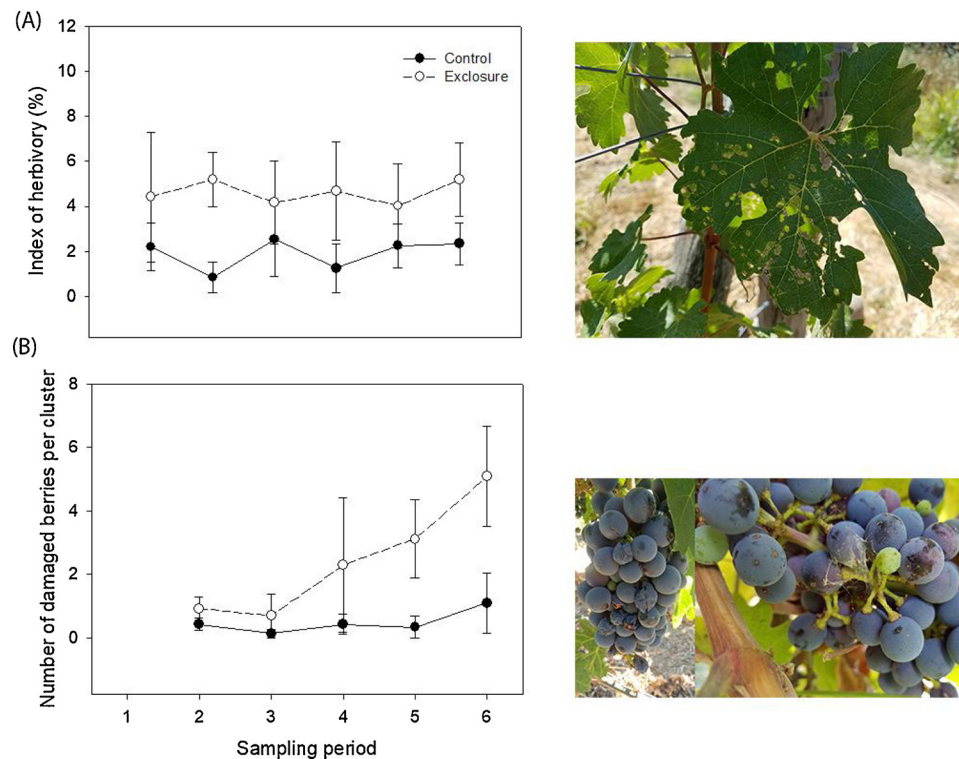


Fig. 2. (A) Mean herbivory index (\pm SE), and (B) mean number of damaged berries per cluster (\pm SE) in nocturnal exclusions (bats absent) and controls (bats present) plots on three vineyards in central Chile over 6 sampling periods from December 2017 to March 2018.

assembler. Sequences were clustered into unique OTUs if there were \leq 2bp difference between sequences. Batch BLAST OTU consensus sequences were performed in the nucleotide collection (nr/nt) of NCBI. Furthermore, the sequences of the 14 insects that were sequenced in this study were added to the database. In order to perform a sequence classifier database from the BLAST hits, we removed duplicates and created a database for the sequence classifier tool. The classification was performed in a Sequence Classifier incorporated in the Geneious prime version 2020.05. A species-level assignment was conceded when query sequences matched the reference sequences with $> 98.5\%$ similarity value (Razgour et al., 2011). When the haplotype coincided with more than one species belonging to the same genera, we made a genus-level assignment (matches on GenBank $> 96\%$ sequence similarity with 100% sequence coverage). Only Arthropoda DNA sequences were considered as potential prey items.

2.5. Statistical analysis

We evaluated the effects of bat exclusion treatments on leaf damage and cluster damage, using a generalized linear mixed effects repeated measures analysis (GLMM), with a Gaussian error structure and identity function. We conducted our analysis with Site (vineyard farm) as a random effect and Treatment (exclusion and control) as a fixed effect. We included Time (sampling period) in the model as the repeated within-subject factor, and each Plot within Site as the subject for repeated measures. We square-root transformed the index of herbivory and the number of damaged berries per cluster prior to analysis to achieve normality. We related bat activity with the level of damage reduction in grape berries with linear regression. All analyses were conducted using SPSS version 23.0 (IBM, Chicago, Illinois).

2.6. Economic analysis

The economic value of the pest suppression services of bats to agricultural production have been estimated by both avoided cost

models (Cleveland et al., 2006; Federico et al., 2008; Puig-Montserrat et al., 2015; Wanger et al., 2014) and by experimental exclusion approaches (Gras et al., 2016; Maas et al., 2013; Maine and Boyles, 2015). The economic value of the pest suppression service provided by bats in our study vineyards was estimated using the data from the bat exclusions following the methodology used by Maine and Boyles (2015) in corn and Karp et al., (2013), in coffee farms. We calculated the increase in the proportion of grape berries damaged after excluding bats by subtracting the percentage of berries damaged in exclusions and controls (Δ damage). We estimated the value of the difference in damage between the exclusions and controls based on 15 grape clusters collected in each plot on the final day of the experiment. We counted the total number of berries per cluster on the 15 clusters from each treatment at each vineyard, and then divided the mean number of grape berries damaged in exclusions and controls by the mean number of berries per cluster to obtain the percentage of berries damaged. To calculate the economic benefit of bats we used the formula: Yield (kg/ha) \times Δ damage \times Price (US\$). We obtained the data of per-hectare yield and price of the winegrape directly from winegrape producers and published data of the Office of Agricultural Studies and Policies (ODEPA, 2018) of the Ministry of Agriculture of the Government of Chile.

3. Results

3.1. Bats exclusion

We found no insect larvae on grapevine plants, in both the exclusion or control plots, during the experiment, and just on one occasion, we found eggs of the brown Chilean leaf-footed bug *Leptoglossus chilensis* (Hemiptera), which is considered a pest for grapes. We also found some Diptera pupae of the family Psilidae, among others that could not be identified, but in very low abundance and thus were not included because of the low robustness of statistical analyses.

Bats significantly reduced herbivory rates in our vineyards under

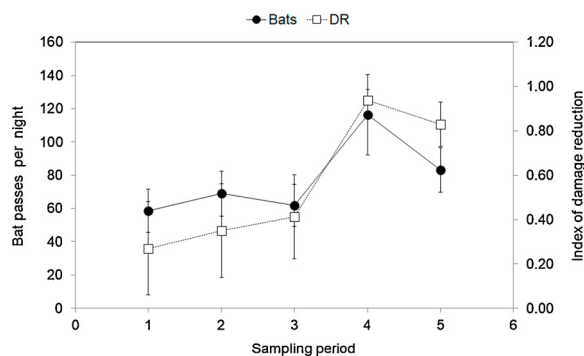


Fig. 3. Bat activity (mean \pm SE) (circles) and the average damage reduction in grape clusters (\pm SE) (squares) by insectivorous bats across time in three vineyards of Paine, central Chile, from December 2017 to March 2018. The index of damage reduction was expressed as the proportional change in the number of damaged grape berries per cluster between exclusions and controls.

study. Levels of leaf damage were significantly higher in plots where bats were excluded (Mean \pm ES; 4.61 ± 0.70) than in controls (1.90 ± 0.41) (Fig. 2A; $F_{1,24} = 9.84$; $P = 0.004$), but there was no significant difference in leaf damage across sampling periods ($F_{5,24} = 0.24$; $P = 0.942$). Likewise, the number of grape berries damaged per cluster was higher in exclusions (2.42 ± 0.66) than in controls (0.48 ± 0.20) (Fig. 2B; $F_{1,20} = 13.94$; $P = 0.001$), and also varied significantly over time ($F_{4,20} = 4.05$; $P = 0.015$).

3.2. Bat activity and damage reduction

We recorded a total of 9872 bat passes, of which 9852 (99.7 %) were identified and attributed to one of five species of aerial insectivorous bats: *Tadarida brasiliensis*, *Myotis chiloensis*, *Lasiurus villosissimus*, *Lasiurus varius* and *Histioglossus montanus*. *Tadarida brasiliensis* was by far the most frequent species in the vineyards, accounting for 67 % of the total bat passes recorded, followed by *M. chiloensis* with 17 %; whereas *H. montanus* was particularly rare with less than 5%. Total bat activity and the average index of damage reduction in grapes followed the same trend over time (Fig. 3), which was supported by a significant positive association between both variables ($r^2 = 0.82$, $p = 0.034$).

3.3. Diet analysis

The molecular dietary analysis was carried out separately for each bat species. A total of 45,718 reads of ~ 365 pb were generated from the faecal analysis of *M. chiloensis*, of which 41,641 were assembled to produce 1789 unique OTUs. Of these, only 112 OTUs were identified to species or genus-level. Dipterans were the most consumed prey, with *Psychoda* sp as the dominant source, accounting for more than 90 % of the sequences in this order. Lepidoptera and Coleoptera were the second most represented orders in the diet of *M. chiloensis*, but also the most diverse in the case of Lepidoptera with six species identified including the Chilean fruit leaf roller *Proeulia auraria* (Tortricidae), and other agricultural pests such as the codling moth *Cydia pomonella* (Tortricidae), the diamondback moth *Plutella xylostella* (Plutellidae), the poplar moth *Leucoptera sinuella* (Lyonetiidae), the tobacco moth *Ephesia elutella* (Pyralidae) and the quinoa moth *Coleophora versurella* (Coleophoridae). Several taxa of Neoptera, Araneae and Thysanoptera were also present in the diet of this species, although at a much lower frequency (Fig. 4). These data represent the first report on the diet of *Myotis chiloensis* in its entire range of distribution.

In the case of *T. brasiliensis*, a total of 26,248 reads of ~ 365 pb were obtained, of which 23,795 were assembled to produce 381 unique OTUs, where only 32 of these OTUs were classified at the species and genus-level. Lepidoptera was the most represented order, which accounted for 78.1 % of the OTUs. Within lepidopterans, we identified the

consumption of *Plutella xylostella* (Plutellidae), *Elasmopalpus angustellus* (Pyralidae), *Elasmopalpus lignosellus* (Pyralidae), *Leucoptera sinuella* (Lyonetiidae), and *Coleophora versurella* (Coleophoridae). Several taxa of Coleoptera and Diptera were also recorded, although at a much lower frequency. A single representative from Neoptera and Hemiptera were also found in the diet of *T. brasiliensis* (Fig. 5).

3.4. Economic analysis

Exclusion plots had 8.9 % of grape berries damaged compared to 1.9 % recorded in control plots, so we estimated that bats increased grapevine yield by 7.0 %. The estimated value of bats is also a function of grapevine yield and the price of winegrapes, which varies annually worldwide. In our studied vineyards, yield was on average 8500 kg/ha. The market value of the winegrape in 2017/2018 ranged between CLP \$190-\$250/kg (depending on the winegrape variety), according to the ODEPA (2018). Considering these figures, we estimated bat predation confers significant economic benefits to winegrape producers in our study area by saving 595 kg/ha/year of berry from pest infections, a value of CLP\$113.050-148.750/ha/year (US\$188-\$248/ha/year).

4. Discussion

The winemaking sector in Chile has a high cultural and economic relevance, with more than 900 million liters produced in a total production area of 136.000 ha in 2017 (ODEPA, 2018), which makes grapevine pest suppression particularly valuable to winegrape producers. Our preliminary results suggest that bats can supply ecologically and economically valuable services to the local winegrape industry in Chile. After Maine and Boyles (2015) in corn, this is the second study worldwide explicitly evaluating the impact of aerial insectivorous bats on crop protection, and the first in vineyards, using large nocturnal exclusions. Previous works focused on tropical and temperate forests and agro-ecosystems (e.g., coffee and cacao) where bats glean insects from vegetation (Böhm et al., 2011; Kalka et al., 2008; Karp and Daily, 2014; Maas et al., 2013; Morrison and Lindell, 2012; Williams-Guillén et al., 2008).

Although the sample sizes in the present study are small (three exclusions and their controls, in three vineyards) and the exclusion experiment was limited to one year, our data support the hypothesis that bat predation both reduced herbivory rates and grape berry damage in vineyards. These findings are consistent with previous bat exclusion studies from other latitudes (Kalka et al., 2008; Maas et al., 2013; Maine and Boyles, 2015; Morrison and Lindell, 2012), supporting the idea that bats may reduce the numbers of economically damaging important pests across a variety of agricultural systems and natural habitats. Even though it was not possible to find direct evidence of the impact of bats in the number of larvae/pupae, our data suggest that bats can provide sufficient predation pressure on the adult stage to reduce herbivory rates and grape cluster damage in vineyards. The positive association between bat activity and the index of damage reduction in grape clusters over time seems to support this statement. The lack of larvae/pupae during field inspections could be a consequence of our observational sampling, and the fact that we did not dissect the damaged berries to look for larvae inside. Nevertheless, previous surveys of nocturnal flying insects in our studied vineyards using light traps, reveal a high diversity of insect orders and families associated to this crop (Chaperon et al., unpublished results), including the presence of the grapevine pests *L. botrana*, *P. auraria*, *Agrotis* sp, and *Athlia rustica* (Coleoptera: Scarabaeidae).

Our molecular dietary analysis results show *T. brasiliensis* as a moth specialist, as lepidopterans vastly outnumbered the remaining four insect orders consumed by the species. This result should be interpreted with caution, since we obtained faecal samples from a single colony and did not collect samples throughout the year. Nevertheless, a dominance of lepidopterans in the diet of *T. brasiliensis* has been reported in

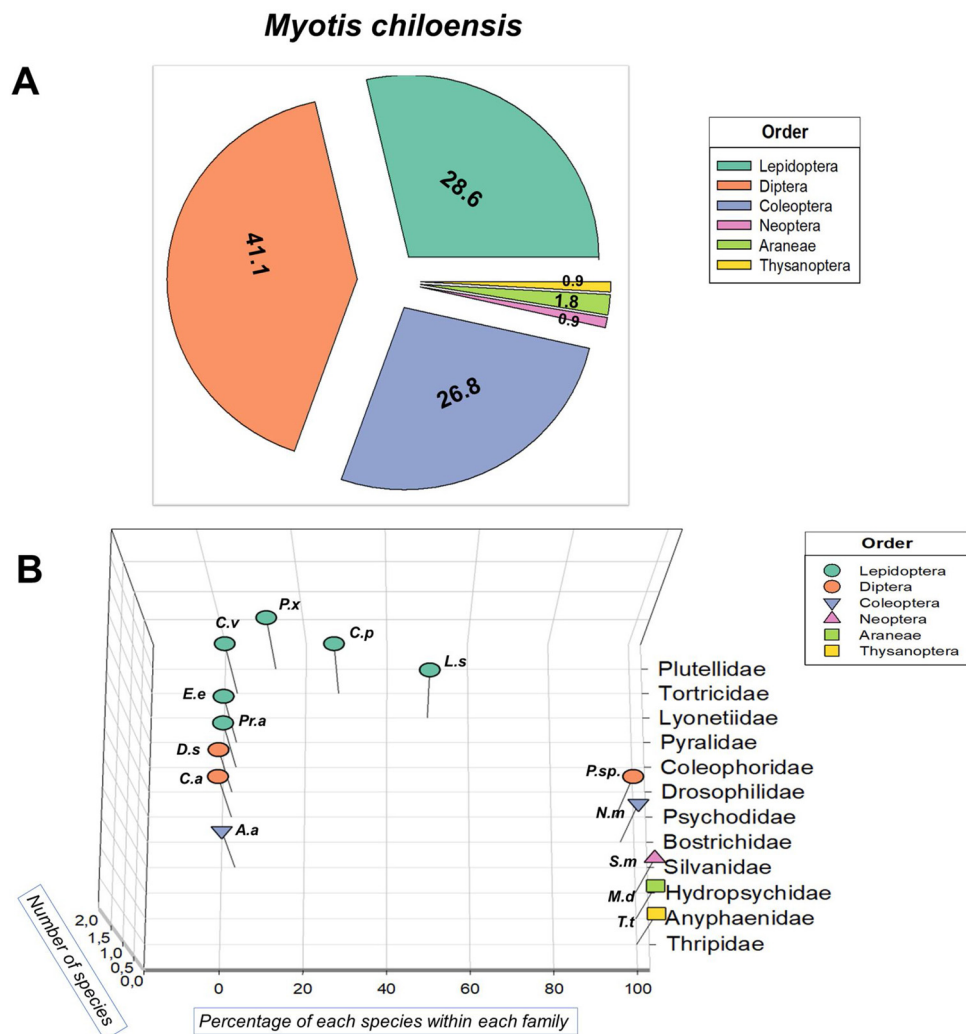


Fig. 4. Relative representation of insect orders (A) and species (B) identified in the diet of *Myotis chiloensis* sampled from two colonies in Paine, central Chile, expressed as the percentage of occurrence (relative number of sequences clustered into OTUs assigned to the taxon). Abbreviation Px: *Plutella xylostella*; Cp: *Cydia pomonella*; Pra: *Proeulia auraria*; Ls: *Leucoptera sinuella*; Ee: *Ephestia elutella*; Cv: *Coleophora versurella*; Ds: *Drosophila simulans*; Ssp: *Psychoda* sp; Ca: *Clogmia albipunctata*; Nm: *Neoterius mystax*; Aa: *Ahasverus advena*; Md: *Monapia dilaticollis*; Tt: *Thrips tabaci*; Sm: *Smicridea murina*.

previous studies based on morphological identification of prey remains in the droppings (Gamboa-Alurralde and Döaz, 2018; Lee and McCracken, 2005), although not in such disproportionate percentages. On the other hand, *M. chiloensis* showed a more varied diet, feeding mainly on dipterans, lepidopterans and coleopterans, consistent with diets reported for other species of *Myotis* from the southern cone of South America (Gamboa-Alurralde and Díaz, 2019). Although it was not possible to find evidence of a predatory effect of bats on the major pest *L. botrana* in our study, other grapevine pests such as *P. auraria*, were detected in the diet of *M. chiloensis*, supporting its role as predator of grapevine insect pests in Chilean vineyards. The Chilean fruit leaf roller *Proeulia auraria* is native to Chile and causes damage to vines and blueberries very similar to that of *L. botrana*. It is considered a quarantine pest for the United States, Mexico, Japan and Canada, being the main cause of the rejection of shipments to these export markets (González, 2017). Despite the fact that our research was focused on vineyard systems, we found moth pest species associated with other crops (i.e. cabbage, tomato, apples and tobacco). Similar findings were reported by (Baroja et al., 2019), and may be associated with the different ecological requirements of prey species throughout different life stages (Arrizabalaga-Escudero et al., 2015). Whereas the larval host plant of a given prey species may be linked to trees and shrubs, adults can occur in other habitats such as pastures or crops due to their

dispersal abilities, trophic needs and phenology (Betzholtz and Franzen, 2011; Slade et al., 2013). Further analyses based on species-specific primers, and faecal samples collected throughout the full sampling season will be essential for a more complete assessment of grapevine pest consumption by the bat species and their role as natural pest controllers in our region.

Insectivorous bats prevented significant pest damage to grapevines, representing a 7% (US\$188-\$248 per ha and year) of the total wine-grape production in our studied vineyards. The value of this service likely varies with the type of vineyard (i.e., organic or conventional), pest abundance, and bat assemblage structure; therefore, extrapolations from our results to other types of vineyards should be done with caution. Our study was conducted in organic vineyards, which represent 3.2 % of the winegrapes planted in Chile in 2017 or 4.446 ha ODEPA, 2018. In conventional vineyards, where synthetic agro-chemicals are commonly used to manage grapevine pests, bats may reduce the cost of pesticide use by suppressing adult insect populations below outbreak thresholds (Cleveland et al., 2006; Federico et al., 2008). However, our economic analysis only addresses suppression of direct damage to grapevines and does not include the effects of pesticides sprayed on crops, which may decrease the estimated value of bats suppression.

It has been suggested that rising temperatures due to climate change may increase the severity and intensity of outbreaks of insect pests, due

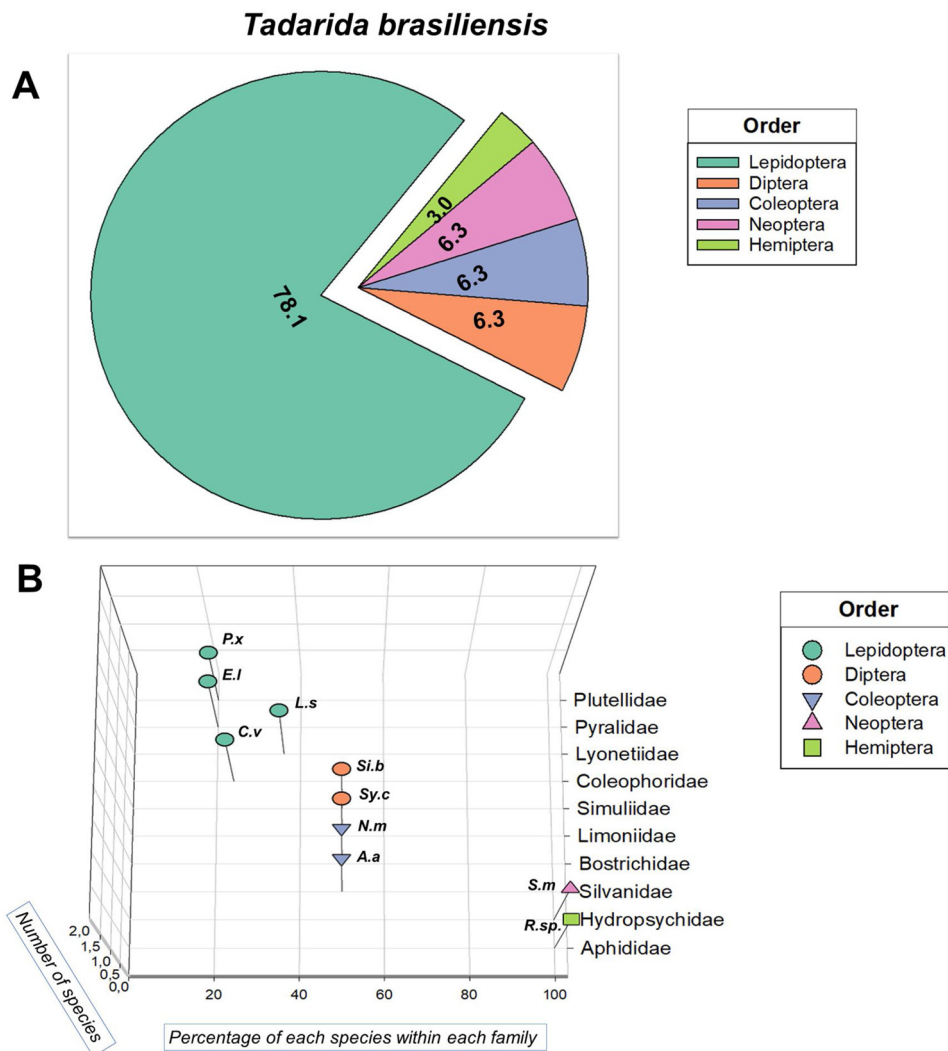


Fig. 5. Relative representation of insect orders (A) and species (B) identified in the diet of *Tadarida brasiliensis* sampled from one colony in Paine, central Chile, expressed as the percentage of occurrence (relative number of sequences clustered into OTUs assigned to the taxon). Abbreviation Px: *Plutella xylostella*; Ea: *Elasmopalpus angustellus*; El: *Elasmopalpus lignosellus*; Ls: *Leucoptera sinuella*; Cv: *Coleophora versurella*; Nm: *Neoterius mystax*; Aa: *Ahasverus advena*; Sm: *Smicrida murina*; Sib: *Simulium barbatipes*; Syc: *Symplecta cana*; Rsp: *Rhopalosiphum sp.*

to positive response of insects to warmer conditions (Robinet and Roques, 2010; Castex et al., 2018). Higher temperatures might trigger an increase in the number of generations of insect species that are able to produce several broods per year, such as *L. botrana* and *P. auraria* (Caffarra et al., 2012; González, 2015; Martín-Vertedor et al., 2010), which could lead to an increase in population and increased levels of infestation. If infestation increases, pest-control value provided by insectivorous bats, would also likely increase, as grapevine pest insects become a more significant food source.

Maintaining an abundant and diverse assemblage of insectivorous bats may help provide resilience against pest outbreaks. Conserving bat populations by retaining ecological structures at both local and landscape scales may therefore represent a critical component for integrated pest management in vineyards. Bat activity increases in vineyards surrounded by landscapes with a higher diversity of cover types (Rodríguez-San Pedro et al., 2019), and at close proximity to hedgerows and rivers (Froidevaux et al., 2017). Furthermore, our results show that the index of damage reduction is positively associated with bat activity. Winegrape producers and policy makers seeking to enhance bat activity and diversity in vineyards should aim to increase cover diversification in the landscape scale. Similarly, maintaining natural vegetation in and around the vineyards can help to retain bat diversity (Polyakov et al.,

2019; Rodríguez-San Pedro et al., 2019). Further research evaluating the effects of landscape structure and agricultural management (organic vs. conventional) on the efficiency of bats as biological suppression agents in vineyards will be crucial in the context of conservation biological control.

5. Conclusions

To our knowledge, this is the first effort worldwide to evaluate and quantify the ecological and economic services provided by bats in vineyards and represents a first step towards encouraging winegrowers to use bats as biological suppression agents in this agro-ecosystem. Our results, although preliminary, suggest that top-down suppression by bats can reduce herbivory rates and grape berry damage in vineyards. Winegrowers save up to 7% of the annual winegrape production in our study area because of bats. Therefore, bats should be included in future biodiversity conservation plans in vineyard landscapes and also considered within agricultural management approaches based on natural pest control.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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