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## RESEARCH ARTICLE

# Mortality of the outbreak defoliator *Ormiscodes amphimone* (Lepidoptera: Saturniidae) caused by natural enemies in northwestern Patagonia, Argentina

## Mortalidad del defoliador epidémico *Ormiscodes amphimone* (Lepidoptera: Saturniidae) causada por enemigos naturales en el noroeste de la Patagonia Argentina

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### ABSTRACT

Outbreaks of the defoliator moth *Ormiscodes amphimone* are occurring more frequently in numerous *Nothofagus* forests of Patagonia. However, little is known about the life history of this species including its natural enemies as mortality agents. In this work we quantified mortality by parasitoids and generalist predators at the egg, larval and pupal life stages of *O. amphimone* in a *Nothofagus pumilio* (Poepp. & Endl.) Krasser forest in northwestern Patagonia. Parasitism of eggs was relatively low (ca. 11 %), and we did not record significant larval predation by insectivorous birds. However, we recorded elevated mortality caused by larval parasitoids (ca. 50 % in third instar larvae) and pupal predators (ca. 75 %), which suggests that these natural enemies could play a significant role in regulating *O. amphimone* populations. Our research is an initial step towards understanding the influence of natural enemies on *O. amphimone* population dynamics.

**Key words:** entomopathogenic nematode, *Hyposoter*, *Nothofagus*, parasitoids, predation.

### RESUMEN

Las irrupciones poblacionales de la polilla defoliadora *Ormiscodes amphimone* están ocurriendo de manera más frecuente en numerosos bosques de *Nothofagus* de la Patagonia. Sin embargo, se sabe poco de la historia natural de esta especie y, particularmente, de sus enemigos naturales. En este estudio se cuantificó la depredación de huevos, larvas y pupas de *O. amphimone* por parasitoides y otros depredadores en un bosque de *Nothofagus pumilio* (Poepp. & Endl.) Krasser en el noroeste de la Patagonia. Se encontró que el parasitismo de huevos fue relativamente bajo (ca. 11 %) y no se registró depredación significativa de larvas por aves insectívoras. No obstante, registramos niveles elevados de mortalidad causada por parasitoides de larvas (ca. 50 % en larvas en tercer instar) y por depredadores de pupas (ca. 75 %), lo que parece indicar que estos enemigos naturales desempeñan un papel significativo en la regulación de poblaciones de *O. amphimone*. Este estudio representa un paso inicial hacia el entendimiento de la influencia de los enemigos naturales de *O. amphimone* en la dinámica de poblaciones de esta polilla.

**Palabras clave:** depredación, *Hyposoter*, nematodo entomopatógeno, *Nothofagus*, parasitoides.

### INTRODUCTION

*Ormiscodes* caterpillars are Saturniid moths known to defoliate extensive areas of native southern beech (*Nothofagus*) forests as well as plantations of introduced pines (*Pinus radiata* D. Don) in southern Chile and Argentina (Baldini & Alvarado 2008). These outbreaks reduce radial tree growth (Paritsis et al. 2009), can kill saplings and apical shoots (Bauerle et al. 1997, Cogollor 2002), and have been suggested

to cause partial crown dieback on *Nothofagus* stands if defoliation is severe (Veblen et al. 1996). In addition, *Ormiscodes* caterpillars are a nuisance for tourism and outdoor activities in general when they reach epidemic population levels due to their irritating hairs (Artigas 1972, Baldini & Alvarado 2008).

Over the past 30 years, outbreaks of *O. amphimone*, one of the most widespread *Ormiscodes* species in southern South America, have increased in frequency in many *N. pumilio*

(Poepp. & Endl.) Krasser forests in Patagonia, probably due to climate warming (Paritsis & Veblen 2011). These outbreaks, which last a single growing season, can defoliate several thousand hectares of *Nothofagus* spp. forests, but *N. pumilio* is typically the most affected species (Baldini & Alvarado 2008, Paritsis et al. 2011). Recent *O. amphimone* outbreaks (2007, 2008 and 2009) on *N. pumilio* and *N. antarctica* (Forster) Oerst. in the Aysén region (Chile) generated concern among land owners and farmers, and the Agriculture Ministry of Chile took measures to monitor these outbreaks (Anonymous 2007, Baldini & Lanfranco 2008).

Despite the ecological importance of defoliation events caused by *O. amphimone* in *Nothofagus* forests in Patagonia, there are few specific studies on the ecology and natural history of this species. These include tree-ring reconstructions of past outbreaks (Paritsis & Veblen 2011), evaluation of larval performance to diet quality and temperature (Paritsis & Veblen 2010), and biophysical correlates with spatial patterns of defoliation events (Paritsis et al. 2011). However, there are no studies that have quantified the incidence of natural enemies of *O. amphimone* in order to assess their potential role in the population dynamics of this outbreak defoliator.

Population ecologists interested in insect herbivores have often disagreed on the extent to which their population densities are controlled by food supply (bottom-up effects) or by the effects of their natural enemies (top-down effects) (Hunter & Price 1992, Schmitz 1994). Natural enemies are known to have great impacts on the population dynamics of forest Lepidoptera in various ecosystems (e.g., Klemola et al. 2002, Dwyer et al. 2004). Nevertheless, the relative influence of natural enemies on populations of forest Lepidoptera is highly variable depending on the species and location considered. For instance, while predators of pupae appear to play a significant role in gypsy moth (*Lymantria dispar* [L.]) outbreak dynamics in North America (Liebhold et al. 2000), they do not seem to be a major factor in local outbreaks of the winter moth, *Operophtera brumata* L., in southern Finland (Heisswolf et al. 2010). In southern South America multiple species of natural enemies have been observed to attack *Ormiscodes*

species at different stages of their life cycle (Silva 1917, Peigler 1994, Cogollor 2002), and it has been suggested that *Ormiscodes* populations could be controlled by the mortality associated with parasitoid attack (Silva 1917, Artigas 1972, Cogollor 2002). However, quantitative data on mortality of *Ormiscodes* species caused by parasitoids and generalist vertebrate predators, such as birds and rodents, are scarce or, as in the case of *O. amphimone*, non-existent.

Given the recent increase in the frequency of *O. amphimone* outbreak in multiple areas of Patagonia and the potential for more outbreak events to occur in the future (promoted by warming trends) (Paritsis & Veblen 2011), it is essential to quantify mortality caused by natural enemies on these populations in order to assess the potential role of parasitoids and predators on *O. amphimone* demography. Because *N. pumilio* appears to be the most extensively defoliated species (Baldini & Alvarado 2008, Paritsis et al. 2011), our objective is to quantify mortality of eggs, larvae and pupae of *O. amphimone* caused by natural enemies in *N. pumilio* forest stands in northwestern Patagonia.

## METHODS

### Study area

Surveys and field experiments were conducted at Paso Puyehue (40°43' S, 71°55' W; 1150 masl) in a valley bottom location at the foothills of the eastern slope of the Andes in Argentina. This is an area of relatively dense *N. pumilio* forest with an open understory of forbs (e.g., *Adenocaulon chilensis* Less.) and small shrubs (e.g., *Ribes maguellanica* Poer., *Drymis winteri* Forst., and *Gaultheria mucronata* [L. f.] Hook. & Arn.). To account for potential heterogeneity in predation levels within the study area, we selected three sub sites of 2 to 4 ha in size each, separated 0.5 to 2 km from each other, to conduct predation assessments. The climate in this region is characterized by cold and wet winters, and mild but dry summers, and the growing season occurs mainly from November to February. Mean annual precipitation is approximately 3000 mm (Barros et al. 1983).

### Study species

*Ormiscodes amphimone* is a native and polyphagous Saturniid moth that feeds preferentially on *N. pumilio* foliage (Baldini & Alvarado 2008, Paritsis et al. 2010). Outbreaks of this species generally do not cause widespread tree mortality, probably because the defoliation event lasts only a single growing season. *O. amphimone* overwinters in the egg stage, and larvae emerge during early to late spring (Lemaire 2002). Larvae feed gregariously until mid to late summer, going through five instars before pupating in the forest floor litter. Adults emerge after one to two months of pupation (Baldini & Alvarado 2008, personal observation) and,

after mating, females lay their eggs in a single cluster around small diameter twigs of the host plant.

Multiple parasitoids have been described to attack *Ormiscodes* species. The most frequently cited include the egg parasitoids *Horismenus ancillus* Brèthes (synonym: *Dirphiphagus ancilla*) (Hymenoptera: Eulophidae) and *Paridris chilensis* Brèthes (Hymenoptera: Platygasteridae), and the larval parasitoids *Apanteles* spp. (Hymenoptera: Braconidae) (Silva 1917, Cogollor 2002, Baldini & Alvarado 2008). Despite some early observations by Silva (1917) on the life history of parasitoids of *Ormiscodes* sp. (cited as *Dirphia amphimone*) in central Chile, little is known about the identity and the natural endemic-levels of parasitism of *Ormiscodes* species, especially in *Nothofagus* forests. Vertebrate predators of larvae and pupae, such as birds and small mammals, are known to exert significant predation pressure on populations of eruptive Lepidoptera species in forests of the northern hemisphere (e.g., Liebhold et al. 2000, Barbaro & Battisti 2011). However, the potential effects of vertebrate predators on *Ormiscodes* populations are largely unknown.

#### Egg parasitoids

During mid-February 2004 (i.e., ca. three months after egg hatching), we collected 15 egg clusters that were laid over fall 2003 (i.e., March-May) on *N. pumilio* saplings. Egg clusters laid in previous seasons (recognized by a pronounced weathering and discoloration of the egg shells) were not included in this analysis because it was not possible to accurately assess parasitism incidence. We counted the number of hatched eggs, parasitized eggs, and unhatched eggs in each egg cluster with a 70x magnification dissection microscope. Parasitized eggs can be readily differentiated from successful *O. amphimone* larval emergence by the size of the emergence opening, which is of significantly smaller diameter for the parasitoid (Fig. 1A) than for *O. amphimone* (Fig. 1B). We verified that the smaller emergence holes were created by parasitoids by observing and photographing *O. amphimone* larvae and parasitoid emergence from eggs with a 70x magnification dissection microscope on two fresh egg clusters collected earlier in the same season. To test for a potential influence of the total number of eggs per cluster on the number of parasitized eggs we conducted a linear correlation between these variables using SPSS (2007).

#### Larval parasitoids

To assess mortality caused by parasitoids and to determine parasitism per instar, we collected groups of larvae from the field at their first, second, third and fourth instar and reared them until pupation or parasitoid emergence. We did not examine parasitism at the fifth instar because larvae are mostly solitary during this instar, which makes it difficult to obtain a sufficiently large sample size. We first located groups of larvae in the field and monitored them at weekly intervals until they reached the desired instar. Instars were identified by the approximate width of the head capsule (Llanderal 1993) and from previous knowledge of their relative body size. Larval collection in the field was conducted in two different summers. In the first summer (2003-2004; hereinafter 2003) we collected a total of 28 groups of larvae from the three sub sites, totaling 560 larvae. When collected, two groups were in first instar (29 larvae), five groups were in second instar (117 larvae), eight groups were in third instar (143

larvae), and 13 groups were in fourth instar (271 larvae). In the second summer (2006-2007; hereinafter 2006) we collected a total of 14 groups of larvae (474 larvae total). At the time of collection, two groups were in first instar (31 larvae), seven groups were in second instar (292 larvae) and five groups were in third instar (151 larvae). No fourth instar larvae were collected in the second summer. Groups of larvae were reared in plastic containers in the laboratory at room temperature (18 to 20°C) with a 14:10 L:D photoperiod and constant supply of fresh *N. pumilio* leaves until pupation or parasitoid emergence. We quantified the number of larvae killed by parasitoids per group and instar. Parasitoid specimens were preserved in 70 % ethanol and were taxonomically classified using the keys and/or taxa descriptions in Townes & Townes (1966) (Ichneumonidae), Johansen (2010) and Silva (1917) (Braconidae), Hansson (2009) (Eulophidae), and Poinar (1983) (Nematoda). To assess temporal variation and variation in the incidence of different parasitoid species in larval mortality we used the data for third instar larvae (i.e., the most representative instar for estimating parasitism in this system). These data were analyzed with a two-way analysis of variance, with year, parasitoid species and their interaction as the main effects using SPSS (2007).

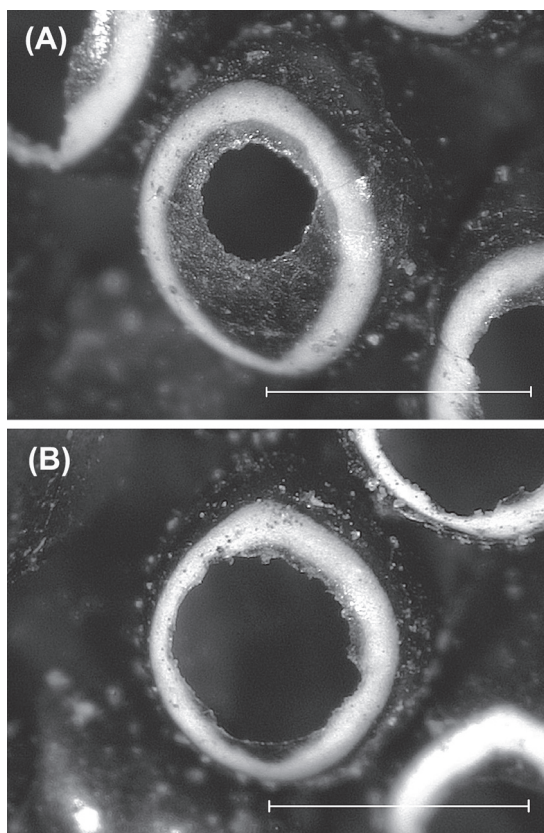


Fig. 1: (A) Emergence opening of the egg parasitoid *Horismenus ancillus*. (B) Emergence opening of the *O. amphimone* larva. Scale bars represent 1 mm.

(A) Orificio de emergencia del parasitoide de huevos *Horismenus ancillus*. (B) Orificio de emergencia de la larva de *O. amphimone*. La escala representa 1 mm.



### Bird predation on larvae

Bird predation on larvae was estimated by quantifying larval mortality on *N. pumilio* saplings with bird exclosures and on saplings with free access to birds. In late December 2003 we identified 24 *N. pumilio* saplings 1.5–3.5 m in height in the study area, which had one *O. amphimone* egg cluster attached. On January 23, 2004, when larval groups were in second to third instar, we randomly selected 12 saplings and covered each of them with a bird-proof mesh (mesh size 2 × 2 cm) and left the 12 remaining saplings uncovered. Bird-proof meshes allow parasitoids and other insect predators free access to larvae, but protect larvae from bird predation. After bird-proof mesh placement we counted the number of larvae per group on each sapling, which ranged from 12 to 150 ( $67 \pm 12$ , mean  $\pm$  SE) larvae each. Bird-proof meshes were installed on the saplings for seven days. During the sampling period, the commonest birds feeding on insects on canopy foliage in these forests are the thorn-tailed rayadito, *Aphrastura spinicauda* Gmelin (Furnariidae); the white-crested elaenia, *Elaenia albiceps* Orbigny & Lafresnaye (Tyranidae), and the house wren *Troglodytes aedon*, Vieillot (Deferrari et al. 2001, personal observation). Seven days after mesh installation and before larvae reached the fourth instar and actively disperse, we re-counted larvae in each group to estimate mortality (or disappearance) in both covered and uncovered saplings. Bird predation was estimated as the difference in mortality between treatments (i.e., mesh-covered vs. uncovered). Because during the second time we counted the larvae we were unable to find three groups of larvae on uncovered saplings and one group on a mesh-covered sapling, the final sample size was reduced to 11 bird exclusion samples and nine control samples. The effect of bird exclosures on larval mortality was assessed with an independent samples t-test using SPSS (2007).

### Predation of pupae

To assess predation of pupae in the field we placed pupae in the forest litter from February 24 to March 12, 2004 (i.e., 17 days) –which coincides with a fraction of the time pupae are naturally found in this area– and quantified predation. To test for potential effects of density of pupae on pupal predation we established two sets of plots with different pupal densities. We defined eight 2 × 1 m high pupal density plots and placed 18 uniformly distributed pupae in each plot (i.e., six pupae per square meter). We also defined eight 1 × 1 m low pupal density plots where we placed two pupae on each (i.e., two pupae per square meter). These eight low density plots were paired with the eight high pupal density plots (i.e., at 10 to 15 m from these). Plot pairs (high-low densities) were at least 40 m away from any other pair of plots. By February 24, 2004, when *O. amphimone* pupae are typically found in these forests, pupae were buried in the forest litter at a depth of 1 cm at the base of a wooden stick which indicated their location within the plot. Predation of pupae was estimated by quantifying missing or partially eaten pupae after 17 days in the field. When partially eaten pupae were found, we discarded potential adult emergence by examining the pupal case for lines of weakness typical of successful adult emergence. Common species that could predate on pupae in our study area are ground birds, such as the chucac tapaculo, *Scelorchilus rubecula* Kittlitz (Rhinocryptidae) (Correa et al. 1990), and various small mammals, such as *Geoxus valdivianus* Thomas (Cricetidae) (Meserve et al. 1988, R. Sage, personal communication, 2011).

Additionally, invertebrates, such as *Ceroglossus* spp. (Coleoptera: Carabidae) may also predate on pupae (Devotto et al. 2007). We assessed the effect of pupal density on predation with a paired t-test using SPSS (2007).

## RESULTS

### Egg parasitoids

Egg clusters ranged from 87 to 229 eggs and had  $167.8 \pm 10.9$  eggs on average. The only species of egg parasitoid we observed emerging from fresh eggs was *Horismenus ancillus* Brèthes (Hymenoptera: Eulophidae); consequently, it is likely that this species is responsible for most of the parasitism we observed on *O. amphimone* egg clusters (Fig.

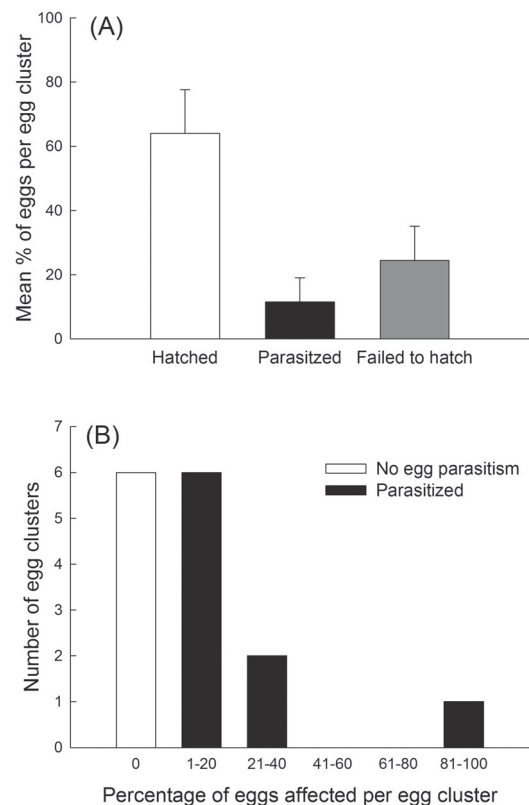


Fig. 2: (A) Percentage ( $\pm$  SE) of successfully hatched, parasitized, and unhatched *O. amphimone* eggs per egg cluster collected in the field three months after caterpillar emergence. (B) Frequency of egg clusters according to their percentage of parasitism.

(A) Porcentaje ( $\pm$  EE) de huevos eclosionados, parasitados y no eclosionados de *O. amphimone* por grupo de huevos recolectados en el terreno tres meses después de la emergencia de las larvas. (B) Frecuencia de grupos de huevos según su porcentaje de parasitismo.

2A). However, it is possible that other species of egg parasitoids (e.g., *Paridris chilensis* Br  thes) might have also contributed to the egg parasitism documented here. Mean egg parasitism per egg cluster was  $11.5 \pm 7.5$  % (Fig. 2A) and ranged from 0 % to 92.5 %. Mean percentage of eggs per egg cluster that failed

to hatch was  $24.4 \pm 10.7$  % (Fig. 2A) and ranged from 0 % to 98.2 %. Twelve out of the 15 egg clusters collected had less than 7 % parasitism, while three egg clusters had more than 27 % (and up to 92.5 %) parasitism (Fig. 2B). There was no significant linear correlation between the number of parasitized eggs and the total number of eggs per cluster ( $r = -0.08$ ;  $n = 15$ ;  $P = 0.8$ ).

### Larval parasitoids

*Ormiscodes amphimone* larvae were parasitized by a total of three parasitoid species in our study area and parasitism varied substantially; not only among species of parasitoids ( $F_{2,39} = 8.9$ ;  $P = 0.001$ ), but also between survey years (as demonstrated by a significant parasitoid species by year interaction;  $F_{2,39} = 12.0$ ;  $P < 0.001$ ) (Fig. 3). An undescribed species of *Hyposoter* F  rster (Hymenoptera: Ichneumonidae) (D. Wahl, personal communication, 2011) was the most common parasitoid affecting *O. amphimone* larvae during 2003, while *Apanteles* sp. Forster (Hymenoptera: Braconidae) and an unidentified species of mermithid nematode (Mermithida: Mermithidae) caused markedly less parasitism (Fig. 3). In 2006, the nematode species was the most common parasitoid attacking *O. amphimone* larvae, while *Hyposoter* sp. considerably decreased its parasitism and *Apanteles* sp. was absent from our samples (Fig. 3). Parasitism by *Hyposoter* sp. varied markedly among groups of larvae ranging from 0 % to 96 %. *Hyposoter* sp. parasitized *O. amphimone* larvae as early as during their first instar (Fig. 3A) and larvae were typically killed during their fourth instar when the parasitoid pupated inside the mummified larva (Fig. 4A). However, we also observed individuals of *Hyposoter* sp. emerging from pupae of *O. amphimone*. Because *Hyposoter* sp. emergence from pupae was substantially lower compared to the emergence from fourth instar mummified larvae, we did not include these parasitized pupae in the analyses. *Hyposoter* sp. proved to be a solitary endoparasitoid, as only one adult (Fig. 4B) emerged per *O. amphimone* larva (or pupa). *Apanteles* sp., the rarest of the three documented parasitoids in our study area, parasitized *O. amphimone* larvae as early as in their third instar (Fig. 3B). Multiple larvae (ca. 15 to 25) of *Apanteles* sp. emerged from single *O. amphimone* larvae when these were in their

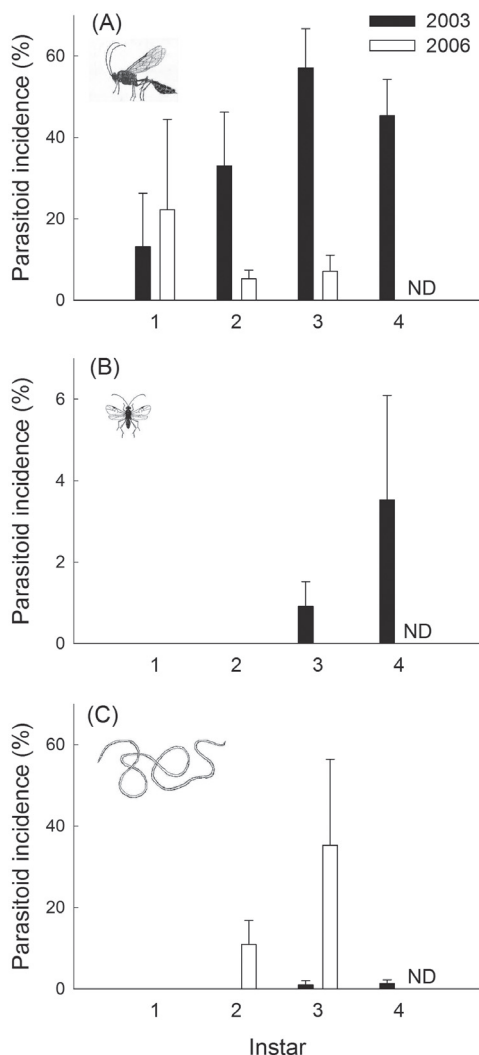


Fig. 3: (A) Mean ( $\pm$  SE) larval parasitism for groups of caterpillars collected in the field in their first to fourth instar in 2003 and 2006 caused by *Hyposoter* sp., (B) *Apanteles* sp., and (C) a nematode species. "ND" indicates that no data are available for that instar/year. Note the change in the scale of the axis for plot B.

(A) Parasitismo medio ( $\pm$  EE) larval por instar en 2003 y 2006 causado por *Hyposoter* sp., (B) *Apanteles* sp. y (C) la especie de nem  todo. "ND" indica que no existen datos disponibles sobre ese instar/a  o. N  tese la escala diferente del eje en el gr  fico B.

fifth instar, and each formed a silk cocoon to pupate attached to the body of the larva. The nematode species parasitized *O. amphimone* larvae as early as in their second instar (Fig. 3C) and emerged and killed the larvae during their third or fourth instar. Typically, one single nematode emerged per larva of *O. amphimone*, but in rare occasions we also recorded two individuals emerging from the same larva.

#### Bird predation on larvae

There was no significant difference in larval disappearance between groups of larvae on saplings with ( $9.4 \pm 2.3$  %) and without ( $12.8 \pm 4.7$  %) bird-proof mesh ( $t_{18} = 0.7$ ;  $P = 0.5$ ), which suggests that bird predation on *O. amphimone* larvae was not significant over the seven-day study period (Fig. 5).

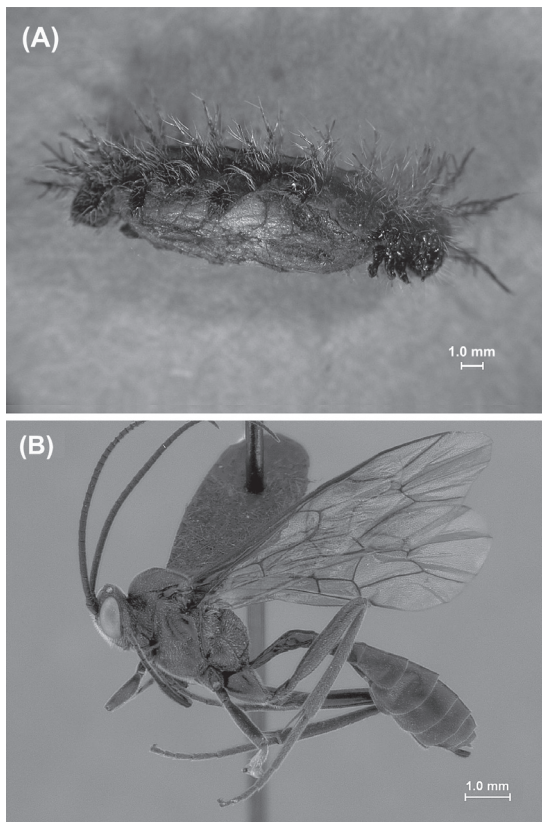


Fig. 4: (A) Mummified fourth instar larva of *O. amphimone* with a *Hyposoter* sp. pupa inside. (B) Adult specimen of the undescribed species of *Hyposoter*. Photo by D. Wahl.

(A) Larva momificada de *O. amphimone* (cuarto instar) con una pupa de *Hyposoter* sp. en su interior. (B) Individuo adulto de la especie no descrita de *Hyposoter*. Foto por D. Wahl.

#### Predation of pupae

Pupal predation was the highest compared with predation and parasitism in the egg and larval life stages. Nevertheless, pupal density did not significantly affect predation levels ( $t_7 = 0.9$ ;  $P = 0.4$ ) (Fig. 6). Most predated pupae were likely consumed by vertebrate predators because they disappeared leaving no remains (Frank 1967, Heissenwolf et al. 2010). We observed only four (i.e., 3 %) partially eaten pupae, which may have been predated by invertebrates. However, the significance of invertebrate predators is

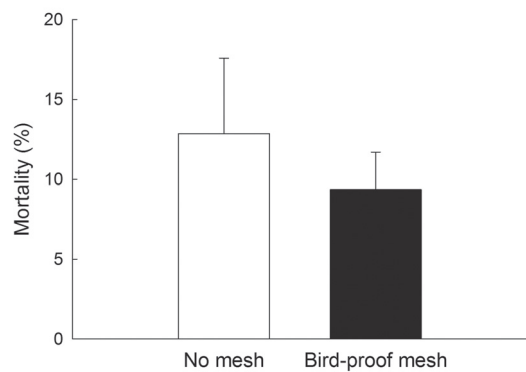


Fig. 5: Percent of mortality (mean  $\pm$  SE, estimated from larval disappearance) of larval groups on uncovered (no mesh) saplings and saplings covered with bird-proof mesh.

Porcentaje de mortalidad (media  $\pm$  EE, estimada de la desaparición de larvas) en grupos de larvas sobre renovales sin redes y con redes antipájaros.

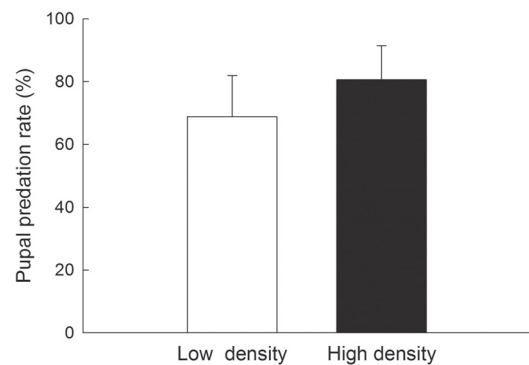


Fig. 6: Percent pupal predation (mean  $\pm$  SE) in the forest litter at low and high pupal densities.

Porcentaje de depredación de pupas (media  $\pm$  EE) en la hojarasca del bosque en densidades bajas y altas.

unknown because partially eaten pupae by invertebrates could have been subsequently consumed by vertebrates.

#### DISCUSSION

Our study constitutes the first quantitative assessment of mortality caused by natural enemies in an *Ormiscodes amphimone* population during endemic levels of abundance. The relatively high parasitism we recorded confirms previous qualitative observations indicating a high incidence of parasitoids on *Ormiscodes* populations (Silva 1917, Cogollor 2002). In addition, the high predation levels of pupae, a stage with possibly a much higher per capita reproductive value than earlier larval stages (Caswell 2001), suggests that pupal predation may also be important in regulating *O. amphimone* population dynamics.

Egg parasitoids are effective controls of herbivory because they kill larvae before these start damaging the host plant (e.g., *Trichogramma* spp; Smith 1996). Therefore, despite the relatively low levels of egg parasitism recorded here (ca. 11 %) egg parasitoids could regulate herbivory levels caused by *O. amphimone* in *N. pumilio* forests. In addition, a portion of the unhatched eggs could have also been parasitized by *Horismenus ancillus*, but the adult parasitoids failed to emerge, and thus egg parasitism may have been higher than what was observed here. Our preliminary data also suggest that egg parasitism follows an aggregated distribution pattern in which a few egg clusters are heavily parasitized while the majority suffers minimal or no parasitoid attack (Fig. 2B); however, a larger number of egg masses is needed to confirm this trend.

Larval parasitism was substantially higher than egg parasitism, but it was highly dependent on the timing (i.e., instar) that larvae were collected in the field. Collection of early instar larvae typically resulted in lower levels of parasitism than collection of more advanced instars (Fig. 3), most likely due to the shorter time period that larvae had been exposed to natural enemies in the field (Benrey & Denno 1997). In addition, parasitism by *Hyposoter* sp. and the nematode species documented for fourth instar larvae (Fig. 3) is likely underestimated given that these parasitoids

generally killed *O. amphimone* larvae during their fourth instar (and also third instar in the case of the nematode). Consequently, a considerable number of fourth instar larvae may have died due to parasitoid emergence before being collected in the field and therefore the proportion of parasitized fourth larvae in the field was probably higher than in our samples. These observations should be taken into account when quantifying larvae parasitism in *O. amphimone* populations, because collection of early (i.e., first and second) or late (i.e., fourth and fifth) instar larvae only, could result in underestimation of parasitism levels. Thus, based on our results, collecting third instar larvae should provide the most realistic estimates of larval parasitism in *O. amphimone* for the parasitoid species evaluated here.

Two of the three species documented here that parasitize *O. amphimone* larvae can be effective at decreasing herbivore damage in these forests. Both *Hyposoter* sp. and the mermithid nematode species typically killed larvae during the fourth instar at the latest. *Ormiscodes amphimone* larvae start increasing foliage consumption exponentially at their fourth instar. During the fourth and fifth instar, larvae consume ca. 90 % of the total foliage they consume over their lifespan (J. Paritsis, unpublished data). Therefore, the relatively high mortality caused by these natural enemies (i.e., ca. 50 % in third instar larvae, Fig. 3) in combination with the timing of parasitoid emergence implies that mortality caused by both species of natural enemies may have important implications in controlling levels of herbivory by *O. amphimone* in *N. pumilio* forests.

The substantial change in the relative abundances of parasitoids between years implies that the parasitoid community of *O. amphimone* is highly dynamic over time. Multiple causes may be responsible for the marked reduction in the parasitism incidence by *Hyposoter* sp. in 2006. First, climate variability and stochastic population fluctuations are well-known causes of changes in rates of parasitoid attack and may explain the observed variation in relative parasitoid abundance. Second, a low severity *O. amphimone* outbreak occurred during the 2001-2002 austral summer in the study area (i.e., two years before we collected the 2003 samples) (Paritsis et



al. 2009). Consequently, the relatively high *Hyposoter* sp. parasitism values recorded in 2003 could be associated with a post-epidemic (declining) population phase of *O. amphimone* and the values in 2006 may be more representative of an endemic population phase. Finally, the higher incidence of the nematode species in 2006 may have caused a failure of emergence of *Hyposoter* sp. The nematode species generally killed *O. amphimone* larvae earlier than *Hyposoter* sp., which may have caused a decline in successful emergence of *Hyposoter* sp. (Begon et al. 1997). This suggestion is reinforced by the observation that in 2006 five out of the six groups of larvae that were parasitized by *Hyposoter* sp. (with at least 5 % parasitism) were simultaneously parasitized by the nematode. Susceptibility of parasitic Hymenoptera to simultaneous use of the host with entomopathogenic nematodes is a well-known cause of parasitoid emergence failure in other host-parasitoid systems (Zaki et al. 1997, Lacey et al. 2003).

In contrast to parasitoids, birds did not exert significant predation pressure on second and third instar *O. amphimone* larvae. Previous studies conducted in our study area that evaluated the effect of birds on folivory by insect chewers on *N. pumilio* saplings showed contrasting trends. Studies by Mazía et al. (2004, 2009) found that bird exclusion over the entire growing season increased folivory, suggesting that birds may reduce populations of insect chewers such as *O. amphimone*; however, Garibaldi et al. (2010) did not find a significant effect of bird exclusion on folivory levels by insect chewers. It is likely that the potential contradiction in the role of birds as predators of *O. amphimone* larvae among studies (including ours) stems from the temporal variability of bird predation pressure. Furthermore, in our study some larvae may have dispersed during these early instars adding random variability to our dataset. Hence, further research assessing bird predation across all larval instars and over longer periods of time should provide more definitive answers regarding the role of birds as predators of *O. amphimone* larvae.

Predation on advanced life stages, such as pupae, has a crucial influence on population dynamics, given its immediacy to the reproductive stage (Caswell 2001). Predators of pupae can exert significant control of

forest Lepidoptera during endemic population phases maintaining populations at stable levels (Tanhuanpää et al. 1999, Liebhold et al. 2000). When generalist predators decrease predation pressure on pupae due to availability of alternative food items, lack of pupal predation could favor the onset of an outbreak, as has been suggested to occur with small mammal predators and the gypsy moth, *Lymantria dispar*, in North America (Liebhold et al. 2000). Consequently, predation of pupae may be a critical top-down control regulating outbreak dynamics of *O. amphimone*. The high levels of pupal predation documented in our study (i.e., > 70 %) warrants further research on the identity and food habits of the potential pupal predator species.

Despite the limited spatiotemporal extent of our study, this research constitutes a first step towards understanding the potential role of natural enemies in regulating populations of *O. amphimone*. Because the mechanisms responsible for *O. amphimone* outbreaks remain largely unknown, there is a need to explore how parasitoids and generalist predators (mainly of pupae) influence changes in *O. amphimone* populations. The high predation levels documented here suggest that natural enemies could be a key factor influencing outbreak dynamics of *O. amphimone*. The validity of our results, however, needs to be verified at spatiotemporal scales relevant to outbreak dynamics. Therefore, to better understand the dynamics in population fluctuations of this key herbivore in *Nothofagus* forests, future research should focus on assessing temporal variability in mortality due to multiple natural enemies attacking egg, larvae, pupae and adult stages across larger areas of the geographic distribution of *O. amphimone*.

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