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Phenology and Voltinism of *Paropsisterna cloelia* and *Paropsis charybdis* (Coleoptera: Chrysomelidae) in Temperate Maritime New Zealand

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ABSTRACT

The *Eucalyptus* variegated beetle (*Paropsisterna cloelia*) was established in New Zealand in 2016 and has caused substantial damage to selected host species. Previous field observations suggested that *Pst. cloelia* larvae may feed for a longer period during the year than the closely related *Eucalyptus* tortoise beetle (*Paropsis charybdis*), New Zealand's current most damaging eucalypt defoliator. Phenology and voltinism of these two invasive paropsine leaf beetles were quantified over two eucalypt growing seasons at two sites planted with *Eucalyptus bosistoana* in Marlborough, New Zealand. Results show that the availability of new foliage determined the voltinism and phenology of *P. charybdis* and *Pst. cloelia* and that the phenology of both species coincided at both field sites. As the availability of new leaves in spring and mid-summer prompts oviposition, both species had two generations at the site where trees produced new leaves in spring and mid-summer and one generation at the site where trees only produced new leaves in spring. Additionally, field observations indicate that both species have the potential for a third generation if the growing season is extended and trees produce new foliage three times. These conditions may be met in the Northland and coastal Bay of Plenty regions. Consequently, we conclude that *Pst. cloelia* does not produce more generations than *P. charybdis* and that larval activity coincided during the sampling seasons. *Pst. cloelia* is expected to spread throughout New Zealand over time and may become as damaging as *P. charybdis* on its preferred eucalypt hosts. We suggest future research to quantify phenology and voltinism of both species in warm/wet regions of New Zealand, to establish development models to inform pest management and to define host preferences for risk assessment.

1 | Introduction

Eucalypts were established in New Zealand more than 150 years ago (Poole et al. 2017). Although eucalypt plantations currently cover only ~22,000 ha or 1.3% of New Zealand's planted forest estate (New Zealand Forest Owners Association 2023), there are several economically important species grown for different purposes. *Eucalyptus nitens* currently covers the largest area (Radics et al. 2018). Although mainly used for short fibre pulp production (Miller et al. 1992), *E. nitens* has recently been considered

for solid wood (Lausberg et al. 1995) and engineered wood products (Gaunt et al. 2003). In the North Island, plantations of ash eucalypts (e.g., *Eucalyptus fastigata* and *Eucalyptus regnans*) are increasing for pulp production and carbon sequestration (Miller et al. 2000; Kennedy et al. 2011). Expansion of eucalypt forestry with other species to supply the domestic hardwood market is in progress (Millen et al. 2018).

Eucalypt-feeding insects have followed their host trees to new shores, and at least 36 eucalypt specialists have established

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in New Zealand to date (Weser et al. 2024). Paropsine leaf beetles or paropsines (Coleoptera: Chrysomelidae) are the most damaging group of eucalypt pests in Australian plantations (Elek and Wardlaw 2013). Seven eucalypt-defoliating paropsines have established in New Zealand to date: *Paropsis charybdis* Stål (Thomson 1922), *Trachymela sloanei* Blackburn (Withers 2001), *Trachymela catenata* Chapuis (Withers 2001), *Paropsisterna beata* (Newman) (Yamoah et al. 2016) (genus *Paropsisterna* hereafter abbreviated to *Pst.*), *Pst. cloelia* (Stål) (Rogan 2016), a third *Trachymela* Weise species (B. Rogan, personal communication) in the *tincticollis* group and most recently *Pst. morio* (Fabricius) (Ministry for Primary Industries 2024). *P. charybdis* was first detected in 1916 (Thomson 1922) and has spread nationwide (Bain and Kay 1989). *Pst. cloelia* was first detected in 2016 in the Hawke's Bay (North Island of New Zealand) (Rogan 2016; Lin et al. 2017). By 2025, it had been observed from the central North Island to the upper South Island, including Gisborne, Taupo, Hawke's Bay, Manawatu-Wanganui, Wellington, Nelson, Marlborough and north Canterbury (iNaturalist 2025b). The largely overlapping Australian distributions of *P. charybdis* and *Pst. cloelia* range from subtropical Queensland to cool temperate Tasmania (Styles 1970; De Little 1989; Nahrung et al. 2020; iNaturalist 2025b, 2025a), suggesting wide climatic tolerances for both species. Hence, climate is unlikely to limit *Pst. cloelia* spread throughout New Zealand.

Both *P. charybdis* and *Pst. cloelia* prefer eucalypts from the subgenus *Symphyomyrtus* (De Little 1979; Bain and Kay 1989). In Australia, *P. charybdis* only became a pest on eucalypts planted outside their natural range and is only considered problematic in a few areas (De Little 1989; Nahrung 2006). In New Zealand, it has caused the most damage of any paropsine throughout the country with repeated defoliation of preferred hosts, such as *E. nitens*, *Eucalyptus globulus* and *Eucalyptus camaldulensis*, leading to low establishment and reduced height growth of trees (Withers and Peters 2017). *Pst. cloelia* is regarded as a pest of various eucalypt species in several regions of Australia (i.e., Queensland, New South Wales, Victoria, South Australia, Western Australia and Tasmania) (Carne et al. 1974; Simmul and de Little 1999; Loch 2005; Nahrung 2006), which covers the species' entire current Australian distribution, including both the natural and invasive ranges. Its pest potential in New Zealand remains uncertain.

Oviposition strategies differ between paropsine species. *P. charybdis* oviposits egg batches on mature leaves adjacent to new leaves, but never on new flush leaves (Styles 1970; McGregor 1989), whereas *Pst. cloelia* lays egg batches directly on new flush leaves (De Little 1979). Like other paropsine species, larvae of *P. charybdis* and *Pst. cloelia* develop through four larval instars (L1–4) (Moore 1967). Only neonate larvae of *P. charybdis* feed gregariously (De Little 1979; McGregor 1989), whereas all larval instars of *Pst. cloelia* show aggregation behaviour and feed gregariously during the day (De Little 1979). Fourth-instar larvae of both species develop further into prepupae, drop from trees and pupate in earthen chambers or in leaf litter (Styles 1970; McGregor 1989; Elliott et al. 1998). Adult *P. charybdis* are sexually dimorphic, and males have darker-coloured elytra and are smaller than females (Steven 1973). *Pst. cloelia* adults change colour as they mature from red over green to brown (Weser, Withers, and Pawson 2025),

and there is a black/melanistic colour morph in eastern mainland Australia (Nahrung et al. 2020).

Development of paropsine life stages and phenology is highly dependent on temperature (Nahrung et al. 2004). Temperature-dependent development rates of all life stages can be quantified in laboratory trials, and the data can be used to build statistical phenology models that predict appearance, development and abundance of paropsine pests in the field (Nahrung et al. 2004; Nahrung et al. 2008; Lin 2017). Development starts at the minimum temperature threshold, from which development rates increase and peak at the optimum temperature and thereafter tend to decrease sharply towards the maximal temperature threshold, at which development ceases (Quinn 2017). Temperature development thresholds are species and life stage specific (Nahrung et al. 2004; Nahrung et al. 2008; Lin 2017). Development thresholds of *Pst. agricola* and *Paropsis atomaria* (Olivier) eggs are 8.6°C and 8.9°C, respectively (Nahrung et al. 2004; Nahrung et al. 2008), whereas *P. charybdis* and *T. catenata* (Chapuis) eggs have a lower threshold of 4.8°C and 5.0°C, respectively (Barrett 1998; Lin 2017), indicating adaptation to cooler climates. Development thresholds and temperature-dependent development rates for *Pst. cloelia* life stages have not yet been researched.

The full development of *P. charybdis* from egg to adult takes approximately 7–9 weeks in the field; however, this varies with eucalypt host species and temperature (Styles 1970). Studies of *P. charybdis* voltinism (number of generations per year) showed two generations per year in the central North Island of New Zealand (Styles 1970; McGregor 1989; Murphy and Kay 2000). McGregor (1989) predicted more than two generations in very warm climates; however, this has not been investigated. Lin (2017) reported one generation in two consecutive seasons at a dryland site in the upper South Island (Marlborough), most likely a result of limited food supply following severe summer droughts. *P. charybdis* is known to have generally one generation in cool temperate Southland and occasionally two generations if warm spring and late summer temperatures extend the eucalypt growing season (J. Rope, 2023, personal communication). However, *Pst. cloelia* phenology (timing and abundance of different life stages) and voltinism in New Zealand have not been studied. Larvae and adults of *Pst. cloelia* were observed on trees in the North Island later in the season than other paropsine species (Rogan 2016; Murray and McConnochie 2019), suggesting that *Pst. cloelia* may have a longer activity period during the year than *P. charybdis*. In Australia, the number of generations of *Pst. cloelia* varies depending on the climatic region: two generations in temperate climates (Australian Capital Territory and Tasmania) (P.B. Carne, unpublished data, as cited in De Little 1979; De Little 1979) and between two and possibly five generations in subtropical climates (SE Queensland and northern coast of New South Wales) (P.B. Carne, unpublished data, as cited in De Little 1979; Kent 1996 as cited in Elliott et al. 1998; Nahrung 2006). These observations suggest that *Pst. cloelia* will produce two generations in cooler regions of the South Island of New Zealand, three generations in the warmer central North Island and possibly more than three generations in the subtropical northern parts of the North Island.

Knowledge of *Pst. cloelia* phenology and voltinism in New Zealand will contribute to our understanding of the species' pest potential compared to *P. charybdis*. It informs the development of management strategies and is a precursor to the development of sustainable control methods (Nahrung and Allen 2004b). For example, the timing of insecticide application is essential to achieve the best results, as they are generally only effective against particular life stages (Herms 2004). Biological and natural more 'environmentally friendly' insecticides, such as *Bacillus thuringiensis* (Bt) and spinosad, are most effective at controlling early-instar larvae (Elek and Beveridge 1999; Carnegie et al. 2005). Phenological knowledge is also crucial in the selection of appropriate biological control agents, where success depends on a close phenological and ecological match between the target pest and its proposed biological control agent (Rowbottom et al. 2013; Gerard et al. 2021).

The aim of this study was to quantify and compare the phenology and voltinism of *Pst. cloelia* and *P. charybdis* in Marlborough under field conditions to answer the following two questions:

1. Does *Pst. cloelia* have more generations during a season compared to *P. charybdis*?
2. Does the timing of the different *Pst. cloelia* life stages coincide with that of *P. charybdis*?

2 | Methods

2.1 | Field Sites

Sampling occurred at two temperate maritime dryland sites planted with young *Eucalyptus bosistoana* in the Marlborough region in the upper South Island of New Zealand, where *Pst. cloelia* and *P. charybdis* were known to be present and cause damage. *Eucalyptus bosistoana* was selected as it is a known host for both paropsines (White 1973; Lin 2017; Murray and Kuwabara 2017). The Dillon site is an *E. bosistoana* clonal breeding trial planted in 25 blocks of 14×14m scattered in an area of approximately 48800m². It was established on ex-pasture land in 2018 in the Waihopai Valley, 27km SW of Blenheim (41°38'35" S, 173°40'26" E, 220m a.s.l.). The trial area consists of a flat part and a W-facing slope with a stream running through the length of the trial. The areas close to the stream become waterlogged in spring and after heavy rainfall. The blocks of the clonal trial are scattered in the flat part and along the bottom part of the slope. The entire ground is completely covered with thick vegetation consisting predominantly of long grasses. Willow trees and wetland vegetation grow in and along the stream. The clonal trial adjoins a demonstration trial planted in 2018 along the slope with blocks of *Eucalyptus quadrangulata*, *Eucalyptus cladocalyx*, *E. bosistoana*, *Eucalyptus macrorhyncha*, *Eucalyptus globoidea* and *Eucalyptus tricarpa* and is bordered by a gravel road, grazed paddocks with high grass cover and a planted pine forest. Estimated monthly average rainfall and temperature based on interpolations of long-term weather data (1991–2020) (Wratt et al. 2006) were provided by Earth Sciences New Zealand. The Dillon site has a mean annual rainfall of 672mm and a mean annual temperature of 11.9°C. The Lawson site is an *E. bosistoana* breeding trial that was planted in

150 blocks of 12×10.8m in an area of approximately 30700m², established on ex-pasture land in 2009 in the Awatere Valley, 6km SW of Seddon (41°43'13" S, 174°2'2" E, 140m a.s.l.). The trial was planted on a slope within a smaller N-facing and a larger E-facing part. Trees were randomly thinned within each block in 2020, and coppices growing from the cut stumps in the shelter of the canopy trees after the thinning operation were sampled as host trees. A few *E. quadrangulata* and *E. globoidea* were randomly interplanted throughout the trial. The canopy trees are >10m high and overshadow the ground; hence, the understory is extremely sparse except for the coppices, and ground cover is mostly absent with exposed, dry and compacted soil. The trial is bordered by a tar-sealed road, a vineyard and grazed paddocks with low grass cover. The Lawson site has a mean annual rainfall of 616mm and a mean annual temperature of 12.7°C and is slightly warmer and drier in comparison to the Dillon site in most months of the year (Wratt et al. 2006) (Figure 1).

2.2 | Sampling Design

During each of two consecutive sampling seasons (Season 1: 11 September 2021 to 29 March 2022; Season 2: 13 September 2022 to 28 March 2023), 15 assessments were conducted at 2-week intervals. Sampling covered the reproductive and larval developmental period of both paropsine species at both sampling sites and coincided with prior field observations in similar climatic regions from Australia and New Zealand (Ramsden and Elek 1998; Rogan 2016; Murray and McConnochie 2019). Field sampling finished in March each season, as no immature stages remained on the trees. In Season 1, sampling was conducted at the Dillon site (Dillon 1) only, and in Season 2, both the Dillon (Dillon 2) and Lawson sites (Lawson 2) were sampled. Ten different trees were sampled on each sampling date per site. At both sites, trees belong to genetic lines ('families') with a varying number of genetically related genotypes per family, and at the Dillon site, there are one or more genetically identical trees per genotype (clones). As paropsine defoliation varies by family (Mann 2023), trees were not chosen randomly throughout the site, but instead, 10 *E. bosistoana* families were chosen at each site along the full spectrum of defoliation (based on Mann 2023) to account for the variation in their resistance to defoliation. Trees of 1.6–3.0m height were selected for sampling. Due to the number of suitable trees available per family, only two of the 10 *E. bosistoana* families that were selected for sampling at Lawson corresponded with those assessed at the Dillon site. Trees at both sites were small enough to visually assess the canopy without having to cut branches. Families served as replicates. *E. bosistoana* trees per family were randomly assigned to sampling dates, resulting in 10 independent replicate samples for each sampling date and site. These were randomly distributed in the blocks.

2.3 | Phenology

Pst. cloelia egg batches and larvae and *P. charybdis* larvae can be found on new leaves, but *P. charybdis* egg batches are oviposited on mature leaves adjacent to new leaves (De Little 1979; McGregor 1989; Mo and Farrow 1993; Whyte 2012). Consequently, five easily accessible branches consisting of a branch section with 50 (±10%) new leaves,

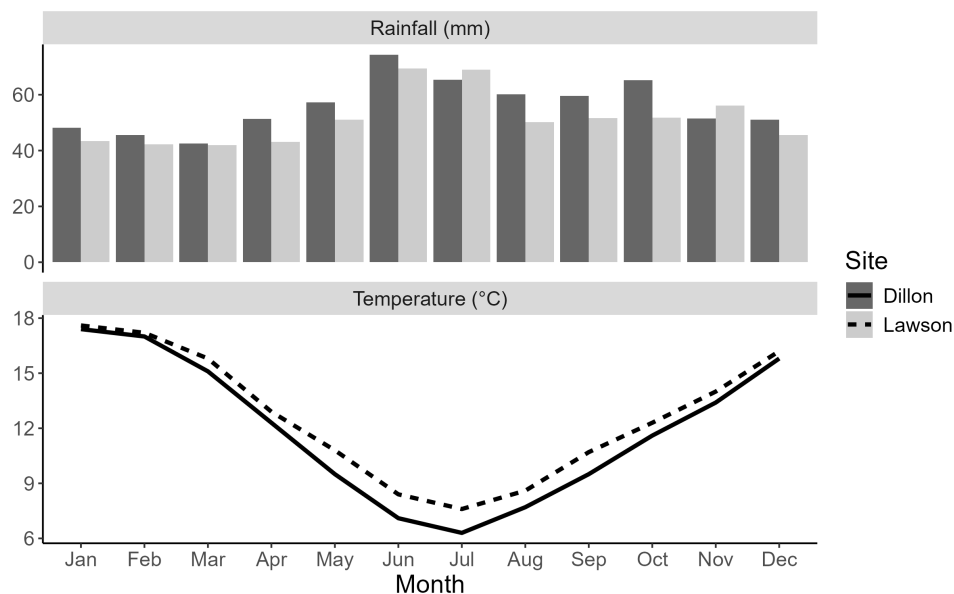


FIGURE 1 | Estimated monthly average temperature and rainfall based on interpolations of 30-year weather data (1991–2020) for the Dillon and Lawson sites (Wratt et al. 2006).

as well as an equivalent number of adjacent mature leaves, were sampled from the entire tree perimeter on each sampling tree. To ensure consistency, the number of leaves on each sample branch was counted at the first sampling date. During all following sampling dates, the number of leaves was counted on the first branch of each sampling tree to recalibrate the observer's eye to the appropriate branch section size. The number of egg batches and larvae of each paropsine species was counted and recorded on each sampling branch. Egg batches of the two species are easily distinguished. *P. charybdis* oviposits pale yellow-greenish eggs (~2.6 mm long) in two or three neat rows on the underside of mature leaves (Styles 1970; McGregor 1989). *Pst. cloelia* lays loosely aggregated or messy batches of bright yellow eggs (~2 mm long) exclusively on young leaves (De Little 1979). Only neonate larvae of both species look similar, but *Pst. cloelia* larvae can be distinguished as they are smaller than those of *P. charybdis* (Weser et al. 2024). Eggs and larvae of both paropsines co-occur on trees (L. Mann, 2022, personal communication); however, it is unknown if they oviposit on the same branch.

The first sampling confirmed that the disturbance drop reflex of adult paropsines prevented their accurate observation while counting larvae; hence, no adult counts are available from that date. Subsequently, adult abundance was quantified by shaking each sampling tree with a wooden stick over a beating tray for 1 min while traversing the tree perimeter. Adult maturity was evaluated by carefully compressing the elytra of both species with soft tweezers to test their rigidity. Adults were classed as 'teneral' (soft elytra, sexually immature) and 'hard' (hard elytra, sexually mature) (Nahrung and Allen 2004c). The presence of teneral beetles indicates the recent completion of one generation.

2.4 | Availability of New Leaves

New leaves were defined here as young, tender leaves that are still expanding in their lamina or have already expanded but

are still soft with a light green colour compared to older leaves. Availability of new leaves on the sampling branches was scored categorically by visual assessment as New Leaf Index (NLI) at four levels (0–3). Not expanded leaves were defined here as leaves just after bud burst that were not fully unfolded (still wrinkled) or small in size and still expanding in their lamina. Expanded leaves were fully unfolded and had expanded to a size suitable for oviposition (at least 1.5-cm length). Hence, the NLI levels describe the changes in new leaves visible on the trees, combining presence/absence, developmental stages (from bud to expanded leaf), expansion of leaf area and relative abundance of new leaves on the trees (% of branches bearing new leaves).

- 0 =. 0%–10% expanded leaves (no new leaves or mainly buds/not expanded leaves)
- 1 =. 11%–35% expanded leaves (some new leaves, ~25% of all new leaves already expanded/big enough for oviposition)
- 2 =. 36%–75% expanded leaves (more new leaves, most of them expanded)
- 3 =. > 75% expanded leaves (tree covered in new leaves, all expanded)

2.5 | Statistical Analysis

Data analysis was done with Bayesian mixed-effects models (GLMMs) using WinBUGS software (Lunn et al. 2000) and R package R2WinBUGS (Sturtz et al. 2005) in R (R Core Team 2023).

For each paropsine species, the number of egg batches and larvae per branch and adults (teneral and total) per tree were modelled per date and site. As is common when modelling counts, the number of organisms was assumed to have a Poisson distribution. Site and season were combined into a single categorical variable; hence, there are three site-season combinations (Dillon 1, Dillon 2 and Lawson 2) that map

directly on different dates, so that on each date, only one site was observed. The two species and three site-season combinations were used as fixed effects, and date, family, plot and tree were used as random effects. NLI classes on the trees were modelled using ordinal logistic regression. The class-specific cumulative probabilities were modelled as a function of calendar time with family, plot and tree as random effects. The dependence of *Pst. cloelia* eggs on the availability of new leaves (NLI) was modelled using a Bayesian GLMM with Poisson response. The abundance of *P. charybdis* was too low to be included in the analysis. NLI and the three site-season combinations were used as fixed effects, and date, family, plot, tree and branch were used as random effects. In all of the above models, the fixed effects were given a vague normal prior, whereas the random effects were all given vague normal priors with common precision parameters, which, in turn, were given vague gamma priors. See the [Supporting Information](#) for detailed model formulations and WinBUGS code. The results of the models were summarised by obtaining posterior means and 95% central credible intervals (CIs) for the parameters of interest. A Bayesian central credible interval is limited by the 2.5% and 97.5% percentiles of the posterior distribution and contains 95% of the posterior probability mass. In addition, for hypotheses of interest, posterior probabilities of a specific statement given the data can be calculated from the posterior distribution. These are sometimes referred to as Bayesian *p*-values. The higher they are, the likelier the statement is to be true. For all the models, a 5000 burn-in followed by 5000 iterations with no thinning were run. Convergence was visually assessed based on posterior densities and trace plots.

3 | Results

3.1 | Phenology

Paropsisterna cloelia was more abundant than *P. charybdis* in all life stages at both sites in both seasons on *E. bosistoana*. At the Dillon site, *Pst. cloelia* had three clear peaks of egg batches in Season 1 (Dillon 1) and one continuous peak stretching over mid-summer from late November to the end of January in Season 2 (Dillon 2). *P. charybdis* had two clear egg batch peaks in Season 1 and a third increase in egg batches at the end of the season. In Season 2, only one peak of egg batches could be observed (Figure 2). Both paropsines produced two coinciding clear larval peaks in both seasons, and *Pst. cloelia* showed a third low peak with some eggs developing into larvae at the end of Season 1 (March). Abundance peaks of *P. charybdis* were more obvious in the larval stages than in egg batches due to the species' low abundance. For both paropsine species, the start and end of the peak reproductive period (first egg peak to last larval peak) coincided but varied between the seasons. In Season 1, the first egg peak was recorded in mid-October and the last larval peak at the beginning of March. In Season 2, the continuous mid-summer egg peak started in late November, and the last larval peak occurred in mid-February. For *P. charybdis*, the second larval peak was lower than the first in both seasons, whereas *Pst. cloelia* larval peaks were equal in Season 1, and the second peak was higher than the first in Season 2. Adults ('Total adults') were present on the trees throughout both seasons and were higher at the beginning of Season 1 at

the Dillon site compared to the beginning of Season 2. Two more distinct peaks in teneral adults with soft elytra were observed for *Pst. cloelia* in Season 1 (end of December and beginning of March) and two indistinct peaks or one continuous peak in Season 2 (beginning of January to end of March). Teneral *P. charybdis* only peaked once in each season, simultaneously with the first peak of teneral *Pst. cloelia* (Figure 2).

At the Lawson site (Lawson 2), both paropsine species produced one egg and one larval peak. *Pst. cloelia* egg batches peaked at the end of September, 2 weeks earlier than at the Dillon site, and stayed high until the end of October. Larvae peaked from the end of October until the end of November. Only one *P. charybdis* egg batch was recorded at the end of October, and larvae were observed on the trees in very low numbers from mid-September until mid-December. No immature stages of either paropsine were found in the second half of the season after early January (Figure 2). At the beginning of the sampling season, the abundance of *Pst. cloelia* adults was higher than at the Dillon site. Adults of both paropsines were present on the trees throughout the season, but *P. charybdis* adults were only occasionally found. Teneral *Pst. cloelia* adults peaked in mid-December; one teneral adult was also found at the end of September, causing a small peak. *P. charybdis* teneral adults were never recorded at the Lawson site (Figure 2).

3.2 | Availability of New Leaves

At the Dillon site, production of new leaves started in Season 1 at the end of September and peaked three times with high probabilities of NLI Levels 2 and 3: the end of October, the end of January and the end of March. In Season 2, trees started to produce new leaves at the end of October, a month later than the year before, and kept growing until mid-December, when the new leaves score plateaued, and then started dropping again at the end of January to low NLI levels at the end of February. There was also a small increase in new leaves in late March during Season 2 (Figure 3). At the Lawson site in Season 2, new leaf availability was already high when sampling began in mid-September and continued until late October. New leaves decreased sharply in early November and declined consistently until January; thereafter, no new leaves were produced (Figure 3). The model shows that the expected number of *Pst. cloelia* egg batches was positively correlated with higher levels of the NLI (Figure 4). Overall, the posterior probability that the expected number of *Pst. cloelia* egg batches, N , increases with the level of NLI ($\Pr(N_{NLI=0} \leq N_{NLI=1} \leq N_{NLI=2} \leq N_{NLI=3})$) by site and season is 0.7722 for Dillon 1, 0.9978 for Dillon 2 and 0.9780 for Lawson 2.

4 | Discussion

Our results show that voltinism and phenology are driven by the availability of new leaves on trees, which is a precursor to oviposition by *Pst. cloelia* and *P. charybdis*. Both paropsine species produced one generation at sites where trees only produced new leaves once during the summer, two generations at sites where trees produced new leaves twice and may produce three generations at sites that produce three cohorts of new leaves over the summer.

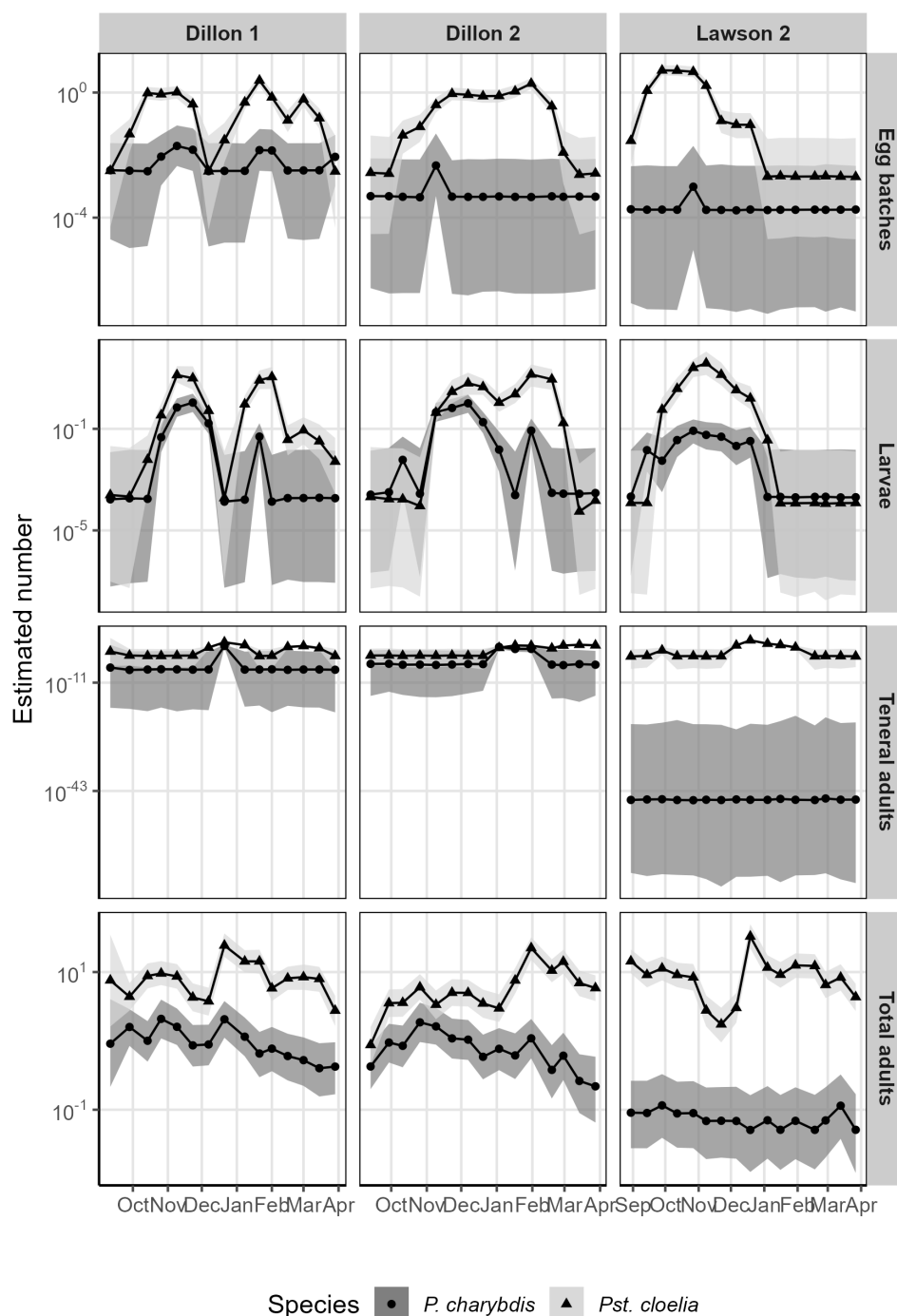


FIGURE 2 | Estimated counts of life stages and 95% credible intervals for *Pst. cloelia* and *P. charybdis* over two sampling seasons at the Dillon site and one season at the Lawson site. *Note:* Estimated numbers of all life stages are displayed on the log10 scale to show the low abundance peaks of *P. charybdis*.

At the cooler, wetter Dillon site, *Pst. cloelia* successfully completed two clear generations in Season 1 (Dillon 1), indicated by two clear peaks of immature stages (i.e., egg batches and larval stages) and soft teneral beetles. The second generation finished in autumn. It is possible that two generations were also produced in Season 2 (Dillon 2); however, this assumption was only supported by the two clear larval peaks, whereas egg batches only showed one continuous peak and teneral adults showed one continuous peak or two indistinct peaks. We hypothesise that the second generation seamlessly merged into the first generation because the continuous availability of new leaves

during the middle of Season 2 triggered steady egg production. Additionally, it cannot be confirmed whether *P. charybdis* also completed two full generations at the Dillon site in either season, as there was only one egg peak recorded in Season 2, and in both seasons, soft teneral adults were only found on the trees after the first, but not the second larval peaks that would mark the completion of the second generation. It is possible that the few second-generation teneral beetles had already dispersed to other eucalypt trees or had matured and their elytra hardened at the next sampling, making them indistinguishable from mature beetles. It has been observed in *Pst. agricola* that soft

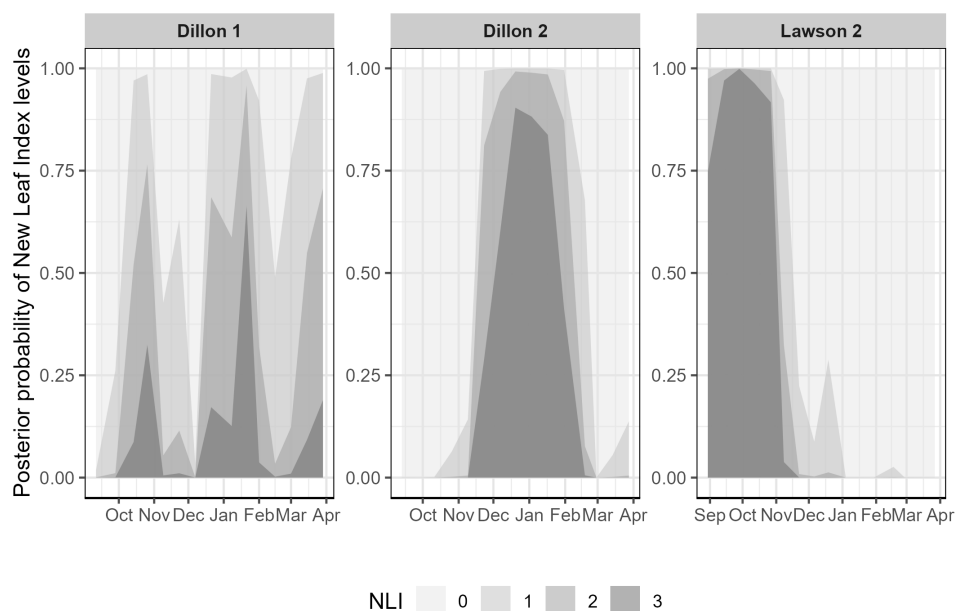


FIGURE 3 | Cumulative posterior probability of New Leaf Index (NLI) levels over two sampling seasons at the Dillon site and one season at the Lawson site.

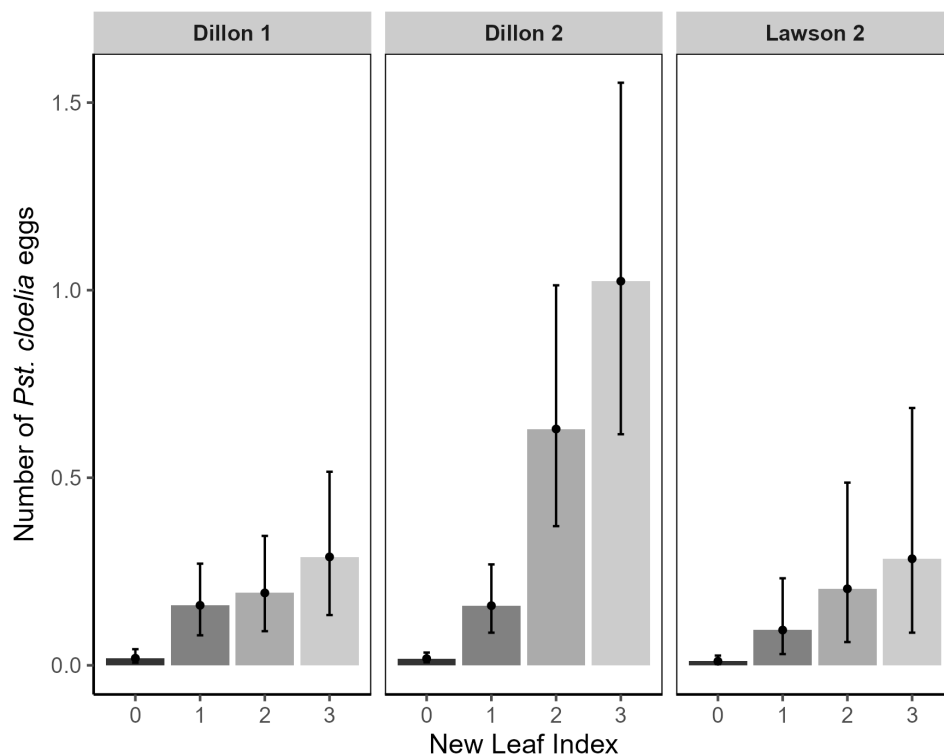


FIGURE 4 | Posterior estimated expected number of *Pst. cloelia* eggs at different levels of New Leaf Index.

elytra of teneral beetles harden within 2 weeks (Seeman and Nahrung 2004), and this could be similar in other paropsines. At the warmer, drier Lawson site in Season 2 (Lawson 2), there was only one generation of *Pst. cloelia* and *P. charybdis* due to the lack of new leaves in the second half of the season, with flushing likely being prohibited by water limitation from the summer drought. Consequently, no new oviposition sites were available for first-generation paropsine adults. Lin (2017) also reported one generation of *P. charybdis* in two consecutive field seasons

(2015/2016 and 2016/2017) at another dryland eucalypt site in Marlborough near Lake Grassmere (41°44'11" S, 174°07'19" E), 10 km from Lawson, which was attributed to summer droughts. *P. charybdis* generally has one generation in cool temperate sites in Southland with cold spring and late-summer temperatures that restrict new leaf availability and larval survival (J. Rope, 2023, personal communication). Occasionally, there are two generations of *P. charybdis* at Southland sites when spring (and late summer) temperatures are warmer than average and

emergence of overwintering adults and new leaf production starts earlier (J. Rope, 2023, personal communication). The start of a third generation was observed at the Dillon site with an increase in *Pst. cloelia* and *P. charybdis* egg batches when more new leaves were produced at the end of Season 1. This suggests that three paropsine generations may be possible in warmer and wetter regions, such as Northland and the coastal Bay of Plenty, with longer periods of tree growth stimulating a third cohort of new leaves later in the season. However, this needs to be confirmed by consistent field sampling. Along the coast of northern New South Wales in Australia, *Pst. cloelia* is known to complete at least three generations per year (De Little 1979; Elliott et al. 1998). However, the pattern of new leaf production in this region and the link to *Pst. cloelia* voltinism has not been recorded.

High availability of new leaves in spring stimulates the early onset of oviposition, whereas low availability of new leaves delays the onset of oviposition. This was observed both when comparing Season 1 with Season 2 at Dillon, and Dillon with Lawson in Season 2. At Dillon in Season 1, the availability of new leaves and the abundance of overwintering adults was higher at the beginning of the sampling season, and oviposition of the first paropsine generation was advanced by almost 1 month compared to Season 2. Paropsine adults overwinter under loose bark and emerge in spring for feeding on new foliage before they start oviposition (Selman 1994; Nahrung and Allen 2004a). The late onset of new leaves and continuous production of new leaves during Season 2 at the Dillon site resulted in one long period of oviposition and larval presence from late November until the end of January. Lawson is a warmer site compared to Dillon; hence, at the beginning of sampling in mid-September in Season 2, there were already abundant new leaves on the trees, and a high abundance of overwintering adults had already emerged. This stimulated oviposition a month before Dillon and supported a large number of *Pst. cloelia* immatures and teneral adults (although the vastness in numbers is not immediately visible in Figure 2 due to the log scale). Conversely, at Dillon during Season 2, the later production of new leaves delayed oviposition of the first generation by almost 1 month compared to Season 1. Additionally, the low availability of new leaves in late summer did not facilitate a third oviposition period that was observed in Season 1. Carne (1966) also observed variations in the phenology of *P. atomaria* between seasons and sites due to a lack of new leaves as a result of severe defoliation from the first generation. Similar to the observations in the present study, Carne noticed that the initiation of oviposition shifted by approximately 1 month due to new leaf availability.

Previous field observations in the North Island led to the assumption that *Pst. cloelia* has a longer larval feeding period in the field compared to *P. charybdis*, possibly resulting in greater defoliation (Rogan 2016; Murray and McConnochie 2019). Contrary to this, our study found that the larval feeding period and phenology (egg and larval peaks) of *Pst. cloelia* and *P. charybdis* at the Dillon site were synchronous. Phenological synchrony could not be assessed at Lawson, as *P. charybdis* was practically absent.

At the Dillon site in Season 1, second-generation egg batch and larval peaks of *Pst. cloelia* were higher or equal compared to the first-generation peaks. However, for *P. charybdis*,

a second-generation egg peak was not observed in Season 2, and second-generation larval peaks were lower than first-generation peaks in both seasons. Increased mortality due to the activity of natural enemies, such as predators and parasitoids, is a plausible explanation. For *P. charybdis*, the two egg parasitoids *Enoggera nassau* and *Neopolycystus insectifurax* (both Hymenoptera: Pteromalidae) may have led to increased mortality of second-generation eggs in each season, as they can reach high parasitism rates of 70%–100% in the second generation in eucalypt plantations in the North and South Islands (Jones and Withers 2003; Mansfield et al. 2011; Weser, Davy, et al. 2025). Parasitism rates of *Pst. cloelia* in the field are generally low (Weser, Davy, et al. 2025). Moreover, several predatory arthropods feed on paropsines in Marlborough (Weser, Dhimi, et al. 2025) and could have had a noticeable decimating effect on the low numbers of *P. charybdis* on the *E. bosistoana* trees. Although the identity of arthropod predators has been identified (Weser, Dhimi, et al. 2025), their impact on paropsine populations has not yet been quantified.

Besides the availability of food sources, paropsine phenology is dependent on temperature (Nahrung et al. 2004). Future research should determine temperature-dependent developmental requirements and development rates of all life stages in laboratory trials and use the data to build phenology models that predict the appearance, development and abundance of *Pst. cloelia* in the field (Nahrung et al. 2004; Nahrung et al. 2008; Lin 2017). Such models are excellent integrated pest management tools for forest managers to predict the timing and abundance of the damaging larval stages, inform the timing of population monitoring in the field and estimate the risk of damage to make decisions on pest control operations (Candy 1999). Moreover, laboratory oviposition and feeding trials can identify *Pst. cloelia* host preferences and determine foliage consumption (De Little and Madden 1976; Nahrung 2004), which can help estimate the pest potential of the species.

In summary, we showed that voltinism and phenology of *Pst. cloelia* and *P. charybdis* depend on the timing of new leaves on the trees. Both paropsine species produce two generations with coinciding peaks of life stages at wetter temperate sites, are restricted to one generation at sites with summer drought and may have the potential to create a third generation in sites where the length of the growing season is extended and moisture does not limit a third cohort of new leaves. Abundance peaks of *Pst. cloelia* and *P. charybdis* life stages coincided. It can therefore be concluded that *Pst. cloelia* larvae do not feed for a longer period in the field and that *Pst. cloelia* does not produce more generations than *P. charybdis* in the temperate maritime region of Marlborough. Despite growing knowledge, considerable information gaps remain regarding *Pst. cloelia*'s potential impacts. Investigating *P. charybdis* performance and its potential to produce three generations in the warm and wet regions of New Zealand, for example, Northland, would give an indication of how many generations *Pst. cloelia* may have in these regions once it arrives there. *Pst. cloelia* phenology should be monitored once its distribution reaches the subtropical parts of the northern North Island. *Pst. cloelia* is expected to spread throughout New Zealand over time and may become as damaging as *P. charybdis* on its most preferred eucalypt hosts. Moreover, *Pst. cloelia* may be capable of higher population outbreaks than *P. charybdis*.

owing to its high reproductive output and advantageous life strategies; however, this remains a subject for future research. Laboratory trials can be used to build phenological models, estimate the pest potential of *Pst. cloelia* and guide decision-making for monitoring and control operations.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Our datasets are available on the Figshare data repository under <https://doi.org/10.6084/m9.figshare.30768221>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.