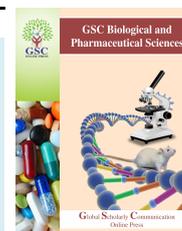


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(RESEARCH ARTICLE)



Quantitative analysis of the causes of outbreaks in leaf-mining insects: application to the common leaf-miner *Leucoptera malifoliella* (Lepidoptera: Lyonetiidae) on apple tree

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Abstract

Leaf-mining by insects usually have limited detrimental consequences on host-trees. Yet, *Leucoptera malifoliella*, a common leaf-mining moth on Rosaceae, is among those leaf-mining species that can exhibit occasional, sometimes even regular eruptive impacts on their hosts, in particular on apple trees. Here, we address the different causes involved in a particular case of nascent outbreak of this moth observed in the wild that is independently of the artificial conditions that prevail in densely planted apple orchards. Relevantly analyzing the reasons of eruptive outbreaks remains difficult however, as multiple causes are involved and their respective influences on mining-impact level are largely intermingled. Thus, in order to disentangle the respective contributions of each cause in quantitative terms, a specifically dedicated approach, the “Melba” procedure, was implemented and applied to the data issued from an exhaustive sampling of the foliage of the studied wild apple-tree. Out of the three main causal components of mining impact level, neither the average clutch-size nor the severity of mated females in selecting those leaves acceptable for oviposition substantially differ from the ranges of values encountered in other leaf-mining species having high but non-eruptive mining impacts on their respective hosts. In fact, the recorded nascent outbreak is mainly attributable to the unusually high density of mated females attracted to the investigated host tree. Accordingly, metapopulation effects obviously play a major role in triggering the recorded eruptive impact.

Keywords: Leaf-mining moth; *Leucoptera malifoliella*; *Malus*; Mining impact; Leaf selectivity; Metapopulation

1. Introduction

The impact of leaf-mining insects on their host-trees (in term of the average number of mines per leaf) may vary over quite a large range, from vanishing level up to eruptive outburst [1] and, in the latter case, may have significant consequences of practical concern.

Several types of causal factors govern together the pattern of mines distribution among host-leaves, the resulting level of insect incidence and its variations in space and time. In particular, quantitative aspects of ovipositing mothers' behaviour prior to egg-laying and their local density within the host canopy are explicitly involved in determining the level of incidence and impact of leaf-mining, as detailed below [2-5].

In leaf-mining insects, ovipositing mothers actively search, at first, for individuals belonging to the proper host species and then, having reached the foliage of the host, they seek for the most convenient host-leaves to be egg-laid. To this end, mothers actively visit and probe host-leaves, prior to egg-laying, in order to assess their respective level of quality and ultimately select those leaves only that meet their own minimum requirements (the latter intended to

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mirror, more or less tightly, the future needs of larvae - beyond the prime necessity of developing upon the appropriate host-species [3-4, 6]). Schematically, the impact of mines upon host-leaves depends upon:

- The average number of mothers probing visits (μ) received per host leaf, directly related to the density of mothers within the host canopy ([*]: see Appendix 1)
- The proportion (α) of leaves of the selected host which would be considered acceptable for egg-laying by mothers, i.e. which satisfy mothers' requirements; this proportion hereafter designed as "leaf acceptability ratio", varies according to the average foliar quality of the host ([**]: see appendix 1)
- The mine clutch-size (n_c), is defined as the average number of mines actually resulting from the hatching of one clutch of eggs (eggs deposited as a single bout after one mother visit to an acceptable leaf [***]: see Appendix 1).

Yet, each of these three causal parameters is very difficult to quantify in the field, for such tiny insects as those usually involved in leaf-mining. Moreover, this quantification becomes even impossible later, *a posteriori*, when the mining impact has become clearly evident and call for the attention of the researcher. This is why a detailed, quantitative analysis of the actual causes of a particular mining outbreak actually encounters so strong difficulties.

To overcome this obstacle, an efficient way is to trace back from the resulting, as-recorded mining-impact pattern to the causal factors ' μ ', ' α ', ' n_c '. This way has now become practicable, using a recently derived procedure [4-5, 7-8] which allows accurate estimates of parameters ' μ ', ' α ', ' n_c ', retrospectively. Thus, the respective contributions of (i) the mothers' density of visits μ , (ii) the leaf-acceptability ratio α and (iii) the mine clutch-size n_c may be adequately disentangled, thereby casting new light upon what actually makes the mining impact of a given insect either high or low, according to sites or years.

In the following, we implement this procedure to investigate about the causes involved in the particular case of a localised eruptive occurrence of a leaf-mining moth, *Leucoptera malifoliella* (Costa) belonging to order Lepidoptera and family Lyonetiidae, which commonly occurs on apple trees (*Malus sylvestris* Miller). Specifically, we ask whether this nascent outbreak may result:

- From values of the parameters ' α ' and/or ' n_c ' that would be significantly larger than usually encountered in the system $\{L. malifoliella \text{ and } M. sylvestris\}$, as a consequence of either the *insect behaviour* (that is: n_c and α pro parte) or the average quality of host-foliage (that is: α pro parte);
- From an exceptionally high value of the density ' μ ' of mothers' probing visits to host leaves, resulting from a correspondingly unusually high local density of mated females within host-canopy.

For this purpose, the derived values of parameters α , n_c , μ , are compared to the corresponding values of these parameters in a series of non-eruptive stands with levels of mining impact no more than one mine per leaf on average [1]. Brief information on the natural history of *Leucoptera malifoliella* is provided in Appendix 2.

2. Material and methods

2.1. The procedure implemented for the retrospective estimations of parameters α , n_c , μ

As mentioned above, the evaluations of the driving parameters α , n_c , μ face important practical difficulties, since none of these parameters is easily observable directly in the field, especially considering such tiny insects as leaf-miners. Moreover, at the moment when the mining impact level has sufficiently progressed to be recorded, the time for monitoring the parameters α , n_c , μ , has already passed for long.

Accordingly, a specific method, the "Melba procedure" was formerly derived so as to overcome these difficulties. This procedure provides indirect estimations of α , n_c and μ , on the only basis of field observations that may be easily recorded when the mines have developed: namely, the distribution $\Pi(\eta)$ of the number of leaves according to the number η of mines they support, as recorded within a sampled portion of canopy.

In short [see the references 4-5, 7-8 for full details], the "Melba" procedure relates the hard-to-observe parameters α and n_c to the resulting, easily field-recorded distribution $\Pi(\eta)$. The procedure is based on the fact that, thanks to commonly accepted assumptions [4-5], the distribution $\Pi(\eta)$ should theoretically answer a specific equation with the adaptable parameters such as α and n_c . Conversely, the inferred values for α and n_c are those that yield the best fit between the recorded distribution $\Pi(\eta)$ and the corresponding theoretical distributions $\Pi(\eta)$, parameterised in terms

of α and n_c . After that, the inferred value of parameter μ is immediately derived from α and n_c [4-5]. Note that, here, the recorded data implemented in the “Melba” procedure involves the distribution, $\Pi(\eta)$, of *mines* instead of eggs, as already mentioned above. Accordingly, the resulting estimated clutch-size n_c represents the “mines clutch-size”, i.e. the number of mines resulting from the (more or less complete) hatching of the corresponding eggs-clutch [4-5]. Indeed, in term of mining impact, it is well the resulting “mines clutch-size” (rather than the eggs clutch size) which contributes to rule the mining impact level ([***]: see appendix 1).

The proportion ‘ ε ’ of actually exploited leaves within the subset of potentially acceptable host-leaves and the average number ‘ v ’ of clutches per occupied leaf are subsequently derived from the evaluations of α , n_c and μ : $\varepsilon = 1 - \exp(-\mu)$ and $v = \mu / (1 - \exp(-\mu))$ [5].

Now, for practical purpose, two indices relevantly account for two complementary aspects of the mining impact *sensulato* (Figure 1):

- The impact ‘*stricto-sensu*’, defined as the average number ‘**I**’ of mines per leaf, which depends multiplicatively upon the three preceding factors:

$$I = \alpha \cdot n_c \cdot \mu$$

- The incidence ‘**i**’, defined as the proportion of mined host-leaves [5]:

$$i = \alpha \cdot \varepsilon = \alpha \cdot (1 - \exp(-\mu))$$

In short, within the set of available host-leaves, only a fraction α (the leaf acceptance ratio) meets mothers’ requirements. In turn, only a fraction ε of the set of displayed leaves is actually visited and probed by ovipositing mothers and, accordingly, the same fraction ε only of the sub-set of potentially acceptable host-leaves is actually exploited, i.e. mined or galled. The complementary fractions, $(1-\alpha)$ and $(1-\varepsilon)$ account for the ‘bottom-up’ and the ‘horizontal’ + ‘top-down’ constraints, respectively.

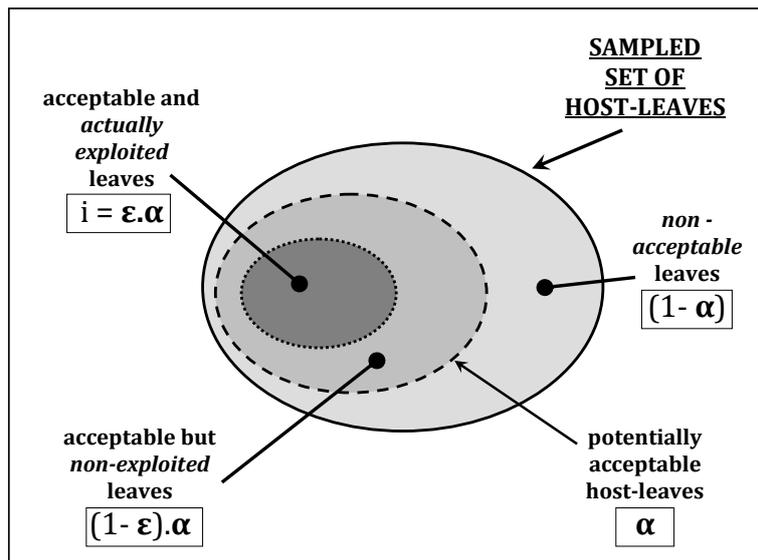


Figure 1 A sketch showing schematically the process and pattern of preliminary probing and subsequent egg-laying upon host-leaves by ovipositing mothers in leaf-mining (or leaf-galling) insects.

The clutch-size n_c proves to be independent of leaf-acceptance ratio α , and, in addition, both α and n_c vary independently of μ and, thus, feature insensitive to local mothers’ density [4, 9-10]. Accordingly, any given level of mining impact may thus result from a virtually infinite variety of combinations of values of α , n_c , μ . This makes the causal interpretation (in quantitative terms) of a given level of impact so far from being straightforward.

Thus, trying to disentangle and quantify the respective contributions to the level of mining impact of each of the three governing factors α , n_c , μ is a prerequisite for a fruitful causal analysis of the reasons which make the mining impact on the host either weak, medium, strong or, even, reaching outbreak levels.

2.2. The field recorded stands

The data for *Leucoptera malifoliella* was obtained by sampling the whole canopy of a young wild apple tree (*Malus sylvestris*), included within a grove hedgerow near the city of Le Creusot (Centre of France, southern Burgundy). A total of 638 leaves were examined for mining occurrence, among which 326 leaves were actually mined by *L. malifoliella* for a total of 806 mono-occupied mines, that is:

- An incidence level (proportion of mined leaves): $i = 51\%$ and
- An impact level (average density of mines per leaf): $I = 1.27$,

Both values above correspond to a nascent outbreak, according to the criteria proposed by Auerbach et al. [1]. These levels of impact are far beyond the usual, quite lower impacts of *L. malifoliella*, with incidence levels that most often do not exceed one or of a few per cent (personal observation). At so low levels, however, it becomes difficult to derive statistically significant evaluations of α , n_c , μ [5]. This is why, for the purpose of comparisons, we considered another mining insect that frequently provides higher rates of mining impacts. Accordingly, we considered, for comparison, a series of 22, non-eruptive, stands of the mining moth *Phyllonorycter maestingella* (Müller), commonly mining the leaves of beech trees *Fagus sylvatica* L.. These 22 non-eruptive stands of *Phyllonorycter maestingella* were selected from a large survey of several hundred stands located in the centre of France, retaining those stands only reaching impact levels comprised between 0.1 and 0.9 mine per leaf on average, that is approaching but never reaching the eruptive threshold of 1.0 mine per leaf on average.

3. Results

Estimates of the leaf acceptance ratio α , the mine clutch-size n_c and the average number μ of mothers probing visits per leaf, derived from using the “Melba” procedure, are given at Table 1 and Figures 2 and 3, with their associated 95% confidence domains. For the purpose of comparison with the nascent eruptive situation under study (1.27 mine per leaf), Figures 2 and 3 provide the estimates of α , n_c and μ obtained from the 22 non-eruptive stands of *P. maestingella* mentioned above, with impact values comprised in a wide range, between 0.1 and 0.9 mine per leaf.

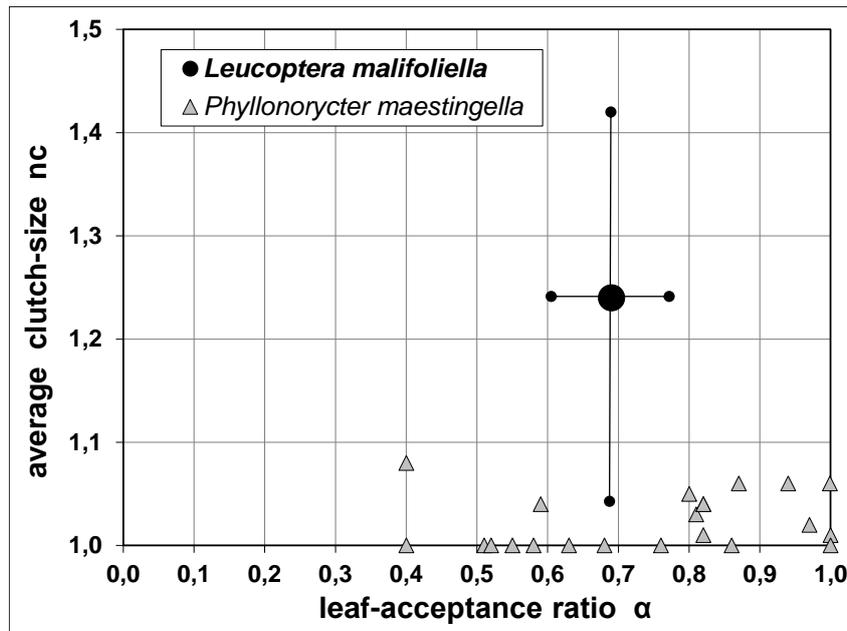


Figure 2 Estimates of the leaf-acceptance ratio α and the average clutch-size n_c for (i) the studied sample of *Leucoptera malifoliella* (with their 95% confidence domains) and for (ii) 22 non-eruptive stands of *Phyllonorycter maestingella*.

Table 1 Estimates and the limits of the 95% confidence domains for α , n_c , μ and ε for the studied stand of *Leucoptera malifoliella*

Parameters	Estimates	95% confidence domains
α	0.69	0.62 - 0.76
n_c	1.24	1.07 - 1.40
μ	1.48	1.17 - 1.90
ε	0,77	0.69 - 0.85

α - the leaf-acceptance ratio, n_c -the average mines clutch-size, μ - the average number of mothers probing visits per leaf and ε - the exploitation ratio

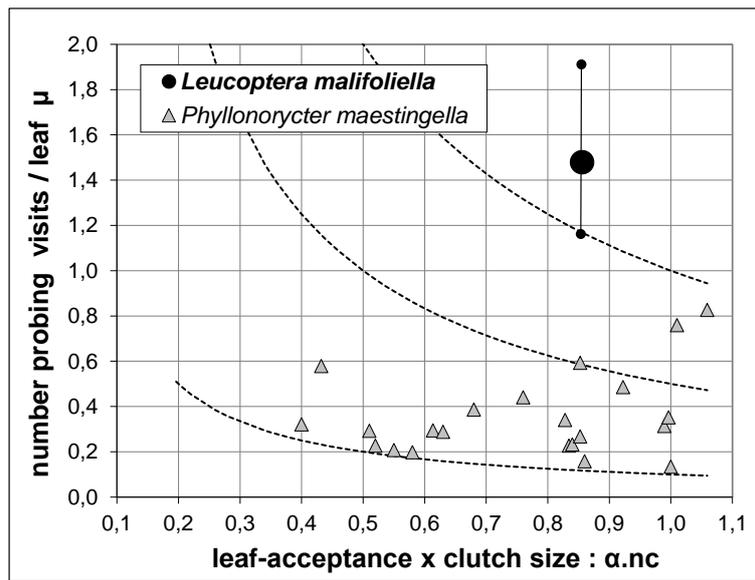


Figure 3 Estimates of the number μ of mothers' probing visits per leaf, plotted against the product $\alpha.n_c$ of the leaf-acceptance ratio times the average clutch-size(i) for the studied sample of *Leucoptera malifoliella* (with the 95% confidence domain) and (ii) for 22 non-eruptive stands of *Phyllonorycter maestingella*. Also depicted are the curves of iso-impact levels $I = \alpha.n_c.\mu = 0.1, 0.5, 1.0$ mines per leaf: dashed curves.

4. Discussion

L. malifoliella, is a common leaf-mining moth which occurs on many trees and shrubs belonging to Rosaceae, especially apple trees. Mining impact by this species may occasionally and locally reach outbreak levels, the origins of which yet remain to be clearly and quantitatively understood. Three driving factors, (i) the local density of ovipositing mothers in term of the number ' μ ' of their probing visits per host leaf, (ii) the proportion ' α ' of host-leaves that meet mothers requirements and are thus acceptable for egg-laying and (iii) the mines clutch-size ' n_c ', are involved multiplicatively in determining the levels of mining impact ' $I = \mu.\alpha.n_c$ ' and mining incidence ' $i = \alpha.\varepsilon = \alpha.(1-\exp(-\mu))$ '.

Disentangling the respective contributions of each of these three parameters is thus a prerequisite to understand the causes of the occasional strong outbreaks by *L. malifoliella* (as is the case also in some other mining species: Auerbach et al. [1]).

In the nascent outbreak of *L. malifoliella* studied here, the major aim was to discover which, among of the three driving parameters μ , α , n_c , actually singularise(s) specifically when the comparison is made with non-eruptive stands of either that species or other leaf-mining species (here *P. maestingella*) The results above (Figures 2, 3 and 4), show that:

- The leaf-acceptability ratio α of *L. malifoliella* falls within the typical range of values estimated for the non-eruptive stands of *P. maestingella*;
- The average mines clutch-size n_c of *L. malifoliella* is only slightly (and just significantly) greater than for *P. maestingella*.

In fact, it is the average density μ of mothers' probing visits to host-leaves, reflecting the local density of mated mothers in the host canopy, which mainly contribute, here, to the nascent outbreak of *L. malifoliella*: the estimated value of μ for *L. malifoliella* clearly exceeds all the corresponding values for *P. maestingella* stands, at the $p=0.05$ level of statistical significance (Figures 3 and 4). In other words, here, the nascent outbreak of *L. malifoliella* is not principally related to an especially high acceptability of the host-leaves nor to a particularly "prolific" egg-laying behaviour of mothers (which would have contribute together to higher values of α and/or n_c) but mainly results from an environmental factor: the high local density of ovipositing mothers in the host-canopy.

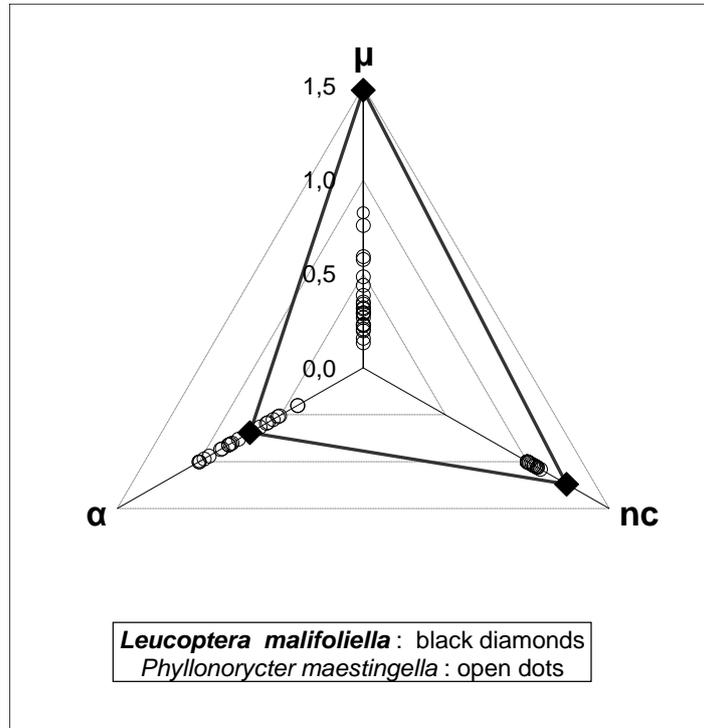


Figure 4 Synthetic sketch: the three parameters, α , n_c , μ , controlling the level of leaf-mining impact [plotted comparatively for the studied eruptive stand of *L. malifoliella* ($I = 1.27$ mines per leaf) and for a series of 22 non-eruptive stands of *P. maestingella* ($I = 0.1$ to 0.9 mines per leaf). For the eruptive stand of *L. malifoliella*, α is well inside the range, n_c is just a little beyond the range and μ is strongly beyond the range of the corresponding values of these parameters in the non-eruptive stands of *P. maestingella*]

This, indeed, is in line with results derived previously for the highly eruptive leaf-miner *Cameraria ohridella*: in this highly invasive species, the extremely high density of ovipositing mothers is the decisive (although non unique) cause of the massive and regular outbreaks of this pest [7, 11]. Such exceptionally high levels of mothers' density are resulting, in turn, from the lack of efficient top-down control by parasitoids. Note, incidentally, that the trend for clutch-sizes substantially exceeding unity in outbreak-generating insects [12] is not verified for *L. malifoliella* (nor for *Cameraria ohridella* [11]).

Now, the impact of *L. malifoliella* may exceptionally rise still beyond the nascent eruptive level considered here, and reach plain outbreak levels, thus becoming a pest of economic importance in apple-fruit producing regions throughout much of Europe and Asia, reducing photosynthetic area, and, consequently, fruit quantity and quality [13-14].

Considering this issue and using the "Melba procedure" as a modelling tool, it is possible to approximately forecast what would likely happen, in term of process, when the local density of mothers (and the resulting density μ of mothers probing visits to leaves) grows continuously. At first, it should be kept in mind that both the leaf-acceptance ratio α and the clutch-size n_c were demonstrated as remaining substantially independent of the local density of

mothers, even at high density levels [9-10]. This trend, acknowledged for three common leaf-mining moth species, likely stands as well for *L. malifoliella*.

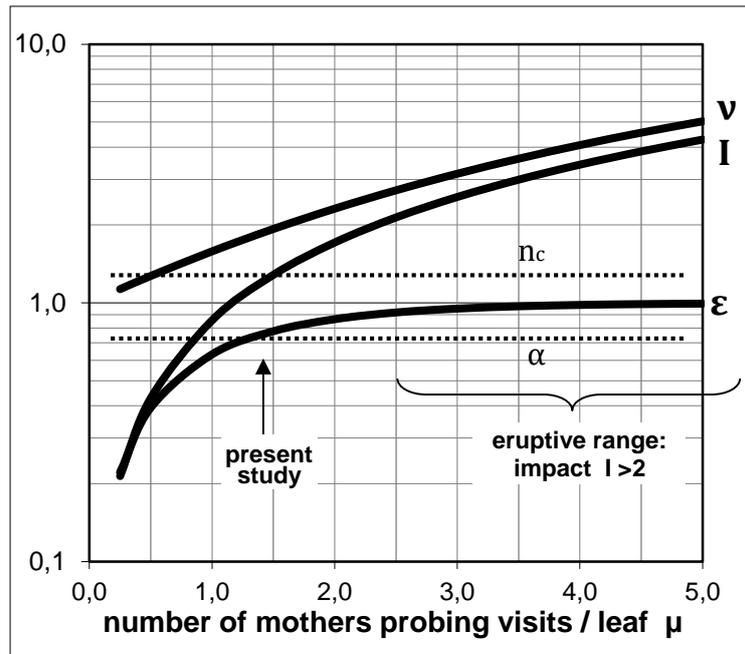


Figure 5 Computed evolutions (using ‘Melba’ procedure) of (i) the exploitation ratio ε of potentially acceptable leaves, (ii) the average number v of mines clutches per mined leaf, (iii) the resulting impact I (average number of mines per leaf) according to the density μ of mothers probing visits to leaves. Values of the leaf-acceptance ratio and the average clutch-size are those derived in this study: $\alpha = 0.69$, $n_c = 1.24$. Estimates using “Melba” procedure: $\varepsilon = 1 - \exp(-\mu)$ and $v = \mu/[1 - \exp(-\mu)]$: cf. [5]. Note the logarithmic scale for the ordinate axis.

Accordingly, as expected, the further increase of μ would result mainly in the growth of both (i) the exploitation ratio ε of the subset (proportion α) of potentially acceptable leaves and (ii) the average number v of clutches per mined leaf (Figure 5), as already suggested in introduction section.

But, more precisely, when the growing density μ of mothers’ probing visits eventually leads to eruptive impact levels (say, impact $I > 2$ mines per leaf), the exploitation ratio ε approaches saturation and, for still higher density of oviposition, it is then the number v of clutches per mined leaf which takes over and, ultimately, becomes the main factor driving the continuously increasing eruptive impact of the insect on the host.

5. Conclusion

This study provides a contribution to the understanding of what may be the main cause involved in outbreaks by the leaf-mining moth *L. malifoliella*. Yet, this analysis applies to the specific case studied here and is not necessarily intended to be generalized to other cases of leaf-mining outbreaks, either by *L. malifoliella* or by any other leaf-mining (or galling) species. In fact, the present study is intended, primarily, to pave the way for other similar case-studies, by providing a dedicated methodology, well adapted to tackle efficiently the difficult problem of quantitatively analyzing the respective contributions of the main factors governing leaf-mining (or leaf-galling) impact.

Compliance with ethical standards

Acknowledgments

Two Reviewers made relevant suggestions which significantly improve a previous version of the paper.

Disclosure of conflict of interest

The author declares that no conflict of interest exists regarding this study and publication

Appendix

Appendix 1: specific notes

[*] The local density of mothers, and the resulting density ‘ μ ’ of mothers probing visits, are arguably dependent upon both biological traits of the insect (such as fecundity, capacity of dispersion of imagos,...) and *contextual* (i.e. *environmentally-related*) factors which affect directly the supply of mated females to the host-canopy. *Within* a given insect-host system, variations of the local density of mothers (and associated value of ‘ μ ’) are thought to depend mainly upon the *environmental context* (in particular, the spatial distribution of other potential host-individuals around and at distance of the focused host-individual, within the range of mothers’ capacity of spatial dispersion: Tack [3]).

[**] The leaf-acceptability ratio ‘ α ’ may equally be considered either: (i) as a *behavioural* parameter, since it quantifies the degree of mothers’ severity in selecting among available host-leaves, prior to egg-laying and (ii) as a proper *characteristic of the host*, reflecting the average foliar quality of the host-individual “in the eyes of mothers” [15]. In fact, ‘ α ’ reflects the *interaction* between the insect behaviour and the host-quality [16-17] and, thus, ‘ α ’ may equally be qualified as “leaf-*acceptance* ratio” (by mothers) or as “leaf-*acceptability* ratio” characteristic of *the host-individual*.

[***] Understand that way, the “mines clutch-size” (or “residual clutch-size”) conforms to the extended notion of “clutch”, being now related to the *outcomes* of one definite oviposition event (i.e. one egg-clutch), in accordance with the concept of Fordyce [18].

[****]note that in leaf-miners, there seems to be, often, not so large a difference between the ‘eggs clutch-size’ and the resulting ‘mines clutch-size’, since the eggs of leaf-miners ordinarily suffer weak mortality from natural enemies [6, 19-21]. This weak eggs mortality from natural enemies is likely attributed to the minute size of eggs in leaf-miners, which attract only few parasitoids [1].

Appendix 2: Brief information on the natural history of *Leucoptera malifoliella*

L. malifoliella (Lepidoptera: Lyonetiidae) is a tiny moth, the body about 3 mm in length and c.a. 7 mm wing span, with elegant, delicate polychromatic metallic patterns on part of the wings. Adults are on wing in June-July and the mated females oviposit mainly on representatives of Rosaceae and sometimes Betulaceae (larvae are thus narrowly polyphagous). Oviposition is at the leaf underside; eggs are oval, with an average size of 0.30 x 0.23 mm. The resulting, mono-occupied mines are rather large, often fairly circular brown blotches. Around the dark centre, the frass is glued to the upper epidermis and is characteristically arranged in distinct successive circular arcs. Pupation occurs outside the mine [22]. The larva is pale-green, turning to pale brown later, reaching 3-4 mm in length. The moth is distributed in Europe and central Asia and may be considered rather common in most regions of Europe but its incidence may greatly vary according to years. Successful invasions are reported from North and South America, South Africa and Australia. In case of high mining density, *L. malifoliella* may become dangerous for apple or pear orchards, so it is interesting to investigate about the factors that likely govern outbreaks of this species, not only for speculative but also for practical concerns.

In spite of their rather wide host-species acceptance range (Rosaceae and Betulaceae), mothers are further selective among available leaves even within preferred host individuals, as was suggested for a series of other leaf-mining insects [3-5, 9, 15]. Yet, to our knowledge and for the practical reasons evoked above, no evidence has already been reported regarding the range of values for the leaf-acceptance ratio (α), nor regarding the average mines’ clutch-size (n_c) in *L. malifoliella*.

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