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Substrates Preference for Pupation on Sawfly *Notofenusa surosa* (Hymenoptera: Tenthredinidae)

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Abstract The choices made by insects at different stages of their life cycle are critical for the individual and progeny success. In the case of leaf-miners, during larval development they are not able to make choices until the emergence from the leaf, after which the larva falls to the ground and begins pupation. According to needs, preferences and soil properties, the larva could achieve a suitable substrate for the development of the pupa. Our aim was to study the preferences for pupation substrates of *Notofenusa surosa* larvae, leaf-miners of *Nothofagus obliqua,* in relation to soil properties. We selected different types of substrates (including volcanic ash) and conducted paired preference tests. The substrate was considered chosen when the larva selected it and formed the pupa (response variable). According to data obtained, several models were performed to determine the probability of individuals to choose a particular option depending on its preferences and substrates' properties. These larvae are able to discriminate the different options offered and choose their pupation substrate according to the percentage of organic matter.

Keywords Leaf-miners · native forest · *nothofagus* spp · patagonia · phytophagous · thurstone scale

Introduction

During adult life, insects have the ability to search for, and choose, the resources required for their development, reproduction and survival. This searching behavior (i.e.,

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active movement) allows insects to locate different resources: hosts, a particular food source, mates, and sites for oviposition, nesting or shelter (Bell 1990). According to the properties and characteristics of the resources, insects can differentiate them and choose, based on their preferences (Bernays and Chapman 1994).

Most studies that have assessed the preferences of insects, evaluate the choices made by adult females due to the relationship between female preferences and the progeny success (i.e., "The preference–performance hypothesis" or "The mother-knows-best hypothesis"; that is, females maximize their fitness by laying their eggs on plants on which their offspring perform the best) (Rausher 1979; Gripenberg et al. 2010). However, there were cases reported where female preferences are quite different from larval requirement (Rausher 1979; Valladares and Lawton 1991; Mayhew 2001; Ellis et al. 2004; Clark et al. 2011). Finding an appropriate resource largely depends on the integration of intrinsic (e.g., nutritional state, age, motivation, requirement) and extrinsic factors (e.g., presence of info-chemicals or certain environmental conditions) (Bernays and Chapman 1994).

Larvae, as well as adult insects, are able to select certain resources according to their preferences. However, this searching behavior is often limited by the options/resources that the adult females chose to oviposit (Jaenike 1978; Craig et al. 1989; Berdegué et al. 1998). In the case of most of leaf-miner larvae (i.e., insect larvae that feed on internal tissue of leaves), their capacity to choose their resources is also limited until they emerge from the leaf. For minorities that develop their pupa inside the leaf, the limitation is even greater because they cannot make choices until adulthood (Haack and Mattson 1993).

Generally, leaf-miner larvae that emerge from the leaf at their maximum larval stage fall to the ground to form the pupa on substrate. The principal uses which insects make of the soil are for shelter, nesting material, food, moisture, air, heat, and as a means of conveyance. Certain soil conditions and use by insects could determine the distribution, relative abundance, and seasonal activities of insects (McColloch and Hayes 1922). Given that the pupation substrate can be more or less suitable for larval development depending on soil properties and/or the insect needs and preferences (Fye 1978), physical and chemical properties of soil (i.e., organic matter concentration, pH, electrical conductivity, field capacity, transparency, and porosity) determine the environment where an insect will or will not develop (Prudic et al. 2005). For example, high concentrations of organic matter can be detrimental for full development of the pupa as it may increase attacks by pathogens (Altieri 1999). Likewise, soil porosity may also influence the larvae ability to move or bury (Johnson et al. 2006).

The aim of this study was to evaluate the ability of the leaf-miner *Notofenusa surosa* to choose a substrate for pupation and determine its preferences according to soil properties.

Material and Methods

The study system is composed by the leaf-miner sawfly *Notofenusa surosa* (Hymenoptera: Tenthredinidae) and the host plant *Nothofagus obliqua* commonly named "roble pellín" (Fagales: Nothofagaceae).

Notofenusa surosa is distributed in southern Chile and Argentina. These hymenopterans belong to the family Tenthredinidae, and are commonly named "sawfly" (Smith

2003). *N. surosa* adult females lay eggs in the leaf; the larva is leaf-miner and consumes the leaf tissue leaving only the upper and lower leaf cuticle (Smith 2003). When the larva emerges from the leaf it drops to the soil where it digs a 1–4 cm deep tunnel to pupate (Taeger et al. 2010). The insect remains buried until the next reproductive season, when the adult emerges from the substrate.

The *Nothofagus* genus is mainly found in Australia, New Zealand, New Guinea, New Caledonia, Chile and Argentina. *N. obliqua* is one of the most representative and important tree species of the northern temperate deciduous forests of the Patagonian-Andes forest. This is a major forest species of important ecological value, excellent robustness and timber quality (Sabatier et al. 2011). Its distribution covers over 33 thousand hectares in Argentine territory and is used for replacement of exotic forest plantations such as pine (Barbero et al. 2011). It is a deciduous tree and its folivorous insect complex has total synchrony with this leaf-out behavior, demonstrating a pattern of optimal utilization of this leaf resource from a temporal perspective (Lanfranco et al. 1999). *N. surosa* has the capacity to undermine the leaves of *N. obliqua* and *N. nervosa* as well as the hybrids formed between both species (Pietrantuono et al. 2013).

Substrates Material

In order to establish a rating of preferences made by the larvae of *N. surosa*, we selected different types of substrates. Soil samples were taken from six locations in the province of Río Negro (Argentina). These sites were arranged along a West–east rainfall gradient (a map with soil sampling sites in Rio Negro province is included as electronic supplementary material- ESM Figure S1) according to Enriquez (2008). On June 4, 2011, a major volcanic eruption of the "Cordón - Caulle" volcanic complex (Chile) occurred; over 7.5 million hectares of northern Patagonia (including these sites) were affected by ashes (Gaitán et al. 2011). Therefore, we decided to include the volcanic ash within the substrate options. Several studies have demonstrated its harmful effect on insects affecting their welfare, habitat, food availability, and survival (Buteler et al. 2011; Fernández -Arhex et al. 2013; Chaneton et al. 2014). Ashless soil samples that were collected at a depth of 0–10 cm, were air dried and sieved twice (first through a 2 mm mesh and then through a 0.5 mm mesh). Samples from the 2 mm mesh were used to determine pH and electrical conductivity (ECond) (soil: water 1: 2.5) (Sparks et al. 1996). Samples from the 0.5 mm mesh were used to estimate the amount of organic matter (OM) through the Walkley-Black method (Walkley and Black 1934). Samples of volcanic ash were also sieved and classified into two categories according to particle sizes (thick ash ≥500 μm and fine ash <500 μm). Additionally, in all substrates, field capacity (FC) was determined according to the methodology developed by Black et al. (1965). Table 1 shows the characteristics of each of the used substrates.

Experimental Design

To test preferences for pupation, substrates were compared by pairs, establishing a total of 28 combinations with six replicates for each combination (David 1988; Bruzzone and Corley 2011). We used handmade devices consisting of glass containers

Table 1 Description of the substrates used for preference tests

Sites	Mean annual precipitation (mm)	Mean annual temperature (°C)	Predominant Vegetation	pH±SE	Field capacity (FC)±SE	Electrical Conductivity (ECond)±SE	%Organic matter (OM)±SE	Porosity±SE
Llao-LLao (LL)	1400	7.5	Forest of *N. antarctica* and *N.dombeyi*	5.35±0.12	115.92±13.6	0.21±0.03	38.34±9.70	81.82±2.5
INTA Bche. (INTA)	580	8.8	*N. obliqua* and *N.nervosa* plantation	5.65±0.05	13.12±0.33	0.11±0.01	7.48±0.29	78.23±3.1
El Cóndor (EC)	580	8.8	Pine plantation	6.95±0.18	12.02±1.63	0.04±0.01	10.93±2.98	60.06±2.2
San Ramón (SR)	580	8.8	Herbaceous shrub steppe	6.81±0.16	19.10±5.63	0.29±0.04	22.61±1.93	68.15±1.5
Quintupanal (QU)	290	9.0	Herbaceous shrub steppe	8.83±0.22	88.88±11.3	0.16±0.02	3.42±0.54	56.05±3.4
Pilcaniyeu (PI))	270	7.4	Herbaceous shrub steppe	8.79±0.22	74.15±18.9	0.16±0.01	1.77±0.06	54.84±2.2
Thick Ash (TA) (500 µm)	–	–	–	5.23±0.16	12.87±2.17	0.43±0.06	0.04±0.02	74.38±0.0
Fine Ash (FA) (<500 µm)	–	–	–	8.16±0.16	21.37±2.67	0.50±0.02	0.09±0.02	63.44±0.0

Extracted and amplified from Enriquez (2008)

(10x15x1cm). Each device was marked with two guide lines: one vertical half line, in order to maintain equal proportions of the two substrates to compare; and one horizontal line to level the surface of both substrates. According to field capacity (Table 1), we moisturized each substrate with distilled water before starting the experiment.

Mined leaves of "roble pellín" with *N. surosa* (n=180) were collected from the nursery of Instituto Nacional de Tecnología Agropecuaria-EEA Bariloche (INTA EEA-Bariloche). The experiment began when the leaf containing the insect (one larva promptly to emerge per leaf) was placed at the intersection of the guide lines marked on the device. After 1 week, we observed through the glass under which of the two substrates the pupa had developed (response variable). From the total of tested individuals, only 169 pupated and were included in the data analysis.

Data Analysis

To analyze the data of the preference tests we first established a scale of preferences based on the Thurstone model of comparative judgments case V (Thurstone 1927; Bradley and Terry 1952). This "Thurstone scale" provides a continuous unidimensional dimensionless variable of preferences. Through this variable we were able to determine the gradient of preference for each substrate according to its properties by means of a regression between the Thurstone scale and the measured properties of each soil type.

To determine specifically which soil property best explains the scale of preferences, several models were proposed. These models were generated from the null model (only preference) becoming more complex by adding parameters in each step (e.g., porosity, ECond, FC). Therefore, models grow in a tree-like pattern from the null model to one-parameter simple linear models (the preference is a linear function of a single parameter), then to two-parameter bilinear models (the preference is a function of a linear combination of two parameters) or quadratic models (the preference is a quadratic function of a single parameter), and so forth. The development of these models continues until the model complexity exceeds the improvement in the likelihood function (best balancing fit and complexity model, Bayesian approach).

The model generation and selection was performed using the algorithm "Reversible Jump Markov-Chain Monte Carlo" for each additional parameter the log-likelihood function was penalized with a value of minus two. The first 40,000 iterations of the reversible procedure were discarded as a burn-in model selection, and the last 10,000 were used to calculate the weight of each model in the model averaging procedure. Expected values as a function of substrate variables were calculated using a weighted average of the models proposed. In the selected model, 1000 iterations of Markov Chain Monte Carlo were performed for each iteration of the Reversible Jump algorithm (Gill 2008). In addition, we established a normal distribution with mean zero and deviance ten for all the parameters since we did not have a priori information of the variables distribution. On the selected models, convergence was tested using Geweke plots and visual inspections of the variable traces (Geweke 1992; Gelman et al. 2004). All analyzes were performed using a PyMC library modified version for Bayesian estimation (Patil et al. 2010) in the Python programming language.

We used a Bayesian approach since its convenience due to the two steps of the analysis (creation of the preference scale and regression to the soil properties) may be performed simultaneously on each proposed model, thus increasing the sensitivity and precision of the analyses. It provides a more straightforward way to fit and simultaneously select a great number of models unlike frequentist statistic methods. Furthermore, it is being used widely by ecologists in animal behavior studies (Ellison 2004; McNamara et al. 2006; Valone 2006; Pereira et al. 2013; Pietrantuono et al. 2014).

Results and Discussion

In the process of model selection, 84 models were generated, from which 13 were selected according to the percentage of iterations in which each model was chosen (a plot of the distribution of the model coefficients is included as electronic supplementary material- ESM Figure S2). Model 1 has the highest percentage of iterations (47.715 %), and represents a cubic function between the percentage of organic matter and the Thurstone scale of insects' preferences (Table 2). Thus we could determine that the amount of organic matter was the parameter that best explained the choices made by *N. surosa*. The optimal value within the preference curve indicates that the preferred value of organic matter lies within 10 to 15 %. Therefore, we can infer that the substrate preferred for pupal development corresponds to "El Cóndor" (EC) location (Fig. 1). The substrates from INTA- EEA Bariloche and San Ramón present values that continue

Table 2 Selected models. According to the percentage of iterations, model 1 was selected as the one that best explains substrate preferences of *N. surosa*

Model	Parameter	Function	N° of parameters	Percentage of iterations in which the model was chosen	Log like average	Log Like SD
1	Organic matter	Cubic	1	47.715	−185.10	5.42
2	Organic matter+Porosity	Cubic+Linear	2	16.278	−184.24	6.50
3	Organic matter	Quadratic	1	13.759	−190.71	3.97
4	Organic matter+Light	Quadratic+Linear	2	7.509	−186.23	4.68
5	Organic matter+pH	Cubic+Linear	2	4.300	−186.19	6.80
6	Organic matter+Electrical conductivity	Cubic+Linear	2	3.440	−191.17	6.16
7	Organic matter+Field capacity	Cubic+Linear	2	2.710	−189.95	8.53
8	Organic matter	Quarter	1	1.980	−184.8	5.03
9	Organic matter+Electrical conductivity	Linear+Quadratic	2	1.450	−189.88	4.90
10	Electrical conductivity	Quadratic	1	0.560	−193.13	3.90
11	Electrical conductivity	Cubic	1	0.230	−186.19	5.09
12	Organic matter+Light	Cubic+Linear	2	0.050	−187.66	5.33
13	Organic matter+Field capacity	Linear+Quadratic	2	0.020	−192.57	4.89

These preferences are determined by a cubic function of the organic matter content of the substrates

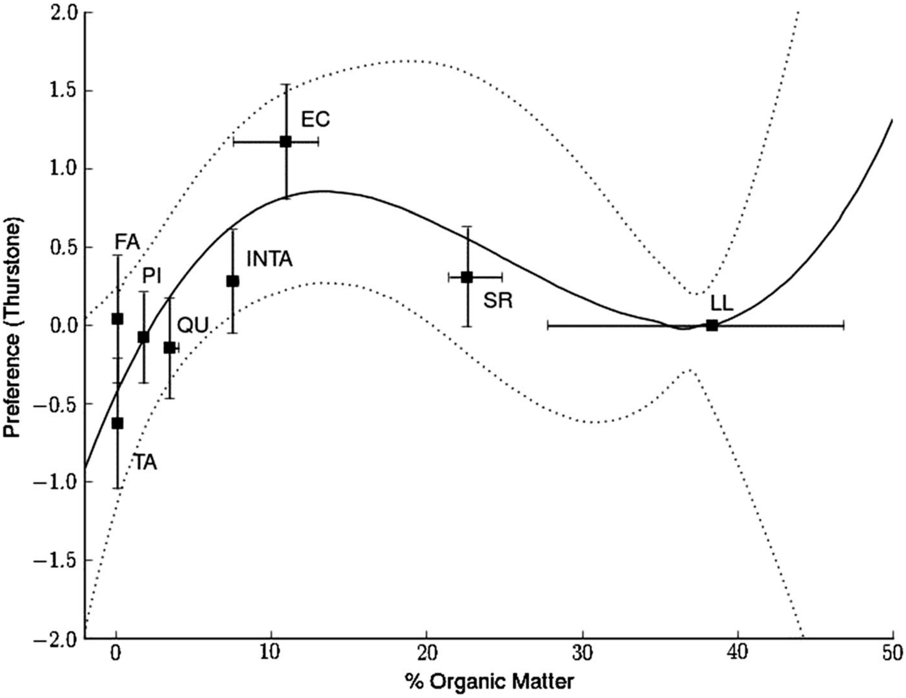

Fig. 1 Preference curve as a function of percentage of organic matter. This function was calculated from the weighted average of model 1. The weight of each model in the calculation of the weighting curve is the percentage in Table 2. The Y axes represent the Thurstone scale of attractiveness / preference. The X axis is the percentage of organic matter at each substrate (FA: Fine Ash, TA: Thick Ash, QU: Quintupanal, INTA EEA Bariloche: Instituto de Tecnología Agropecuaria, EC: El Cóndor, SR: San Ramón, LL: Llao-Llao). Negative values on the Y axes indicate a lower preference for the parameter. The dotted line represents the 95 % of credibility intervals

on the gradient of attractiveness. While the ash (fine or thick), which does not contain organic matter, is practically repelled.

Notofenusa surosa demonstrated that not all substrates were equally attractive for pupation. The larvae actively choose their pupation substrate and are capable to discriminate between different concentrations of organic matter in the soil. According to Edwards et al. (1970), soil organic matter appears to be a key factor to soil life and the diverse functions provided by the range of soil organisms. The amount of organic matter is strongly related to the amount of air available for insect breathing, texture, structure, moisture, and porosity of the soil (McColloch and Hayes 1922). It should be noted that, as *N. surosa*'s diapause lasts several months, locating a suitable habitat to endure this highly fragile and susceptible period is of great importance for individual success. Organic matter could become an important parameter for the development and survival of the larvae (Marrone and Stinner 1984; Dimou et al. 2003; Hulthen and Clarke 2006).

The preferred substrate (EC) belongs to a site with pine plantation (*Pinus ponderosa*) which gives specific properties to the substrate. In Río Negro province (Argentina) 10 % of the land suitable for planting *N. obliqua* is currently forested with pines susceptible to replacement with *Nothofagus* species (Barbero et al. 2011). Some of these plantations were established in the area of native species; as a result, the new plantations to be developed with native species could be exposed to the action of the same insects of the forest (Milligan 1974; Denno and McClure 1983). It has been demonstrated that certain leaf-miners associated to other species of the Fagaceae family have a high rate of foliar consumption and the ability to accelerate leaf abscission (Pritchard and James 1984; Claros and Serey 2001). Consequently, trees may suffer a reduction in photosynthetic capacity, weakening and loss of wood quality (Bernays and Chapman 1994).

Regarding volcanic ash, this substrate is not one of the preferred substrates and exerts a repellent effect on *N. surosa* larvae. This may be because volcanic ashes have high abrasive capacity and cause mechanical damage making the insect epicuticle permeable and accelerating dehydration (Buteler et al. 2011; Fernández Arhex et al. 2014). According to Barker and Reynolds (2004), desiccation is one of the main factors that seriously affect the development of sawfly pupae. Hence, even though the effect of the ash is not the same for all insects, we may suppose that the ashes will have a long term effect on the insects' development (Fernández Arhex et al. 2013; Pietrantuono et al. 2014). While during early stages the larva of *N. surosa* is fully protected within the leaf epidermis, after the emergence from the leaf the larva must dig in the substrate and, like other sawflies, could possess low resistance to mechanical damage (Burret et al. 2005; Pietrantuono et al. 2013). Given the magnitude of the ash deposition, larvae are inevitably exposed to volcanic ashes and face the difficulty to find a suitable habitat according to their substrate preferences. Consequently, the leafminer population of the area affected with volcanic ash and the rate of damage associated could result negatively in the following seasons after eruption (Chaneton et al. 2014).

We conclude that *Notofenusa surosa* larva is able to choose the habitat for pupa development. However, it should be noted that under natural conditions these insects do not possess the same range of substrates to choose from due to the distances between the sampling sites and their limited ability to mobilize. Under natural conditions, the larva must form its pupa in the soil beneath the host plant selected by the adult female. For this reason, we consider that studying only the preferences of the female during the host plant selection is not enough to determine the insect preference (Berdegué et al. 1998; Huk and Kühne 1999). It is also important, especially if they have different habits and/or habitats, to analyze the preferences and requirements at different stages of development.

According to Gripenberg et al. (2010) the study of behavioral choices contributes to the knowledge of evolutionary and adaptive aspects. From an applied perspective, this information is of great interest for restoration and conservation projects of the native forest and even for the productive sector. Research focused on studying preferences of insects that develop in the ground, provides a useful tool for the development and implementation of control techniques for pupal populations as well as to identify factors that could affect the sanitary state of the forest and plantations (Alyokhin et al. 2001; Chen and Shelton 2007). Particularly in cases where insects are associated with native host plants, such as *Nothofagus,* which are already included in plans of domestication and preservation (Gallo et al. 2006).

In addition, Vergara and Jerez (2010) establish the need to perform future projects focused on the interaction between soil and insects associated to *Nothofagus* foliage. They suggest that increased stress of the soil regarding the amount of water and nutrients, may affect the diversity of insects. Therefore, these types of studies also contribute to greater understanding of insect diversity, insect behavior, the role of leaf-miners and their interaction with the environment and host plants.

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