

Insect biodiversity reduction of pinewoods in southern Greece caused by the pine scale (*Marchalina hellenica*)

P. V. Petrakis^{1*}, K. Spanos² and A. Feest³

¹ N.AG.RE.F. Mediterranean Forest Research Institute. Laboratory of Entomology. Terma Alkmanos. 11528 Athens. Greece

² N.AG.RE.F. Forest Research Institute. 57006 Vassilika (Thessaloniki). Greece

³ Water and Management Research Centre. Faculty of Engineering. University of Bristol. Bristol BS8 1TR. UK and Ecosulis Ltd. The Rickyard. Newton St. Loe. Bath BA2 9BT. UK

Abstract

This paper deals with the impact of the pine scale (*Marchalina hellenica* Gennadius, Hemiptera, Sternorrhyncha, Margarodidae) on the insect biodiversity of pinewoods in Attica, Greece. The comparison of biodiversities was done by estimating the biodiversity by the Ewens-Caswell's V statistic in a set of nine sites each containing two line-transects. Transects pairs went through free and infested pinewoods from the pine scale and each one had several tenth hectare plots on both sides. The ecosystem temperature (= disorder) of the sites was computed and found high, together with the idiosyncratic temperatures (= susceptibility to extinction) of the 158 species in order to detect local extinctions. The indicator values of insect species were computed on the basis of the relative cover of each plant species. The main findings of this study are (1) the reduction of insect species biodiversity because of the introduction of the pine scale, (2) the moderate increase of disorder in pine scale infested sites, (3) many insect species can characterize site groups but none of them can distinguish infested from pine scale free sites. The introduction of pine scale in pinewoods disturbs their insect fauna before its influence to the floristic composition and the associated vegetation structure appears. The causes behind this reduction of biodiversity and the anthropogenic influences are discussed.

Key words: biodiversity; pinewood; *Pinus halepensis*; anthropogenic disturbance; ecosystem temperature; species indicator value; pine scale; *Marchalina hellenica*.

Resumen

Reducción de la biodiversidad de insectos de pinares en el sur de Grecia, causada por *Marchalina hellenica*

El presente artículo trata sobre el impacto de *Marchalina hellenica* Genadio (Hemiptera, Sternorrhyncha, Margarodidae) sobre la biodiversidad de insectos de los pinares en Attica, Grecia. La comparación de la biodiversidades se llevó a cabo mediante la estimación del estadístico V de Ewens Caswell en un conjunto de nueve sitios cada uno con dos transectos en línea. Cada par de Transectos incluía pinares infestados y libres de *Marchalina hellenica* y cada uno tenía parcelas de varias decenas de hectáreas. Se calculó la temperatura de los ecosistemas (= trastorno) que era alta, junto con las temperaturas idiosincrásicos (= susceptibilidad a la extinción) de las 158 especies de insectos presentes con el fin de detectar las extinciones locales. Los valores de los indicadores de especies de insectos se calcularon sobre la base de la cobertura relativa de cada especie de planta. Las principales conclusiones de este estudio son (1), la reducción de la biodiversidad de las especies de insectos debido a la introducción de *Marchalina hellenica*, (2), el aumento moderado de la enfermedad en sitios infestados con *Marchalina hellenica*, (3), muchas especies de insectos pueden caracterizar grupos de sitios, pero ninguno de ellos puede distinguir sitios infestadas de libres de *Marchalina hellenica*. La introducción de *Marchalina hellenica* en bosques de pinos perturba su fauna de insectos antes de que sea influenciada la composición florística y la estructura de la vegetación asociada. Se discuten las causas de esta reducción de la biodiversidad y las influencias antropogénicas.

Palabras clave: biodiversidad; pinar; *Pinus halepensis*; perturbaciones antropogénicas; temperatura de los ecosistemas; valor de especies indicadoras; *Marchalina hellenica*.

* Corresponding author: pvpetrakis@fria.gr

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Introduction

Human induced introductions or augmentations of insects are able to influence the succession trajectory of biotic communities by being able to alter their species composition towards different, and usually lower, biodiversity (Balleto and Casale, 1991; Brockerhoff *et al.*, 2006). The structure and function of ecosystems is affected in various ways usually making the respective ecosystems more susceptible to disturbances (Luck *et al.*, 2003; Ruiz-Jaén and Aide, 2005; Spanos and Feest, 2007). In Europe, the extension of managed forests at the expense of natural ones has significantly decreased biodiversity (Luque *et al.*, 2007, for moth assemblages). The restoration process is assessed through a diverse array of specialized techniques for many taxa with a particular emphasis on standardization (*e.g.* Hilty and Merenlender, 2000; Feest, 2006).

Insect assemblages prone to extinction are affected by episodes of glaciation and human occupation. In Mediterranean areas the insect rich gymnosperm forests of Neogene origin receive human impacts that replicate glacial episodes in severity and possibly in a much shorter time scale (Whitehead, 1997). These depleted insect faunas consist of insects capable of surviving severe winters and extreme summer droughts, (Whitehead, 1997; Mendel, 2000; Topp *et al.*, 2006), but evidently unable to survive the catastrophic events that caused the local extinction surges induced by humans.

Insects are thought to be good bioindicators in the sense that their presence or abundance indicates some character of the habitat within which they live (Dempster, 1991; McGeoch, 1998; McGeoch and Chown, 1998; Nickel and Hildebrandt, 2003). In addition their bioindication value can be efficiently measured (Dufrêne and Legendre, 1997). In effect the insects associated with live and dead wood of pines and other co-occurring woody plants (Topp *et al.*, 2006) are expected to be suitable candidate biodiversity indicators (Warren and Key, 1991; Tscharnkte *et al.*, 1988; Cartagena and Galante, 2002). These insect groups may include (1) insect predators and parasitoids (Pschorner-Walcher, 1977; Pearson 1988; Pearson and Cassola, 1992), (2) pine needle and understory plant foliage eaters (Mendel, 2000; Petrakis *et al.*, 2005), and (3) insects occupying understory plants, soil or small temporary habitats.

Even though many local extinction events go unnoticed as «blurry catastrophes» *sensu* D. Janzen (1986), public awareness and health issues raise the question of the reduction of biodiversity in Attica pinewoods.

This pine formation is the dominant forest type in the region and ranges from coastal areas up to 800 masl where it is replaced by *Abies cephalonica* on Mt Parnitha. The reduction of biodiversity is believed to be the result of deliberate and unregulated introduction by beekeepers (Bikos, 2000) of the pine scale (*Marchalina hellenica* Gennadius; Hemiptera, Sternorrhyncha, Margarodidae) in places where the insect never existed before, at least in the observed population densities. It is an anthropogenic introduction and most possibly it has been introduced in northern Greece from Turkey (hence its resemblance with *M. caucasica*; Hodgson and Gounari, 2006) by late Romans and Byzantines who are responsible for the artificial boundaries of its two principal pine hosts —*i.e.* *Pinus halepensis* and *P. brutia*— (Schiller and Mendel, 1995). There are no references that the pine scale existed in Greece at prehistoric and classical times (*e.g.* Aura Jorro, 1985). The insect exploits in nature a few pine species such as *P. brutia*, *P. halepensis*, *P. nigra* and *P. sylvestris* and some (usually planted) *P. pinea* populations while recent attempts have been made to induce the scale to use *Abies cephalonica* (Bacandritsos, 2004). It spreads very slowly (around 40 m in a year, Nikolopoulos, 1965) and the honeydew production is a reward for ant attendance to control potential natural enemies (Hölldobler and Wilson, 1990; Bourgoïn, 1993). Sap sucking by the scale reduces the vigour of the pine host measured as crown transparency or reduction of wood production and in some places it was found to decrease the width of tree increment growth rings (Yesil *et al.*, 2005).

The insects is parthenogenetic and univoltine in Greece and has three instars before reaching the adult stage. The first nymphal instar is a crawler and does not feed; the 2nd and 3rd instars feed by means of the insertion of the rostrum which is cut at the crumena when the insect changes feeding site and it is replaced by a new rostrum stored within the crumena; the adult is an occasional feeder; it feeds on the sap in the trunk and main branches of its pine host by inserting its rostrum usually in a depth reaching 20 mm (Nikolopoulos, 1965; Hodgson and Gounari, 2006; PVP personal observations). The feeding damage of *M. hellenica* does not remove directly the photosynthetic tissue from the pine tree. The pine scale primarily damages the tracheids of the plant since it taps the nutrient sap stream of the trunk (Víte and Rudinski, 1959; Mendel and Lippschitz, 1988) as do all related insects (Mitchell, 1967). The gradual decline of the pine tree caused by this damage is rarely attributed to

the scale since other insects, such as bark beetles, interfere and use the damaged tree. Some bark beetles are able to detect the weakness of the plant through a drastic alteration of the volatile emission profile (Mita *et al.*, 2002). Most bark beetles are only able to attack and colonize the live bark of weakened, stressed or recently cut or dead pine trees, and they are considered secondary pests, such as *Pityogenes calcaratus* Eichh. and *Orthotomicus erosus* Wollaston (Coleoptera, Scolytidae) (Georgevits, 1974). The latter may become a primary pine killer at high densities. These insects do not normally kill pine trees when their populations are in low numbers but some become important mortality factors when they reach outbreak thresholds (Mendel, 2000; PVP *personal observation*).

Following the induction of tree morbidity, the configuration of pinewood ground flora changes, causing drastic alterations to the associated fauna (*e.g.* Fahy and Gormally, 1998; Ings and Hartley, 1999; Hughes *et al.*, 2000). The alteration is reflected in the biodiversity of the pinewood habitat and insects are used to indicate the new situation. Biodiversity, particularly insect biodiversity, is sensitive to various forest management practices of forests (Woodcock *et al.*, 2003; Luque *et al.*, 2007) and other habitat types (among others Niemelä *et al.*, 2000; Biedermann, 2002).

Moreover, according to Lambshead and Platt (1988) if biodiversity is estimated by the V statistic then it is possible to predict the survival of populations of insects on the basis of processes like exclusion or disturbance.

This work is designed to provide answers (based on the Attica, Greece peninsula region) for the following questions:

1. Do pine scale populations affect the insect biodiversity of pinewoods and in what way?
2. How are the different insect species affected by differential pinewood quality as a result of the presence of pine scales. What is the order of local extinction probabilities of insects (nestedness, Atmar *and* Patterson, 1995; Ulrich and Gotelli, 2007)?
3. Do insect species reflect the situation of pinewood as indicated by the floristic composition?

Material and methods

Study area

The study sites (Fig. 1) have a variegated geological evolution partly reflecting their dramatic past history. Mt Parnitha and the site at Villia on Mt Kithairon are

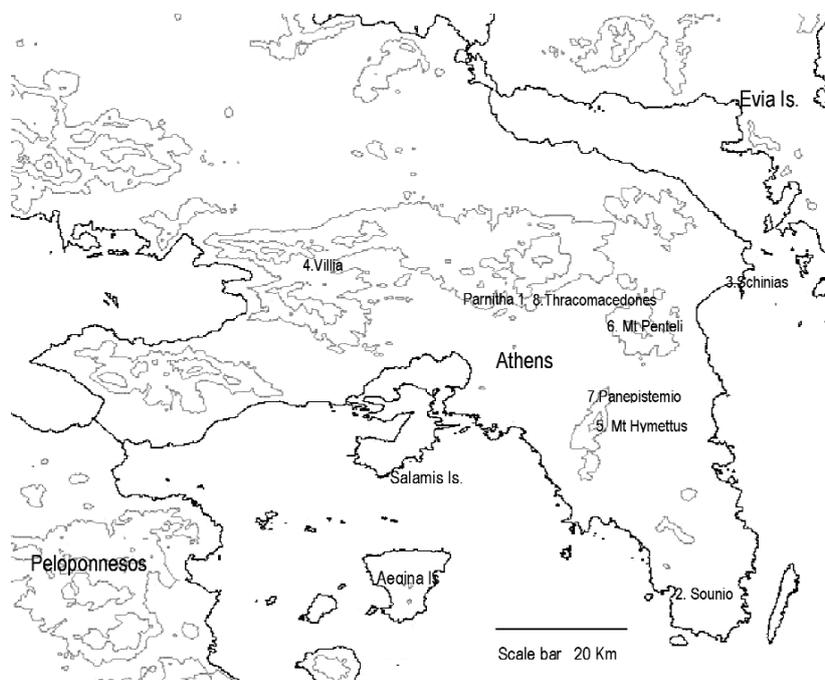


Figure 1. Map showing Attica and the relative position of sites (pine scale free and infested) given in numbers. Site names are: Mt Parnitha, Sounio, Schinias, Villia, Mt Hymettus, Mt Penteli, Panepistemio, Thracomacedones. Altitude isolines are drawn every 400 m.

dominated by Triassic limestones and the dolomites of the Pelagonian zone. At the periphery of limestones there are many natural springs that sustain a rich vegetation cover peculiar to the dry climate of Attica. Schinias is at the easternmost end of Marathon plain. It consists mainly of alluvial and Pleistocene sediments at the foot of mountains of schist and marble of the Attic-Cycladic metamorphic belt. The vegetation cover in this site is considered young. The site at Sounio is located on marble bedrock and is geologically similar to Mt Hymettus and Mt Penteli. Mt Hymettus and Mt Penteli have different parts of metamorphic rocks at the north-east and south-east of Athens. They consist of two layers: old (white) and new (grey) marble. Erosion has acted on both bedrocks to produce the infertile, inhospitable to plants *terra rossa* soil (Higgins and Higgins, 1996) hence the low vegetation cover is in contrast to their floristic richness. The other two sites at Thracomacedones and Panepistemio are located at the foot of Mt Parnitha and Mt Hymettus respectively. All sites were sampled in 2003 from 20 May until 10 October.

The region has a typical thermo-Mediterranean climate with mean annual precipitation 364 mm and mean annual temperature 18.5°C (min 14.3°C and max 22.0°C) and six months drought period. Vegetation and topographic features of the sampled sites are given in Appendix II (supplementary material).

Insect sampling and processing

A line transect in each site was positioned to facilitate access by investigators. The transect length varied among sites according to the variability of the area and ranged from 500 m for the site at Panepistemio to 3 km on Mt Parnitha. With the aid of random numbers a set of 25 to 35 points were selected on each transect. The number of points was roughly proportional to the length of each transect to cover the variability of the area. For each point a random number from a uniform distribution in the interval (-50 ... 50) defined the position of the sampling point. For each pinewood pine scale free site (= PSF), we selected within the same location another site infested by pine scale (= PSI) as close as possible to the first. An exception was the site at Mt Hymettus where it was very difficult to find a pine free site close to the infested one. This PSI site was selected at c. 2 km distance from the first one. Variation in PSI sites was mainly due to the quantity of fissures and

cracks of pine tree trunks. In each PSI site a transect was set and sampled in a similar way as in PSF sites.

At each sampling point a circular plot (to minimise edge effects), 17.84 m in radius, was positioned giving an area equal to tenth hectare. In each plot we set three pitfall traps (diameter 12 cm, depth 6, or 15 cm) at the centre and seven meters on a diameter parallel to the transect line at both sides of the centre. The trap at the centre of the plot was baited with a blend of tuna meat, chicken liver, and honey (replaced every two weeks) in order to collect polyphagous ants and beetles. The other two traps contained only the preservative fluid. In addition, the traps had a 2 W photodiode fed by a 12 V electric battery. The light was automatically turned on by a photosensitive cell 30 min after sunset, triggered by low light intensity. In this way the trap (patent pending) operated for 5-7 night sessions. It was used for Coleoptera that are attracted only to light. These light pitfall traps yield more specimens and at lower variances than passive pitfall traps. Each trap was filled with a killing and preservative fluid containing 50% ethylene glycol, 20% alcohol and 2% boric acid and 28% tap water. In addition one yellow pan trap was set at a convenient open place (suitable for Diptera and Raphidioptera) within the plot and one black window trap (suitable for pine tree Coleoptera) (60 cm × 50 cm, Thyeson trap, Trifolio-M GmbH, Germany) was hung between pine tree trunks. A malaise trap was also set tangentially at the distal end from the transect at the margin of the plot. This trap was used to collect mainly Hymenoptera, Cerambycidae and some Buprestidae flying in and out of the plot. Because malaise traps are easily seen and can be destroyed by people walking the area, such as beekeepers, they were operated for one day between 09:00-19:00 hours. The insect content of the killing bottles was collected and stored. Sweep-netting with dipteran and butterfly nets was performed on all plants and the lower branches of pine trees in each plot for 5 min between 09:30 and 13:00 hours in windless days preferably with sunshine. Hand collecting and butterfly sighting supplemented all other insect collection methods. Moths were initially collected by means of mercury vapour (250 W bulbs) light traps. The long distance attraction of moths and the light pollution of the areas from nearby traffic jeopardized the results and moth trapping was abandoned. All traps were set for one week every month in April-August (and served after two or three days) and every two months in the rest of the year.

Each plot was sampled in the same way at all sites. In this study we report the combined yearly data. The insects were transferred to the laboratory, relaxed and pinned. The initial identification was followed by ongoing intensive and formal taxonomic work. We used our experience with local insect fauna - and some important reference works (Aspöck, 1979; Trautner and Geigenmüller, 1987; Mühle *et al.*, 2000; Niehuis, 2004; Bílý, 2001).

Although the insect collecting methods do not provide absolute population estimates, their accurate identical application in each plot and site offers a useful comparative tool (Luque *et al.*, 2007). These methods are extensively used in similar ecological work (*e.g.* Argyropoulou *et al.*, 2005).

Biostatistical analysis

Sample sizes are different for each site —*i.e.* number of plots, number of traps, sweep-nettings and individuals caught in traps— so we used rarefaction curves (Hurlbert, 1971). For each site and transect type, abundance data for each caught species were used to construct rarefaction curves. We employed Hurlbert's formula as it is implemented in the program *Biodiversity Pro* (McAleece, 1997). As a useful adjunct to rarefaction curves we calculated the diversity equitability index (Ewens-Caswell's V -statistic) since it allows the standardised measurement of the deviation of a real sample from the one predicted by the Ewens-Caswell neutral model. The formula for the calculations is $V = [H' - E(H')] / SD(H')$, where H' = Shannon diversity index; $E(H')$ = diversity predicted by the neutral model; $SD(H')$ = standard deviation of Shannon diversity. It has been empirically shown in many ecological studies (some of them involving insects, reference in Lambshead and Platt, 1988) that this index is capable of predicting the survival of populations, possibly due to abundance of resources ($V > 0$), and density lowering or population crashes ($V < 0$) due to processes like competitive exclusion or disturbance. In sampling units with labile populations the V -statistic becomes even more negative and increases again when populations recover. This property of V is expected to describe communities in a better way than more traditional indices such as Simpson's D or % dominance of commonest species index whilst it is closely related to Shannon index because this index is already calibrated against neutrality (Lambshead and Platt, 1988).

Biodiversity is just one property of the site. To get an idea of the stability of insect communities after the introduction of the pine scale we need to estimate the stability or resilience of the new pinewood insect communities. To that purpose we measured nestedness in the two infestation types of pinewood sites to detect differences among the local extinction order of insects, and as a means to estimate the stability of insect populations. For nestedness calculations we employed the algorithm of Atmar and Patterson (1993) in order to compute the temperature (= disorder) on the basis of presence-absence matrix of each insect species.

The temperature of each site is assumed to be an entropic measure of the disorder in the matrix. The fill of matrix and the calculated extinction boundary threshold line —*i.e.* minimized unexpected presences and absences or equally maximum nestedness— provide information about the stability properties of the matrix. In addition the idiosyncratic temperatures of individual species are important in discriminating between the stochastic noise, coming from environmental, genetic and catastrophic events, and the noise coming from the idiosyncracies of insect species. Patterson (1990) considers that local extinction and immigration are the two most important ecological processes that could generate high idiosyncratic temperature of species, raising thus the temperature of the matrix.

The detection of species that could be indicative of each site and then the detection of species that could predict the occurrence of the pine scale were done by calculating the indicator value index technique for each species (Dufrêne and Legendre, 1997). This technique assigns a specific value (*IndVal*) for each species occurring in a set of habitats classified according to certain criteria (coverage of plant species in this study — *see below*) without explicit incorporation of insects. This value reflects the degree of specificity and fidelity of each species within each group of habitats derived from a certain cut off level of their hierarchical arrangement. Insects fit well with the prerequisites of the method since they can be found everywhere in a multitude of niches in sufficiently large numbers, which is a property of indicator organisms required by the model.

The sites were arranged in a hierarchical typology generated by applying the «Ward minimum variance» algorithm operated on the Euclidean distances of the sites. Sites were described by the coverage of each phanerogamous plant species found within the studied plots with the aid of a wide angle digital camera without barrel distortion and subsequent estimation of the num-

ber of 10^5 pixels corresponding to each plant species (with a computer program written by us). In this way important variables such as the crown transparency of pine trees and cover values understory bushes and herbs is captured in the relative cover of plant species. These values were taken once in the first week of May in all sites, at five equidistant positions located on a diameter in each plot. These values were expressed as percentage coverage approximation of each plant species and transformed in the Domin scale (Van der Maarel, 1979). The statistical significance of the maximum indicator values of species was tested by performing Monte Carlo permutations. All comparisons across sites and site groups were done by means of the Fisher significance of the correlation coefficient (Wilkinson, 1999).

Results

Geographical proximity of sites (Fig. 1) forced the grouping of locations in a hierarchical structure (Fig. 2) on the basis of plant similarity as a result of the uniformity of geological substrates and the overlaying soils. The sampling PSF and PSI sites in pairs, was *a posteriori* important —since all PSF/PSI pairs were grouped together on the basis of plants (Fig. 2). This arrangement of sites delineates any discrepancy of insect diversities to alterations in plant condition and not in floristic composition.

Biodiversity comparisons of site groups

Rarefaction curves for PSI and PSF sites at the northern mountainous parts of Attica prefecture (Mt Parnitha and Villia) are the most diverse in insect species (Fig. 3a and Appendix I). There is a profound and obvious discrepancy among the two site groups —*i.e.* PSI and PSF— (Fig. 3a, b and c). All site groups are similar while all infested sites in the three panels of Figure 3 have rarefaction curves never exceeding 45 expected species.

With regard to the local extinctions of species due to pine scale infestations and dominance, the pinewood temperature matrix is particularly revealing (Fig. 4). Sites grouped on the basis of presence of the pine scale are differently filled with presences; 46% vs. 36.1% of sites in PSI and PSF sites. The lines of extinction thresholds are shown and both are close to the main diagonal of the matrix with little difference in shape between the two groups of sites. Both matrices can be characterized as particularly hot ($T_1 = 54.23^\circ\text{C}$ at $p_1 = 7.03 \times 10^{-3}$ and $T_2 = 49.96^\circ\text{C}$ at $p_2 = 0.313$ each). Pine scale infestation seems to raise slightly the temperature (= disorder). This is in accordance with the prediction that the dominance of one insect species (*M. hellenica* in these pinewoods inferred from abundance data) creates several alterations to the ecosystem reducing the coexistence of species (Hillebrand *et al.*,

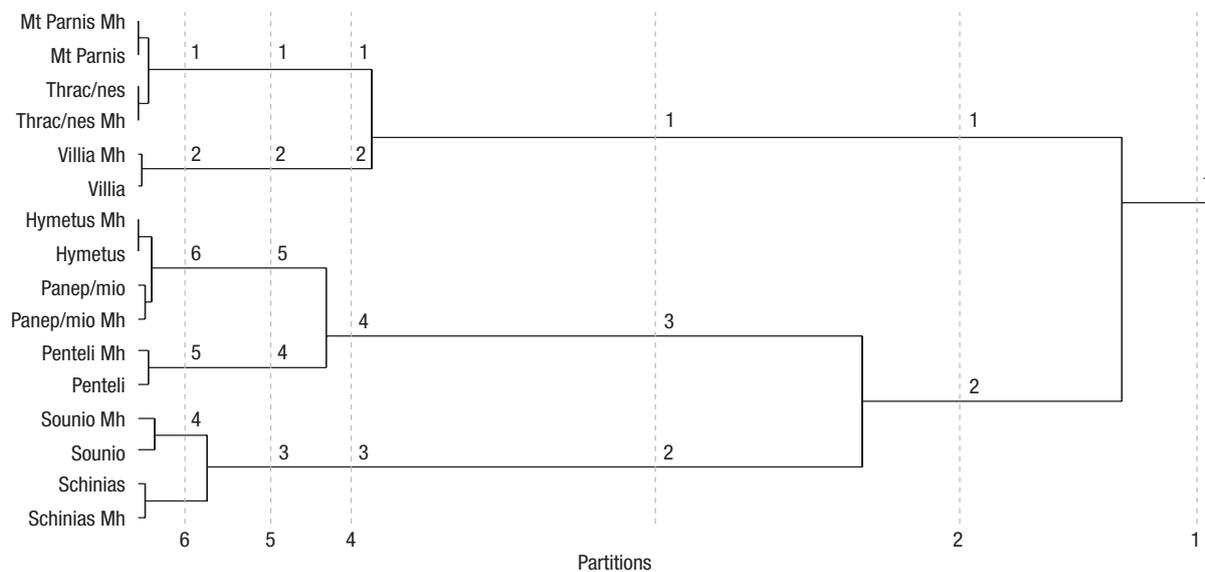


Figure 2. Clustering of pine scale free sites together with pine scale infested sites (Mh). The numbers denote nodes while the numbers characterizing the vertical lines are partitions. Partition levels proceed from coarse (1) to fine (6) which corresponds to site PSF/PSI groups. PSI sites have the trailing «Mh» symbol for the pine scale (*M. hellenica*). The symbol «Mh» denotes infested sites by the pine scale *M. hellenica*.

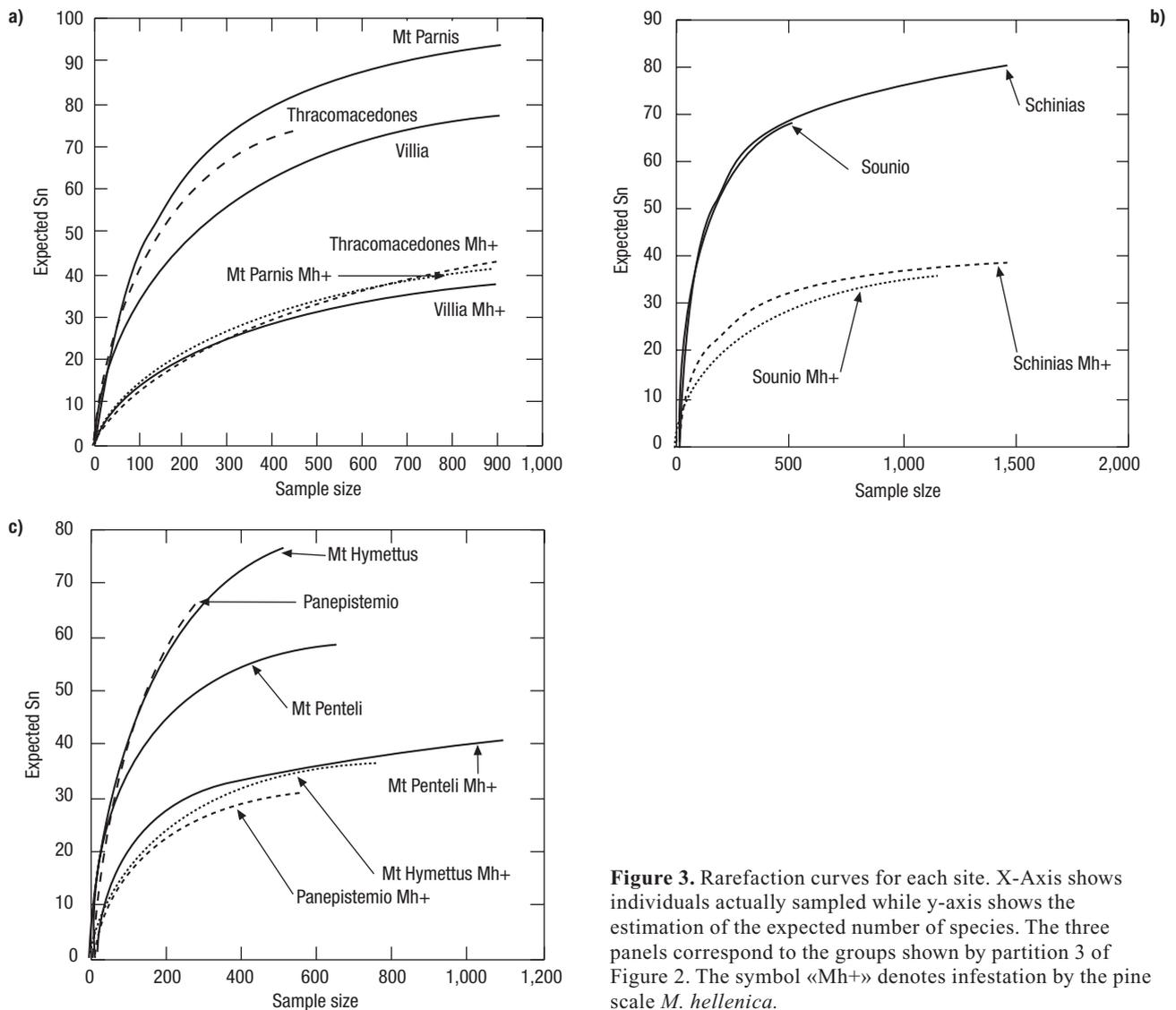


Figure 3. Rarefaction curves for each site. X-Axis shows individuals actually sampled while y-axis shows the estimation of the expected number of species. The three panels correspond to the groups shown by partition 3 of Figure 2. The symbol «Mh+» denotes infestation by the pine scale *M. hellenica*.

2008). The Ewens-Caswell V index (Fig. 5) indicates the same pattern and in addition it shows the lower equitability of insect species in PSI sites.

Indicator values of insect species

Based on the topology depicted in Figure 2 the insect species that show high and significant indicator values are included in Table 1. A salient feature of insect species is that they do not characterize groups of sites above partition 4. There are no species differentially indicating Villia from the sites on Mt Parnitha and Thracomacedones and indicator species occurring only in PSI sites in each location (Table 1 and 2). Also there are no indicator insect species separating the lowland site

at Panepistemio from the sites on Mt Penteli and Mt Hymettus; especially with the site on Mt Hymettus, Panepistemio seems to share the same species pool. However, there are 20 indicator species for the northerly located sites (1, 4 and 8 in Fig. 1) whilst the others have only 10 indicator species.

Individual site comparisons

The V values of individual sites are shown in Figure 5. Sites already receiving anthropogenic impact —*i.e.* Villia, Panepistemio, and Mt Penteli— show an even further decrease of biodiversity. The PSI sites at Villia and Panepistemio show a decrease of V values by 2.646 and 3.557 though their PSF sites had already negative

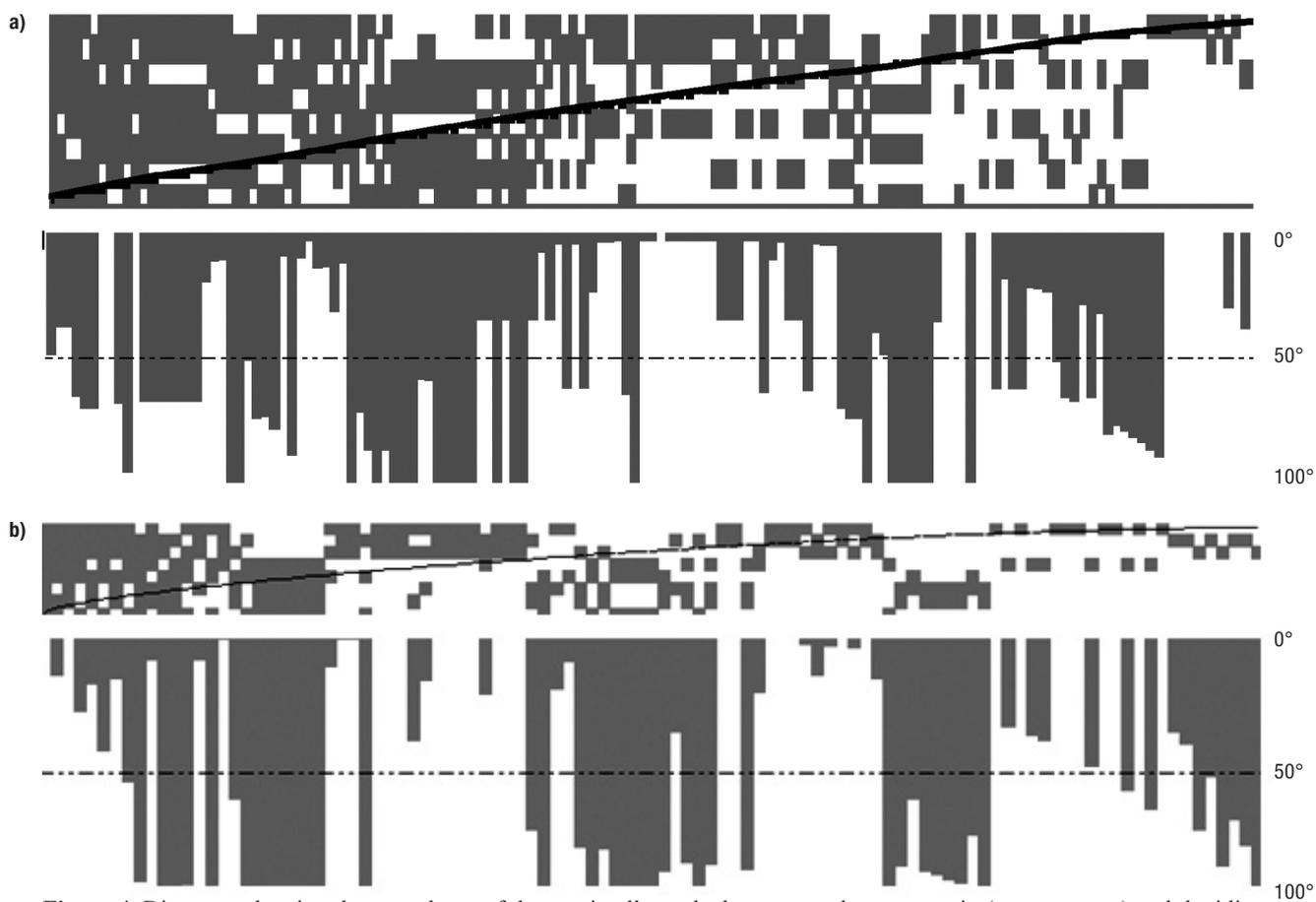


Figure 4. Diagrams showing the nestedness of the maximally packed presence-absence matrix (upper square) and the idiosyncratic temperatures of species (lower square). a) This panel is for sites infested by pine scale and b) for pine scale free sites. The horizontal line in the lower squares of both panels marks system temperatures (explanations in the text). The extinction threshold boundary line is the thick line in each upper square.

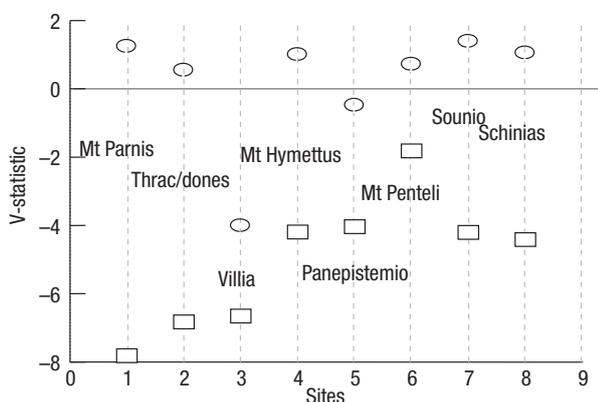


Figure 5. Ewens-Caswell biodiversity-equitability measured by V -statistic in the set of eight sites (16 transects). The algorithm implemented by McAleece (1997) was used. All sites are plotted in PSF-PSI pairs within a location which corresponds to the same x-grid line. PSF sites are denoted by a circle and PSI sites with a square. The $y=0$ line is also plotted to separate the sites with negative V values. Negative values of V as a rule correspond to pine scale infested pinewoods.

values. Similarly the site at Mt Penteli exhibited a decrease by 2.539. The coastal sites (Sounio and Schinias) and Mt Hymettus showed an intermediate decrease by 5.596, 5.467 and 5.199 respectively. The highest decrease in biodiversity happened in the sites on Mt Parnitha and Thracomacedones by 9.059 and 7.375 respectively.

The decrease of biodiversity is weakly correlated to the PSF V values ($r = 0.56$; $p = 0.15$ ns) and weakly correlated with the value of PSI sites ($r = 0.65$; $p = 0.81$ ns). Also, this decrease is neither correlated to the percentage turnover of insect species after the pine scale invasion ($r = -0.2$; $p = 0.97$ ns) nor with the number of species in PSF sites ($r = -0.28$; $p = 0.49$; ns).

Discussion

Due perhaps to the short time since the first introduction of the pine scale, the geological substrates, and

Table 1. Maximum indicator values of all species for the three partitions of Figure 1. All indicator values are significant at $p < 0.01$. For partitions 5-8 there are no significantly valued indicator species

Partition	Order: Family/Superfamily	Species	Indicator value	Group	
2	Neuroptera: Chrysopidae	<i>Dicochrysa flavifrons</i> (Brauer, 1850)	91.67	1	
	Heteroptera: Pentatomidae	<i>Graphosoma lineatum</i> (Linnaeus, 1758)	91.87	1	
	Auchenorrhyncha: Cicadellidae	<i>Euscelis incisus</i> (Kirschbaum, 1858)	81.82	2	
	Coleoptera: Caraboidea	<i>Trechus subnotatus</i> Dejean, 1826	100	1	
	Coleoptera: Caraboidea	<i>Harpalus (Harpalus) rubripes</i> (Duftschmid, 1812)	83.33	1	
	Coleoptera: Coccinellidae	<i>Brumus quadripustulatus</i> (Linnaeus, 1758)	100	1	
	Coleoptera: Staphylinidae	<i>Quedius (Raphirus) coxalis</i> Kraatz, 1858	89.75	1	
	Coleoptera: Staphylinidae	<i>Ocypus (Ocypus) olens olens</i> (O. Müller, 1764)	90	2	
	Coleoptera: Staphylinidae	<i>Leptusa</i> sp.	100	2	
	Coleoptera: Liodidae	<i>Agathidium</i> sp.	100	1	
	Coleoptera: Tenebrionidae	<i>Dichillus</i> sp.	91.67	1	
	Coleoptera: Curculionidae	<i>Pissodes castaneus</i> (?) (De Geer, 1775)	83.33	1	
	Coleoptera: Curculionidae	<i>Pissodes gyllenhalii</i> (C.R. Sahlberg, 1834)	100	2	
	Coleoptera: Cerambycidae	<i>Acanthocinus griseus</i> (Fabricius, 1792)	100	1	
	Coleoptera: Buprestidae	<i>Julodis ehrenbergi</i> Laporte, 1835	83.33	1	
	Coleoptera: Buprestidae	<i>Acmaeodera crinita</i> Spinola, 1838	94.46	2	
	Coleoptera: Buprestidae	<i>Acmaeoderella seminata</i> (Abeille, 1895)	100	2	
	Coleoptera: Buprestidae	<i>Buprestis rustica</i> Linnaeus, 1758	98.56	1	
	Coleoptera: Buprestidae	<i>Melanophila cuspidata</i> (Klug, 1829)	100	2	
	Coleoptera: Buprestidae	<i>Phaenops chalcea</i> Abeille, 1895	100	1	
	Coleoptera: Buprestidae	<i>Phaenops formaneki</i> Jakobson, 1912	100	1	
	Coleoptera: Buprestidae	<i>Anthaxia nigrojubata</i> incognita Bílý, 1974	100	2	
	Coleoptera: Buprestidae	<i>Anthaxia laticeps laticeps</i> Abeille, 1990	100	1	
	Coleoptera: Buprestidae	<i>Meliboeus episcopalis</i> (Mannerheim, 1837)	90	2	
	Coleoptera: Buprestidae	<i>Agrilus marozzinii</i> Gobbi, 1974	100	2	
	Coleoptera: Buprestidae	<i>Trachys problematicus</i> Obenberger, 1918	83.33	1	
	Lepidoptera: Lycaenidae	<i>Polyommatus icarus</i> (Rottemburg, 1775)	83.33	1	
	Hymenoptera: Braconidae	<i>Apanteles</i> sp.	100	1	
	Hymenoptera: Formicidae	<i>Lasius brunneus</i> (Latreille, 1798)	83.33	1	
	3	Neuroptera: Chrysopidae	<i>Chrysoperla carnea</i> Stephens, 1836	91.76	2
		Neuroptera: Chrysopidae	<i>Dicochrysa flavifrons</i> (Brauer, 1850)	91.67	1
		Raphidioptera: Raphidiidae	<i>Ulrike attica</i> (H. Aspöck & U. Aspöck 1967)	96.68	2
		Heteroptera: Lygaeidae	<i>Spilostethus (=Lygaeus) pandurus</i> (Scopoli 1763)	91.06	2
Heteroptera: Miridae		<i>Macrotylus (Alloeonycha) interpositus</i> Wagner, 1951	80.95	2	
Heteroptera: Pentatomidae		<i>Graphosoma lineatum</i> (Linnaeus, 1758)	82.43	1	
Auchenorrhyncha: Cicadellidae		<i>Psammotettix alienus</i> (Dahlbom, 1850)	89.36	2	
Coleoptera: Caraboidea		<i>Trechus subnotatus</i> Dejean, 1826	100	1	
Coleoptera: Caraboidea		<i>Carabus (Pachystus) graecus graecus</i> Dejean, 1826	100	2	
Coleoptera: Caraboidea		<i>Leistus (Pogonophorus) parvicollis</i> Chaudoir, 1869	80.56	1	
Coleoptera: Coccinellidae		<i>Adonia bipunctata</i> (Linnaeus, 1756)	77.95	2	
Coleoptera: Coccinellidae		<i>Brumus quadripustulatus</i> (Linnaeus, 1758)	100	1	
Coleoptera: Staphylinidae		<i>Quedius (Raphirus) coxalis</i> Kraatz, 1858	84.01	1	
Coleoptera: Staphylinidae		<i>Ocypus (Ocypus) olens olens</i> (O. Müller, 1764)	92.23	2	
Coleoptera: Elateridae		Elateridae un02	100	3	
Coleoptera: Tenebrionidae		<i>Akis</i> sp.	81.48	3	
Coleoptera: Tenebrionidae		<i>Tentyria rotundata</i> (Brullé, 1832)	100	2	
Coleoptera: Tenebrionidae		<i>Dichillus</i> sp.	91.67	1	
Coleoptera: Cerambycidae		<i>Acanthocinus griseus</i> (Fabricius, 1792)	100	1	
Coleoptera: Buprestidae		<i>Acmaeodera brevipes</i> Kiesenwetter, 1858	98.64	2	
Coleoptera: Buprestidae		<i>Acmaeoderella cypriota gerae</i> Volkovitch, 1989	100	3	
Hymenoptera: Formicidae		<i>Messor orientalis</i> (Emery, 1898)	95.45	3	
Hymenoptera: Formicidae		<i>Aphaenogaster simonellii</i> Emery, 1894	100	2	

Table 1 (cont.). Maximum indicator values of all species for the three partitions of Figure 1. All indicator values are significant at $p < 0.01$. For partitions 5-8 there are no significantly valued indicator species

Partition	Order: Family/Superfamily	Species	Indicator value	Group
4	Coleoptera: Caraboidea	<i>Harpalus (Harpalus) rubripes</i> (Duftschmid, 1812)	100	1
	Coleoptera: Curculionidae	<i>Pissodes castaneus</i> (De Geer, 1775)	100	1
	Coleoptera: Buprestidae	<i>Trachys problematicus</i> Obenberger, 1918	100	1
	Lepidoptera: Pyralidae	<i>Phycitinae</i> sp. (un. larva)	100	2
	Hymenoptera: Formicidae	<i>Lasius brunneus</i> (Latreille, 1798)	100	1

the soil types among locations, PSF and PSI paired sites are clustered together in the topology of the sites (Fig. 2). This was reinforced by the clustering algorithm which is more sensitive to the presence/absence of a plant rather than to plant coverage. The revealed grouping is in contrast with the findings of other studies (e.g. Luque *et al.*, 2007) who found that different forest management practices produced visible alterations to the plants both in species and coverage. In an attempt to capture subtle differences between PSF and PSI sites, we found no visible in the dendrogram of sites (Fig. 2). Most probably this was caused by the following; (1) There is a large number of plant species with low cover values, especially annual therophytes in the herbaceous layer which do not alter the cluster affiliation of each site; (2) The differences among sites are far larger than those of PSF-PSI couples; (3) Plant species migrate easily from neighbouring sites rather than other areas several kilometres away; (4) At early stages of the secondary succession, the entire plant cover adapted to low sunlight conditions, undergoes the same decrease. The points mentioned above are major guidelines in any forest management application.

Biodiversity comparisons of site groups

The small difference of ecosystem temperature of PSF and PSI sites show a tendency to increased disorder in PSI sites in accordance to the prediction that «biological invasions are breaking down the [ecological and] biogeographic barriers» (Vitousek *et al.*, 1997). However, this situation can be seen only in the abundances of insects and is not reflected in species extinctions but only in the values of V statistic (Lambhead and Platt, 1988).

The Ewens-Caswell (V statistic) has proved a very successful biodiversity index in predicting ecosystem disturbance. All PSF sites, except Villia which is grazed by sheep and goats, have positive V values whilst almost all PSI sites have negative values. The pattern of the insect biodiversity loss (Fig. 5) does not corroborate the view that mountain sites (either as PSF or PSI) are more resistant to the pine scale invasion because they contain more habitat specialists than lowland sites, which presumably receive chronic human impact and this has disrupted any specialised insect-plant association (Brockerhoff *et al.*, 2006). It can be seen that the groups formed by PSI sites are constituted from all types

Table 2. Insect species collected at the three groups of sites corresponding to partition 3 of Figure 2

Site group	All species in the PSF transects	Species exclusive in PSF transects	Species exclusive in transects	All species in PSI transects
Thracomacedones				
Mt Parnitha	120	45	2	77
Villia				
Schinias				
Sounio	81	40	1	42
Mt Penteli				
Mt Hymettus	85	37	5	53
Panepistemo				

of altitude whilst all sites, except Villia, have similar diversities. The low decrease in Villia, Panepistemio, and Mt Penteli can be explained on the basis that both specialist and generalist insects are immune to disturbances already present in PSF sites (Whitehead, 1997). On the other hand the intermediate decrease in V in the coastal sites Sounio and Schinias and Mt Hymettus can be attributed to the intermediate human impact exerted in the form of tourism.

The extensive literature on the adverse effects of—especially pest—invaders in forest ecosystems focuses on the biodiversity of the invaded community as a property that determines its resistance to invasion (Vitousek *et al.*, 1997; Brockerhoff *et al.*, 2006). According to the majority of studies a highly diverse community may have few empty niches so a candidate invader has to compete with native species to exploit them. The invasion of pinewoods by the pine scale does not belong to this category since the entire range of sites has been invaded without regard to diversity. The invasion caused a loss of more than half of the insect species (mean 56.6%; range 41.6–69.5). Interestingly the most diverse site—Mt Parnitha—suffered the largest loss of diversity. This is possibly a manifestation of the disruptive consequences an introduced forest pest may have on the ecosystem. The breakdown of many densely packed niches causes more severe reductions in diversity.

The most intriguing pattern of the rarefaction curves is the consistent similarity in infested sites (Fig. 3). Uniformity seems to be the baseline of biodiversity before the collapse of the ecosystem. This is the result of the uniformity of infested pinewoods since only those species using the declined pine trees dominate the plots (see below). This is the result of the opening up of the canopy that favoured the understory bushes and shrubs. The insects prefer shade so they avoid direct sunlight which is the result of the high transparency of the crown. Therophytes and hemicryptophytes that usually replace these plants in other habitats, in pine forests avoid the higher acidity of the soil. In effect shade preferring insects do not favour infested pinewoods.

Inspecting the idiosyncratic temperatures of insects as indicated by their higher level than the system temperature lines (the horizontal line in the lower squares Fig. 4) we conclude that both site groups are inhabited by insects somewhat disconnected from their normal habitat (Atmar and Paterson, 1993). This parallels the opinion that *P. halepensis* is not indigenous to the

landscapes of mainland Greece but invaded the area possibly helped by humans (Meiggs, 1982). This is mostly manifested in infested pinewoods which contain proportionately more idiosyncratic species than PSF ones. Infested sites also seem to contain more species closer to local extinction. Because these species contribute more noise than the remainder, PSI sites have higher ecosystem temperature. With regard to the hospitability of the sites (Patterson and Atmar, 2000), it is evident that infested pinewoods are more inhospitable as deduced from their reduced insect biodiversity (Fig. 4 and 5). The agreement of rarefaction curves and V values seem to overcome the usual difficulty of which index to use (Hillebrand *et al.*, 2008).

Indicator values of insect species

A feature of Figure 2 is that PSI and PSF sites in the same location can not be separated on the basis of plant coverage alone. Table 1 shows that on the basis of insects, the hierarchy of sites does not produce indicator species at levels above the fourth. The result is the lack of species specializing in PSI sites. Irrespective of the indication ability, the insects occurring only in PSI sites are rare. The insects *Hylotrupes bajulus*, *Hylurgus Micklitzi*, *Tomicus piniperda*, and one unidentified Ptiliidae (Coleoptera) species were found only in PSI sites on Mt Penteli, Mt Hymettus and Panepistemio and only *H. bajulus* in the group of northern PSI sites (Table 2 and Appendix I) in low abundances. These insects feed on dead wood in human establishments while *T. piniperda* is considered as pest of pines (Mendel, 2000). On the other hand, pine scale is not a target of any parasitoid and in many aspects resembles adelgids for which only natural enemies are controlling agents (Brockerhoff *et al.*, 2006). These predators on *M. hellenica* would have been indicator species of PSI sites but they were not found in the study sites.

These findings indicate that the pine scale behaves as a genuine invasive insect species. It deteriorates the ecosystem conditions by increasing the crown transparency of the dominant pine species (*P. halepensis*) and thus increasing light penetration. This alters the predominant conditions of pinewoods causing the local extinction of many insect species either directly or through effects associated with host plants and humidity. In addition the water potential of the pines lowers to such a degree that it alters in an unpredictable way the insect fauna. This favours many wood eaters in the

coleopteran families Buprestidae, Cerambycidae and Scolytidae (Appendix), which are also found in PSF sites as inhabitants of dead wood though in reduced abundance. Also flower visiting buprestids are abundant in PSI sites with light penetration sufficient to sustain a rich ground flora introduced from PSF openings. Hence the similarity of PSF and PSI sites in each location. In partition 3, the three main groups of sites are separated. In this partition, many indicator species from many families can be found (Table 1).

Individual site comparisons

The sites on Mt Parnitha and Thracomacedones at the north of Attica (1 and, 8 in Fig. 1) exhibit the highest discrepancy in terms of V index (Fig. 5) though they are clustered together in the dendrogram of Fig. 2 (partition 2, node 1). The other site at Villia on a similar, in terms of vegetation history, mountain (Mt Kithairon) has negative values of V indicating that the pinewood is highly disturbed. The anthropogenic impact in the PSF site is exerted either as grazing pressure due to excessive demand for local goat meat from summer visitors, or as agricultural practices not found at the other sites in Attica.

This situation is replicated at a lesser degree between the sites on Mt Hymettus and Panepistemio (Fig. 5). The site in Panepistemio has the same pattern of biodiversity decrease with Mt Hymettus but the impact in PSF pinewood is exerted mainly by the traffic in nearby roads. This maybe the reason why its V is negative in the PSF site and the pine scale lowers its biodiversity. The nearby PSI site on Mt Hymettus can not provide insects in the context of a source-sink dynamics (Whittaker and Fernández-Palacios, 2007) because of its lower biodiversity (-4.20 and -0.48 respectively; Fig. 5). In this sense, all insects that abandoned the PSI site on Mt Hymettus have already migrated and can be found in the PSF site in Panepistemio (31 species, Appendix). The site at Mt Penteli receives high anthropogenic influence, but this is purely house building and other establishments associated with human residence. The site is possibly resistant to perturbations (Baletto and Casale, 1991) which is reflected in V values (Lambshhead and Platt, 1988). Mt Penteli exhibits the highest biodiversity among PSI sites but low biodiversity in PSF site, similar to the the PSF site at Thracomacedones.

The lowland sites at Schinias and Sounio behave similarly in terms of V both in PSF and PSI sites. Probably, the lowering of biodiversity comes from the scarcity of predator and parasitoid resources (Lambshhead and Platt, 1988), together with the severe alteration of the microhabitats at PSI sites. It is strange that the sites at Schinias are coastal pinewoods on a sandy ground soft substrate with well developed understorey vegetation consisting of shrubs, bushes and a rich herbaceous layer. In contrast the sites at Sounio receive much lower visitors but are regularly burnt every 5-8 years (data from the Forest Service Extension Office at Lavrion) and grow on a hard limestone derived substrate. In spite of the extremely rich flora and fauna, the PSF site cannot recover easily. The low resilience and the subsequent low V values form a causation-result cycle cannot be unfolded easily. Thus for different reasons they exhibit a reduced (shown as negative) biodiversity as V indicates.

Overall, the introduction of *M. hellenica* in places where it has never existed before, reduced the biodiversity of the entomofauna in pine forest communities. The reduction varied in the study sites according to the history, human impact, and observed insect richness whereas no local extinctions of insect species were observed. Nonetheless, the trend found in ecosystem and idiosyncratic species temperatures could result in a depauperated insect fauna in the short to mid-term.

Any forest management strategy has to take into account that the entomofauna may change in a way not reflected to the individual values of insect species. The high numbers of an insect species such as *M. hellenica*, may cause a decrease of insect diversity before the lowering of plant species and/or vegetation cover is evidenced. Alterations of the insect bioindicator status due to introductions of new species are also subtle and much smaller than the natural differences among biotopes and thus difficult to detect at early stages. One severe limitation of the incorporation of these ideas in a management system is the problem of identification of insect species, which is acute in Greece and other east Mediterranean countries. This limitation is reflected also in the appreciation of the role of specific insect guilds such as the carabid ground predators of pine scales searching for new feeding/oviposition sites. Therefore management practices based on new introductions or augmentation of population densities of existing species should not be undertaken even in highly diverse ecosystems such as Mediterranean pinewoods.

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