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Master thesis

Pine bark beetles of Central America:
Body size and guild structure of the genera *Dendrcotonus* and *Ips.*

Forord

Muligheten til å ta hovedfagsoppgaven utenfor Norges grenser har vært en opplevelse for livet. I februar 2002 dro jeg til Mellom Amerika for å være der i seks måneder å studere bark biller og utføre mitt feltarbeid. Dette gjorde jeg uten helt å vite hva jeg gikk til. Det ble 6 spennende måneder, fra iherdig bark bille jakt i øde skogsområder til å bli ranet i Guatemala City. Gøy har det vært, det er sikkert. Hjemme i Norge tok jeg fatt på oppsetting av 1150 biller, bestemmelse av artene og måling av kroppstrørrelse, det to ikke mindre en i overkant av 6 måneder. For å kunne dra måtte en del ting falle på plass. Å reise fra min nåværende kone var ikke enkel, så jeg vil spesielt takke Mari Anne Skåtun Barstad for at jeg kunne pakke sekken og dra på ekspedisjon. Men det hadde ikke vært mulig å reise uten min veileders iver etter å skape en spennende oppgave, så jeg vil takke Fred Midtgaard for all hjelp, faglig og alt vi har gjort sammen. Ikke minst for de artige turene vi har hatt i Guatemala, Honduras og Belize. Må også takke Lawrence Kirkendall, tror ikke det har vært mulig å gjennomføre etterarbeidet uten den hjelpen jeg har fått. Det var tre veldig lærerike uker. Karl Thunes på Skogforsk i Fana vil jeg også takke for innføringen i oppsetting av biller. Ellers vil jeg takke CONAP i Guatemala for all den hjelpen jeg fikk mens jeg var der nede. Spesielt hovedkontoret i Guatemala som ringte rundt og ordnet avtaler. Må ikke glemme lokal kontorene i Zacapa og Sololá som var meget behjelpelig med å ordne utflukter til furuskogen.

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Abstract

Pine bark beetles are highly assosiated with pine forests in mountain regions of Central America. Difference in host specifity, guild structure and body size in the genera *Dendroctonus* and *Ips* were analysed. Factors such as host species, climatic and altitudinal differences were used to assess if there were any trend in species distribution and guild. Phase of attack was used to test if there was difference in sexual ratio. Body size variation was tested on an altitudinal gradient to see if there was an increase in body size at higher elevation as predicted by theory. Body size difference between the sexes was tested for each locality and species. Most species of *Dendroctonus* and *Ips* showed great geographic distribution and low host specialisation for species in the genus *Pinus*. Sexual composition at the early phase of attack was biased toward more females in all *Dendroctonus* spp. The opposite was the case for *Ips spp*. Body size on an altitudinal gradient gave different results. *Dendroctonus vitei* with low geographic range had no significant difference in body size, even with large altitudinal difference. For the other species, with wide geographich range, *Dendroctonus frontalis* had larger body size at lower altitude and was the only species that did not follow the predicted increase in body size.

Introductions

Central America is situated in the northern Neotropical region with Mexico as a transitional zone between the Neartic and Neotropical regions. Several different plant and animal species originates from North America and plays a large part in the ecosystems in Central America (Salinas- Moreno *et. al.*, 2004). Pine (*Pinus* spp.) forests cover huge areas in the mountainous parts of Central America and is a widespread genus, extending across the Northern Hemisphere of North America and Eurasia to Nicaragua in Central America, but also includes a few species on the Caribbean islands (Farijon and Styles, 1997). Climatic and geological stability in south western parts of North America and Mexico in Miocene (24 million years ago), together with the emergence of the Isthmus of Tehuantepec (lowland tropical forest separating the mountains) favoured the penetration of the cold-temperate biota toward the south and the invasion of Central America. The penetration of *Pinus* into Mexico occurred in two stages from the Rocky Mountains. In the Oligocene (30 million years ago) in the Sierra Madre Occidental and the Pliocene (5 million years ago) at the edge of the Gulf of Mexico along the Sierra Madre Oriental (Salinas- Moreno *et. al.*, 2004). As the penetration of the pine species south into Central America went on, associated phytophagous insects followed (Salinas- Moreno *et. al.* 2004). Several bark and ambrosia beetle species are highly associated with pine species and as the diversity grew with the movement south, the same happened with the bark beetles. Today Central America (excluding Mexico) has ten pine species (Farjon and Styles, 1997) and several associated bark and ambrosia beetles.

Bark beetles of the genus *Dendroctonus* and *Ips* are holartic taxons distributed in North and Central America and across the boreal region of Europe and Asia. Central America (Fig. 1) contains 7 (and one additional new species (Fred Midtgaard, pers. com.)) species of the genus *Dendroctonus*, and 4 species of the genus *Ips*, which are phloemphagous species feeding directly on its host tissue. These species has high specifity toward its host and are found only on the genus *Pinus* (Wood, 1982).

Fig. 1 Study area, Guatemala, Belize and Honduras.

The genus *Dendroctonus* contain species that are perhaps the most destructive force in the coniferous forest of North and Central America. Some species can kill large areas of forest in a relative short period of time. The species are associated with symbiotic fungi and act as an acceleration force to overcome host resistance. The success of these species to overcome host resistance is triggered by the release of aggregation pheromones creating a mass attack (Renwick *et. al.*, 1975). As a primary species, the *Dendroctonus* spp. attacks injured, unhealthy and some species even healthy, vigorous trees (Wood, 1982).
The genus *Ips* is in CA generally not aggressive, attacking injured or unhealthy trees. Some species however, are known to be capable of successful primary attacks. This happens under favourable conditions for population build up. Most *Ips* species act as secondary species and attack the trees after *Dendroctonus* spp. have weakend resistance of the trees (Wood, 1982).
Another group, the ambrosia beetles, is xylemocytophagous and act as tertiary species that do not kill trees. This is a large group of different species of wood borers that cultivate and utilizes symbiotic fungi as food source. They bore into dying or dead trees and are a pest for the wood industry as they have impact on wood quality by making small holes in the wood (Wood, 1982).

Pines reacts to beetle attacks by exuding resin, this mechanism drowns the intruding beetles and plug the entering hole. The amount of beetles infesting a new host is essential for breaking down the host resistance, as only a few beetles will not be able to overcome the defence of the tree. When beetles find a suitable host they bore into the bark to get to the phloem layer, as the beetles reach this layer they produce and release pheromones to attract conspecifics. The pheromones reach the air when the beetles expel frass mixed with feces and the wind spread the pheromones. Both sexes get attracted and upon finding the host they either attack the host (*Dendroctonus*: female; *Ips*: male) or enter the already made entrance holes (*Dendroctonus*: male; *Ips*: female) (Wood, 1982). I will in the following part of the introduction shortly describe the biology of the two genera, the history of attacks, and the pine species of CA, before I describe the goals for this investigation.

Pine bark beetle species biology

The genus *Dendroctonus* and *Ips* have different social organisation associated with reproductions. The genus *Dendroctonus* is monogamous. The female bore new galleries and the male joins after the female have entered the host. Mating occurs in the nuptial chamber;

pair bonds between the female and the male can be minimal or prolonged. Polygyny occurs in the genus *Ips*, here the male excavate the entrance tunnel and the nuptial chamber and admits two to five females to enter. After mating with several females the male remains in the gallery for much of the ovipostition period (Wood, 1982; Reid, 1999).

After entering its host the bark beetles make galleries. When the entrance hole reaches the cambium a flattened cavity is usually excavated. This nuptial chamber has an oval or irregular shape which is bigger than the beetle (three to five times). The female forms egg galleries which extend along the ploem layer, one or more galleries may be found depending on the species. Along the egg galleries the female cut egg niches. After the eggs hatches, the larvas form individual mines (Fig. 2). The galleries can be quite distinct and classification for some species can be done by examining the galleries (Wood, 1982). *Ips* galleries are easily distinguished from *Dendroctonus* as they are long and straight forming a Y or H shape and usually with no frass (Fig. 3) (Billings, 1979).

Fig. 2 Gallerie of *Dendroctonus spp*

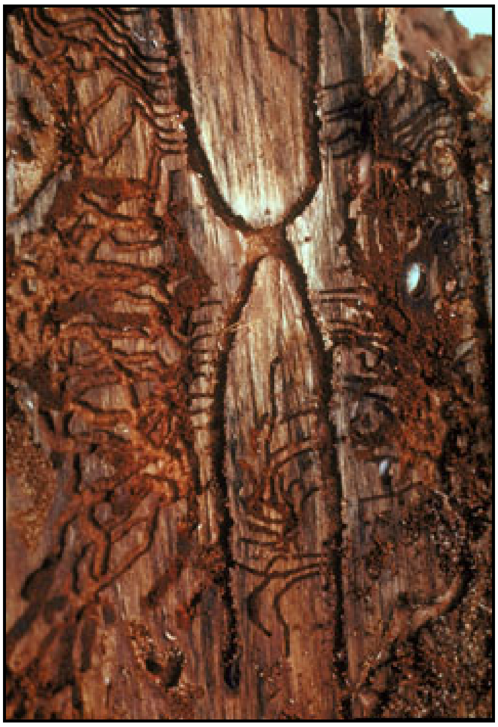


Fig. 3 Gallerie of *Ips spp*

Development is separated in larval instars which vary from two to five and the length of the larva period varies with temperature and geographic location (app. four to eight weeks) (Fig. 4) (Wood, 1982). But apparently the development is only 2-3 weeks in the most aggressive Central American species, *Dendroctonus sp. nov.* and *Dendroctonus frontalis* (Pers. com. Fred Midtgaard). They pupate in the bark and emerge through individual exit holes. The parental beetles can after completing one gallery system construct a second or more galleries (Wood, 1982).

The two genera described here (the genus *Dendroctonus* and *Ips*) can easily be separated by morphological characters. The *Dendroctonus* species are all cylindrical in shape without any prominent turbercles or excavation on the elytra (Fig. 5). The *Ips* species have concavely excavated elytra with several small or large spines along each side of the anterior parts of elytrae (Fig.6) (Midtgaard and Thunes, 2002).

Both genera have been revised on several occasions by various authors; this shows the difficulty of classifying the species. But classification of the different *Dendroctonus* species is especially difficult with use of morphological characteristics. The first monograph of this genus was established by Hopkins in 1909, describing 24 species, based on morphology and biology of the species. Since then much has happened with classification and in 1982, Wood published the work on the bark and ambrosia beetles of North and Central America which stand as the most comprehensive work on these beetles. With the use of karyology and molecular genetics the last decades, there is little disagreement about classification of the genera *Dendroctonus* and *Ips* today (Zúñiga *et. al.*, 2002).

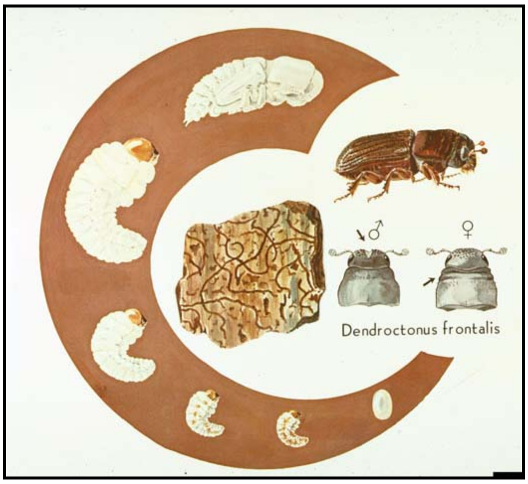


Fig. 4 Life cycle of *Dendroctonus frontalis*.

Fig. 5 *Dendroctonus* spp.

Fig. 6 *Ips* spp.

Guild structure of the pine bark beetles and pine species (*Pinus* spp.) of Central America

Pine bark beetles have a wide distribution and can be found throughout the pine forest of Central America. With utilization of different niches and habitats, the distribution range varies among the species with their specifity towards its host (Wood, 1982; Salinas-Moreno *et. al.*, 2004). *Dendroctonus* and *Ips* species are phloemophagous and specific in host selection, feeding directly on host tissue. Ambrosia beetles are not as restricted as they feed on fungal spores and the beetles survive as long as the fungi do (Wood, 1982). Different species infest the host at different health stage and plays different roles as pests. Succession in attack and infestation give rise to different species composition as the trees resistance breaks down and the tree eventually dies. The primary species are the first to attack and are usually one or a few related phloemophagous species. They are aggressive and break down the trees resistance by infesting it with fungi as they bore into the cambium. As the trees health gets weakened other non-aggressive secondary species are attracted to the tree. Tertiary species usually arrives when the tree is virtually dead and most of the aggressive species have abandoned it. At the different stages of the attack the species composition changes and there is a separation in exploiting the host resources (Wood, 1982; Symmonds, 2004).

The pine forest of Central America is a heterogeneous assembly of forest types dominated by species of the genus *Pinus*. Pines are found from the lowland Atlantic plains to highest mountain areas. Ten pine species (Tab. 1) are divided into four different altitudinal preferences, from lowland to high montane. The climatic and latitudinal differences between lowland and upland areas separate the distribution of the species, but there is great overlap. Lowland areas can have high annual precipitation, but it is unevenly distributed and have long dry season. In upland areas precipitation increases and is more evenly distributed throughout the year. In montane forest there is high diversity among pine species, and Central American mountain regions contain usually more than one species. The climatic zonation of the pine forest is dominated by the precipitation level. The only real separation of the pine species in Central America in between the lowland, containing only *Pinus caribaea* var. *hondurensis*, and the highest altitudes with only a few species (Farjon and Styles, 1997).

Tab. 1 Pine species of Central America (Farjon and Styles, 1997).

Pine species (Farjon and Styles, 1997)	**Elevation range (m)**	**Distribution**
P. caribaea var. *hondurensis*	1- 300 [-700]	Low land
P. devoniana	[100-] 300- 2600 [-2800]	Foothill to montane
P. maximinoii	[100-] 300- 2600 [-2800]	Foothill to montane
P. occarpa	[100-] 300- 2600 [-2800]	Foothill to montane
P. tecunumanii	[100-] 300- 2600 [-2800]	Foothill to montane
P. psedustrobus	[700-] 1100-2600[-2800]	Montane
P. strobes var. *chiapensis*	[700-] 1100-2600 [-2800]	Montane
P. ayachutie	[2000-] 2500-4000 [-4300]	High montane
P. hartwegii	[2000-] 2500-4000 [-4300]	High montane
P. montezumae	[2000-] 2500-4000 [-4300]	High montane

The distribution of pine bark beetles varies and is largest where the highest diversity of pines is (Wood, 1982; Salinas-Moreno *et. al.*, 2004). *Dendrotonus frontalis, Dendroctonus approximatus* and *Dendroctonus valens* have a wide distribution (Salinas-Morneo *et. al.* 2004). *D. frontalis* is aggressive but *D. approximatus* and *D. valens* are non-aggressive, normally found together with more aggressive species (Lanier *et. al.*1988; Sánches-Martínez and Wagne, 2002). *Dendroctonus sp. nov***.** has recently been distinguished from *D. frontalis* through DNA- testing and morphological features (Pers. com. Larry Kirkendall, Fred Midtgaard and Karl Thunes). These two species are very similar in both behavior and morphology (Midtgaard and Thunes, 2003). With the other non-aggressive species the distribution range is not known. The *Dendroctonus vitei* is the only species with narrow distribution, only found in the area around Lago Atitlan, Guatemala (tab. 2) (Wood, 1982; Salinas-Moreno *et. al.*, 2004)

Tab. 2 Pine beetle species (primary and secondary) of Central America (Wood, 1982; Lanier, 1988, 1991 and Zúñiga, 2002), (The name for *D. sp. nov.* has not been established yet).

Pine beetle species (Wood, 1982)	Elevation range (m)	Distribution
D. approximatus Dietz	(Preferred) 2000- 3800	Guatemala and Honduras
D. adjunctus Blandford	(Preferred) >2300	Mountain areas of Guatemala
D. frontalis Zimmermann	(Preferred) 900- 1300	Guatemala and Honduras
D. mexicanus Hopkins	(Preferred) > 700	Guatemala and Honduras
D. parallelocollis Chapuis	No record	Guatemala and Honduras
D. sp. nov.	No record	Belize, Guatemala and Honduras
D. valens LeConte	No record	Guatemala and Honduras
D. vitei Wood	(Preferred) < 2500	Areas in the western highland of Guatemala, region of Sololá
Ips apache Lanier	(Preferred) > 2350	Belize, Guatemala and Honduras
Ips cribricollis Eichhoff	No record	Guatemala and Honduras

Bergmann`rule for change in body size

Since Bergmanns famous publication from 1847, have ecologists been attracted to study the change in body size of animals over an enviromental gradient. He found that body size changes over a latitudinal gradient, and stated that animals with larger body mass suffer smaller losses of energy due to their favourarble relationship between body volume and surface area. This effect is not restricted to latitude gradients alone, because climatic changes do not only occure along latitudinal gradients. Elevations gradients over a small geographic scale have similar effects, and in addition a number of other factors can be responsible for change insect body size. Particulary developmetal temperature in relationsship to generation time (Blackbrun, 1995; Brehm and Fiedler, 2004).

Bark beetle attacks in CA in a historical perspective

Since the late 1800s bark beetle attacks have been recorded in Guatemala and records of attacks during the last century in the 1930s, 1950s, 1970, and 1980s. Most records are from the mountainous areas in western Guatemala, but other areas have also been affected (Schwerdtfeger 1955, Haack 1997). In Honduras outbreaks have been reported from Gualaco in 1939, but in 1962 a large outbreak, possible of *D. frontalis* started in the eastern mountain areas of Olancho. By early 1964 the outbreak had reached catastrophic proportions. Estimations suggested that the outbreak had spread over six million acres with attacking in average 45000 trees a day, but reached 160000 trees killed per day at its peak (Beal *et. al.*, 1964). The proportion of this outbreak gives us an perspective of how aggressive and destructive these beetles can be.

Fig. 7 Outbreak of *Dendroctonus* spp., Virginia, USA.

Fig. 8 Outbreak of *Dendroctonus* spp., Texas, USA.

Outbreaks of *Dendroctonus* (Fig.7 and fig. 8) or *Ips* species of small or large size may be associated with fire, slash or natural disasters, particularly in the case of *Ips*. Even though these species can attack healthy trees, an outbreak can be triggered by attacks on unhealthy trees. Areas with trees injured by forest fire are known to attract *Dendroctonus* and *Ips* species that attacks the injured trees, which is favoured breeding sites at low population densities. Other natural disasters as lightning, tropical storms or drought, that leads to injured or weakened unhealthy trees can be epicentres for epidemic outbreaks. Proper management of the forest is important to keep it healthy and to minimize the outbreak of bark beetles (Wood, 1982).This is particularly true for *Ips*, while the Central American *Dendroctonus* often seem to be much more aggressive and more likely to attack healthy forest (Pers. com. Fred Midtgaard).

Aims of the present study

The aim of this study was to analyze several biological aspects of the genera *Dendroctonus* and *Ips* in Central America. The main foci are:

1) *Dendroctonus* and *Ips* species distribution and diversity are associated with host species, climatic and altitudinal differences. Stage of attack affects mainly species diversity as different species are found at different stages. These factors were used to analyze the distribution and diversity of the species. Difference in the factors would promote difference in species diversity and distribution.
2) The sexual composition of *Dendroctonus* and *Ips* species are different at stages of attack. Females of *Dendroctonus* are the first to attack and the males enters the host some time later and the opposite for *Ips*. The stage of attack determines the sexual composition and at an early stage of an attack there would be bias towards one of the sexes (*Dendroctonus*, female and *Ips*, male). This can be used to distinguish the two first stages of attack and to confirm other features related to these stages.
3) Temperature and host quality determines the size of the species and there is an altitudinal gradient toward bigger body size at higher elevation. Development time and body size increases with decreasing temperature. According to redefinitions of Bergmann`s rule, higher altitude increase the body size.
4) Difference in body size between the sexes is influenced by several factors. Reproduction capacity is body size dependent and females have larger fat reserves used in egg production and oviposition among different insect genera, fitness is known to influence body size and pheromone production is important in fitness. Difference in pheromone production cost between the sexes would also be an important factor, as females invest less than males (Pureswaran and Borden, 2003). In general females tend to have larger body size.

Materials and methods

Samples where collected in mountain areas of Guatemala and Honduras from locations that where known to be infested with pine bark beetles for some while. Also samples collected in Belize and Guatemala by Fred Midtgaard (2002-2003) was included. Phase of attack, general forest type and host tree species were identified at each location.

Locations visited

Fig. 9 Central American countrys with areas visited, 1) Lago Atitlan, 2) Coban, 3) Sierra de Las Minas, 4) Nuevo Santa Rosa, 5) Jocotán, 6) Santa Rosa de Copan, 7) Siguatepeque, 8) Valle de Angeles, 9) Yuscarán, 10) Olancho, 11) Mountain Pine Ridge.

Samples were collected in Guatemala between May till end of July 2003. Data records from CONAP of last years attacks were used to choose locations. They where selected mainly from easy accessibility, different latitude, climatic variation (humid to dry) and pine host species. The areas visited where Lago Atitlan in the western highland, Coban and Sierra De Las Minas in central, Nuevo Santa Rosa east of Guatemala City and Joctotán in the east at the border of Honduras.

From Honduras samples were collected in June 2004. Locations in Honduras where chosen from a course NFG (Norwegian Forestry Group) where holding for ESNASIFOR at different local offices. Locations visited were in Santa Rosa de Copan in the north, Siguatepeque in central and Catacamas in the southeast. I also visited Valle de Angeles near Tegucigalpa and Yurscarán in the south. Quantities of samples collected from each area varied, this had mainly to do with different time spent at each location, size and phase of attack.

A smaller quantity of samples was collected by Fred Midtgaard in 2002 and 2003. Mainly from Mountain Pine Ridge in the south western highland of Belize, but also from different locations in Guatemala. Sampling method varied in this material and will not be taken into consideration in this study.

Sampling method

The samples where hand collected from one or a few attacked trees at each location. Either just picking beetles from the bark or cutting of the bark to collect from the galleries. Samples where taken from the ground and two meters up all around the trees, all insects that were found in the galleries were collected. Exceptions where, Piedra de Amolar (Guatemala) were there had been a forest fire, one tree was cut down and samples were collected from 2 meters up and around the tree. Belen (Honduras) where trees were cut down and samples were collected from the branches (approximately 10- 20 cm thick) in the bowl and San Juan (Honduras) where samples were taken from trees that had been cut down some days before collection were made, and from two trees that had been cut down 1½ month earlier. The beetles where collected in small vials with alcohol (approximately 90%) and labelled. As hand collecting is very time consuming few samples were collected. On a tree with a large attack, it was possible to collect approximately 100 speciments in 4 hours. It was often very difficult to get to and from the different field localities, so the time used at some locations was short and not all localities had large attacks. Therefor sampling often involved not only very much driving to find attacks, but also a considerable amount of walking in rugged terrain to find trees in the right condition.

Preparation equipment

Preparation of samples was necessary to be able to identify and measure the body size of the beetles. The samples where dried before being mounted on pins. Morpho insect pins, black enamelled, number 2, special mounting glue (Shellac gel, BioQuip Products, Inc), thick paper (good quality, 270 g/m^2), were used for mounting. The beetles where attached to the tip of triangular shaped paper, on the right side between elytra and pronotum in a horizontal angel (labelled with species, place, coordinates, collector, date, collection method (tree standing 2 meters up)).

The exception was, *D. valens*, which was pined directly through the body because of large body size, this was done 2/3 in front on the right elytron (mesothoracic).

Identification

A Wild Leitz, Wild heerbrugg M7A microscope was used for magnification. *The bark and ambrosia beetles of North and Central America* (Coleoptera: Scolytidae). *A taxonomic monograph* by Wood (1982) and comparison with already identified beetles were used in the identification. The beetles were classified down to species and sex in the genera *Dendroctonus* and *Ips*.

Body size measurements

Wild Leitz, Wild Heerbrugg M7A microscope where used to do the measurements. Leica HC plan 10x20 measurement ocular was used to get exact measurements and the microscope where calibrated with a Leitz calibrating plate (2mm long, divided into 200 marks). Exact calibration was different at different magnifications and different magnitudes were used for the different species (10❸, 15❸, 18❸, 20❸ and 31❸).The measurements were recalculated to mm.

There is a distortion in measurement of total body length as the lateral angel between elytra, pronotum and head differs between speciements. Measurements done this way would not be accurate, so measurements of elytra and pronotum were done independently from a dorsal view. The lengths from anterior to posterior end of elytra and of pronotum were measured.

Karyology

Defining *Dendroctonus* species by external morphology is difficult and early studies suggested that it was one of the most difficult genera for systematic studies (Lanier *et. al.*, 1988). Large variation in external morphology in different species makes karyology useful. The species found in areas around Lago Atitlan were DNA tested with genetic sequencing to confirm the classification done on morphological futures. DNA was extracted from 12 speciments from 3 locations, 4 from each location (Finca Chuchiya 1, Finca Socorro and Colonia Maria Tecun).

Maps

Maps were used for different purpose, mainly reference to coordinates, latitude and climatic variation.

Guatemala

Maps from IGN (Instituto Geográfico Nacional), 1:50000, coordinates and latitude.
Maps from IGN

- Annual rainfall, maximum, minimum, medio.
- Weather stations, normal rainfall, each month and annual.
- Humidity/ climate zones
- Vegetation

Maps from CONAP (Consejo Nacional De Areas Protegidas), national park and reserves.

- Joctotán, 1:1185751
- Reserva De Biosfera, Sierra De Las Minas, 1:439778
- Parque Nacional " Las Victorias", Coban, 1:22504
- Áreas de usos múltiples cuenca del Lago Atitlán, 1: 189864
- Parque Nacional, Laguna El Pino, Santa Rosa, 1:51949

Honduras

Maps from IGN (Instituto Geográfico Nacional), 1:50000, coordinates and latitude.
No other maps.

Attack detection and definition of phase of attack

Fig.10 Aerial view of attack in progress with all phases present.
The attack is moving from left, dead trees (red canopy) towards the rigth where newly attack trees (ligth green and yellow canpy) can be seen.

Defining the attack phase was done according to the established definitions used for *Dendroctonus* attacks in NA. However, additional data was collected to establish the correct phase of attack, which was necessary for the further analysis.
Attacks occur in different phases by a distinct pattern. This pattern appears when pines are attacked by pine bark beetles and are different from other insect infestation and diseases. Three stages are established for beetle-infested pines, which reflect the different phases of attacks. The practical importance of identifying these stages is to evaluate how an attack will spread so the necessary and correct control measures can be taken. From knowing the different phases one can estimate how long the attack has been going on, say something about the size and aggressiveness of the attack, and if the pines are infected with one or several pine bark beetle species (late attacks can be infested with secondary and tertiary species) (Billings, 1979).

The first thing to look for when monitoring a forest area is dead or diseased single or groups of trees. Pines with yellow- or red canopy would be an indication of pine bark beetle attack (Fig. 10). The next step is to inspect the trees and determine if they are infected with pine bark beetles. Pitch tubes on the bark is the most immediately vivible symptom, which are glossy masses of resina where the adult beetles bore into the trunk of the tree. The pitch tubes are soft and pink when the attack is new and then hardens over time (Fig. 11). When removing the bark the galleries appear. They may vary in length and structure, depending on species and time since attack (Fig. 13).

Phase 1 Pines with fresh attacks

The first pine bark beetles arriving to the tree bore into the bark and produce pheromones (chemical attractant) to attract other conspecifics to the tree. This is necessary to break down the immune system of the pine tree so that the beetles can survive and reproduce. The other beetles that attack the pine also produce and send out pheromones and cause a mass attack and a rapid dead of the tree.

In phase 1 the foliage appears normal, fresh and green, with no discolouring. In CA however, a slight yellowing can often be seen on this stage (Pers. com. Fred Midtgaard). Pitch tubes are found on the bark, but the part of the tree affected depends on the species. Some species begin their attack in the upper part, other species on the lower part of the tree. The pitch tubes are white or pink. The bark still remains tight and hard to remove, and the wood surface looks white and healthy (Fig .12). Cutting of the bark, galleries with adult beetles will appear (Fig. 13) (Billings, 1975)

Fig. 11 Pitch tube.

Fig. 12 colour of the wood is white.

Fig. 13 Adult beetles in the galleries.

Phase 2 Pines with developing broods

When the immune system of the pine is broken down the beetles stop producing pheromones. The beetles have laid eggs which soon hatch into small white larvae that start feeding on the inner bark. The larvae feed away from the adult gallery and move into the outer bark as the larvae develop. Here they change into white pupae and further into brown or black adults occures. So to summarize, at this phase one will find the beetle at all stages in their life cycle.

Fig. 14 Discolouring of the canopy.

Fig. 15 Galleries with larvae.

In phase 2 the foliage starts discolouring, some are still green while others are turning yellow or red (Fig. 14). But the foliage colour varies greatly and is no good indicator at this stage. Apparently, persipitation is an important factor in the rate of discoloration. In moist environment yellowing seems to be slower (Pers. com. Fred Midtgaard) The pitch tubes are hardened and exit holes made by parent beetles may be seen. White dust made by ambrosia beetles may be seenat the base of the trunk. The bark is loose and easy to peel off the trunk and the wood is light brown. The colour may be different, dark brown with blue or black section from fungi. Adults and larvas will be found in the cortex of the bark (Fig. 17).

Fig. 16 The colour of the wood is brown.

Fig. 17 The cortex of the bark has adults and larvae.

Phase 3 Pines killed, the pine bark beetle have left the tree

At this stage the pupaes have developed into adults which have left the tree. The tree is termed "inactive" when no *Dendroctonus* of any stage can be found. This can also be indicated by red foliage colour and needles that have started dropping (Fig. 18). Ambrosia beetle dust is abundant at the base of the tree (Fig.20). The pitch tubes are hard and yellow. Exit holes are numerous and the bark is very loose (Fig 19). The colour of the wood is dark brown to black (Fig. 16).

Fig. 18 Colour of the canopy is red, needles are dropping.

Fig. 19 Exit holes on the surface of the bark.

Fig. 20 Ambrosia beetle dust, at the base the tree.

Species diversity and guild structure

Lago Atitlán

Fig. 21 Sololá, region of Lago Atitlán with locations visited. 1) Finca Chuchyia, 2) Finca Socorro, 3) Colonia Maria Tecun, 4) Barreneché and 5) Argueta.

The localities are divided into to main areas, approximately 3 km north and 3 km southeast of Sololá (Fig. 21). The area north of Sololá includes Barreneché, Argueta and Colonia Maria Tecun, and the area southeast includes Finca Chuchiya and Finca Socorro. The locations are mainly pine forest with some mixed vegetation. My collection from Lago Atitlán contained mainly two primary pine bark beetles, *D. vitei* and *D. valens*. But it also some contained secondary and teriary species.

Area southeast of Sololá

Finca Chuchyia

Finca Chuchyia was one of the main locations I visited and is one of the locations I have collected most samples.The locations collected from in May and July are approximately 300 meters apart, i will differentiate between these trough this paper, as Finca Chuchyia I, II and III from the date of collection. Finca Chuchyia 19.05.03 as I, Finca Chuchyia 17.07.03 as II and Finca Chuchyia 18.07.03 as III.

Finca Chuchyia I

This location has to pine species, *P. occarpa* and *P. pseudostrobus,* collection were taken only from *P. Pseudostrobus*. The area was small, approximately 50 m² with spread attacks, new and old. Collected *D. vitei*, *D. valens* and tertiary species (Tab.5).

Finca Chuchyia II

Collected from three trees which could be either *P. occarpa, P. pseudostrobus, P. tecunumanii* or just one species. Active attacks on most trees, found only *D. valens* on the lower part of the trees, approximately up to 1 meter above ground. This area was different from the other area in Finca Chuchyia, separated about 200 meters apart with agricultural area. This area had long been attack and most of the trees have been cut down and taken out. Only the trees that looked healthy were still there, which now were infected with *D. valens*. This area is an open area with spread pine trees (Tab. 5)

Finca Chuchyia III

The collection was made from *P. occarpa*. After 2 months the attack has moved approximately 200 meters south and the area between I and II had spread attacks, with all phase attacks. Collected *D. vitei* and tertiary species (Tab. 5).

Finca Socorro

Collected from one tree, *P. pseudostrobus*. Spread attacks in the area, two pine species found, *Pinus pseudostrobus* and *Pinus occarpa*. Adult pine forest with mixed vegetation. Found only active attacks on the pine species I collected from. Found only *D. Vitei* on this location (Tab.5).

Area norhteast of Sololá

Colonia Maria Tecun

Collected from one tree, *P. pseudostrobus*. Found dead trees spread over the area that was investigated, approximately 500 m², which had signs of beetle attacks. At this site the attack had not been aggressive and only few trees were infested at this moment. The location was also fairly small with surrounding agricultural areas. Found *D. vitei* and *D. valens* (Tab.5).

Barrenché

Collected form one tree, *P. occarpa.* Large forest area, approximately 2 km², with spread attacks all over, new and old. The forest contained several pine species, *P. occarpa, P. strobus, P. pseudostrobus* and *P. tecunumanii*. From my investigation only *Pinus occarpa* had active infestations. Found old attacks on *Pinus strobus.* Found only *D. vitei* (Tab.5)

Argueta
Collected from one tree, *Pinus tecunumanii.* Approximately 500 m² with spread infestation, only one pine species in the area. Found only *D. vitei* (Tab.5).

Other areas in Guatemala:

Lago el Pino, Nuevo Santa Rosa
Lago el Pino is a Parque Nacional which surrounds a lake. Very few pines were found and only some showed sign of old attacks. Found a little group of about 10 trees with active attack, but the pitch tubes were found high up in the trees. Collected from 1 tree, found 2 specimens, *D. sp.nov.* (Tab. 6).

Parque Victoria, Coban
Parque Nacional Las Victorias is loctated in the north side at the edge of Coban. The approximately 84 ha areas have mixed forest, with large old pines as main vegetation. Chattered pine bark beetle attacks were found all over the park, mainly old attacks. Samples were collected from two trees, *P. maximinoi*, and had phase attack 1. The pine bark beetles found were *D. sp.nov.* and one sample of *D. frontalis* (Tab. 6).

Finca Santa Clara, Sierra de las Minas Biosphere Reserve
in the southern slope/hills in Teculután area, El Cimiento. The samples were collected in Finca Santa Clara, at 1640 meters. The area had chattered attacks, but most were old. Found only few trees with active attacks, collected only from one tree, *P. occarpa* with phase attack 1. This location had only *D. sp.nov.* and 1 specimence of *D. approximates* (Tab. 6).

Piedra de Amolar, Jocotán
Piedra de Amolar contained several pine species, collected from *P. tecunumanii,* phase attack 2. Samples were collected at the edge of a large outbreak.The species found were *D. frontalis* and a smaller amount of *Ips apache* (Tab. 6).

Honduras

Belen, Copan de Santa Rosa
Only *Ips* species found. Pure pine forest which were stressed by drought. Collected from branches of *P. occarpa* with phase 2 attack. Not exact elevation, estimated to be 1500 m (Tab. 7).

San Juan, Siguatepeque
Park area with planted pines. Collected from trees that were cut down some days prior to my vistit. Collected from *P. maximinoi* with phase 1 attack. I found only *I. cribicollis and I. apache* (Tab. 7).

La Colonia, Olancho
Large forest area, phase 1 attacks by *D. frontalis* and *Ips* on old attacks. Not exact elevation, estimated to be 700 m (Tab. 7).

Valle de Angles, Tegucigalpa
Small area attacked by *D. valens* and *D. approximates*. Two pine species were found, *P. occarpa* and *P. maximinoi*. The locality had phase 1attack (Tab. 7).

Finca Santa Rosa, Yuscarán
Pine plantation with 7-8 years old trees. *Ips* attacks in the upper part of the trees, *Dendroctonus approximates* at ground level and in the roots. Galleries were found up to 1 meters down into the roots. The trees had phase 1 attacks. Large area
Infected, possible the entire plantation (Tab. 7).

Belize and Guatemala
Included samples collected by Fred Midtgaard in 2002-2003 from different locations in Guatemala and Mountain Pine Ridge, Belize. Mainly *Ips*, but *D. sp. nov.* was found in Cow trail, Belize. *P. caribaea var. hondurensis* was the main pine species in Belize. Not exact elevation, estimated to be 800 m (Tab. 8).

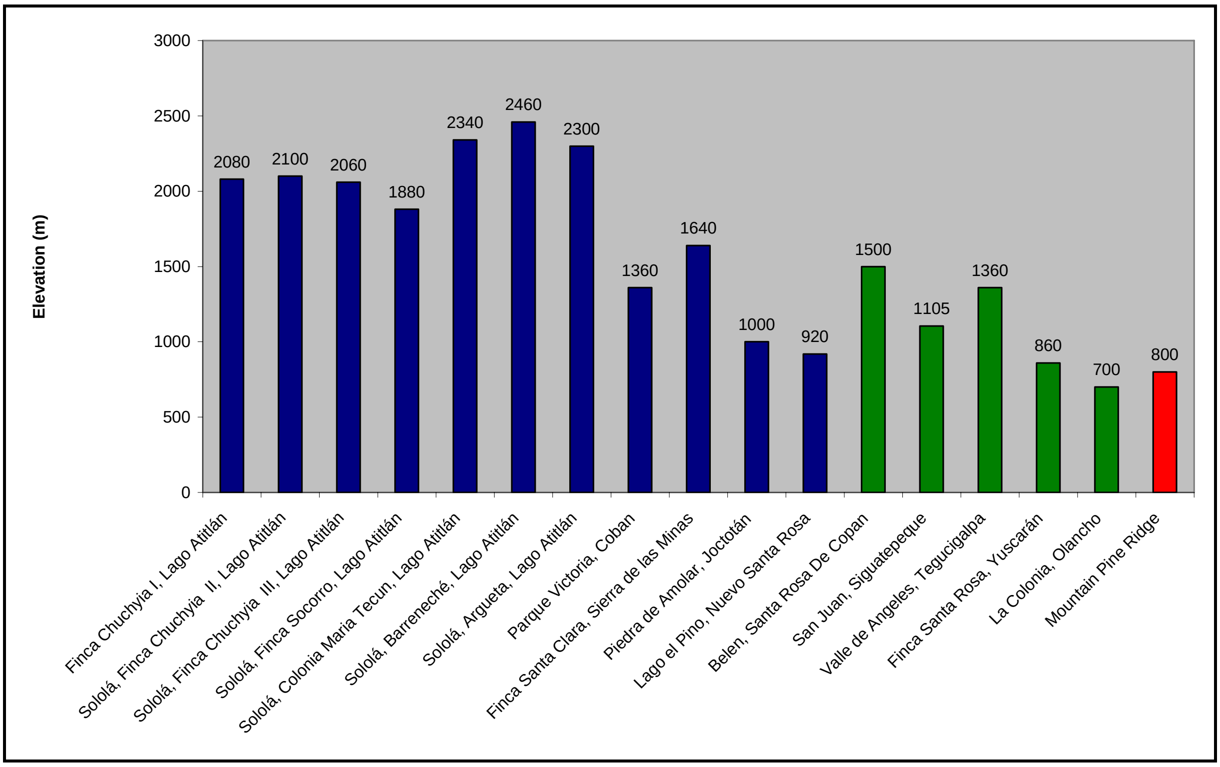


Fig. 22 Elevation at the different location in Guatemala (blue), Honduras (green) and Belize (red)

The main difference between locations around Lago Atitlan and the other locatities is the elevation. The Localities around Lago Atitlan were at1880 to 2460 m, which is higher than all the other locations (Fig. 22). Elevations overlap between the other localities in Guatemala, Honduras and Belize.

Statistics

Analysis of body-size measurements was run through Minitab. Body-size measurements of *Dendroctonus* spp and *Ips* spp samples were used in the analysis. Two analyses were conducted, comparison between the same species at the same location, and between locations were the main objectives.

The purpose of these analyses was to test:
a) Test if there are significant variations in body size of *Dendroctonus* and *Ips* species at different elevations. The H1-hypothesis is that body size increase with increasing elevation.
b) Test if there is significant difference in body size between the sexes. The H2-hypothesis is that females have greater body size than males.

Normality test (Anderson-Darling) was performed to examine if the body-size measurements of the same species followed normal distribution. The normality test was performed prior to the One-way ANOVA analysis to confirm normal distribution.

In order to test the above hypothesis, **One-way ANOVA** (analysis of variance) was used with 95% confidence level. Analysis of both elytra (length) and pronotum (length) were performed.

Locations with low sample size (< 5) were excluded from the analysis **a)**. Localities included are shown in Tab. 3.

All samples of the same species and from all location it was found, are included in **b).**
D. approximates was excluded from the analysis because of low sample size.

Tab. 3 Localities included in **a)**, * elevation is not exact.

Species	Locality	Elevation (m)
D. frontalis	La Colonia, Olancho, Honduras.	700 *
	Piedra de Amolar, Jocotán, Guatemala	1000
D. sp. nov.	Cow Trail, MPR, Belize	800 *
	Parque Victoria, Coban, Guatemala	1360
	Finca Santa Clara, Sierra de las Minas, Guatemala	1640
D. valens	Valle de Angeles, Honduras	1360
	Finca Chuchyia 3	2060
	Finca Chuchyia 1 Lago Atitlan, Guatemala	2080
	Finca Chuchiya 2	2100
D. vitei	Finca Socorro	1880
	Finca Chuchiya 3	2060
	Finca Chuchiya 1 Lago Atitlan, Guatemala	2080
	Colonia Maria Tecun	2340
	Barrenché,	2460
I. apache	D'Silva Forest Station, MPR, Belize	800 *
	Finca Santa Rosa, Yuscarán, Honduras	860
	Piedra de Amolar, Jocotán, Guatemala	1000
	San Juan, Siguatepeque, Honduras	1105
I. cribricollis	D'Silva Forest Station, MPR, Belize	800*
	Finca Santa Rosa, Yuscarán, Honduras	860
	San Juan, Siguatepeque, Honduras	1105
	Belen, Santa Rosa de Copan, Honduras	1500

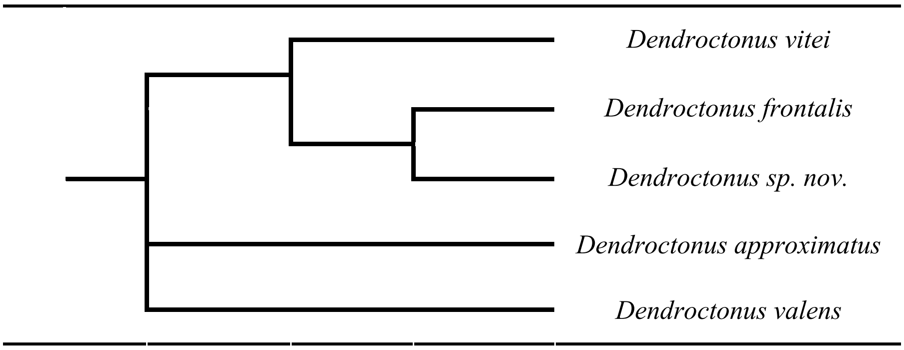
Results

The results from the analysis are shown in figures for the normality test (appendix), box plot of difference in body size versus elevation, difference in body size between the sexes and summary of the one way ANOVA (appendix, worksheet for the one-way ANOVA analysis). Both analysis of elytra and pronotum are shown. It is important to have in mind that pronotum is smaller and that the data are shown on a smaller scale, this also makes it more sensitive to extreme measurements.

Karyology

DNA extractions from the 12 specimens from the 3 locations in Lago Atitlan supported the morphological classification and were identified as *D. vitei*. As there is little data on this species form earlier studies and known to have a very small geographic distribution, genetic sequencing was necessary to be certain of the right identification (Zúñiga *et. al.*, 2002). With the karyology data, phylogenetic relationship between the species may be established (Tab. 4). *D. sp. nov.* was recently distinguished from *D. frontalis* with genetic sequencing data and the species is closely related to *D. frontalis* (Midtgaard and Thunes, 2002). There was no need for genetic sequencing of the other species, as there was no problem identifying these using morphological features.

Tab. 4 Phylogenetic relationship of the species of *Dendroctonus* and *Ips* in CA. Phylogenetic relationship decreases to the downwards. (Wood, 1982; Lanier *et. al.*, 1988; Zúñiga *et. al.*, 2002)



Species diversity and guild structure

The species found at localities around Lago Atitlan (Guatemala) were most diverse and were taken from 4 pine species at attack phase 1 and 2. The samples contained most samples of *D. vitei* and *D. valens*, but also teriary species were found (Tab. 5). The other localities in Guatemala contained mainly *D. sp. nov.* and *D. frontalis* (Tab. 6). The localities in Honduras had either *Dendroctonus* species or *Ips* species as main beetle infestation (Tab. 7). Samples collected by Fred Midtgaard in Guatemala and Honduras contained mainly *Ips* species, but *D. sp. nov.* was found at one locality (Cow Trail, Belize) (Tab. 8). The species found in Guatemala and Honduras are summarised with host species, which shows that *P. occarpa*, *P. pseudostrobus* and *P. maximinoii* contained most species (Tab. 9).

Tab. 5 Species found around Lago Atilan with number speciments collected, host species and phase of attack. (P. ps, P. pseudostrobus; P. tec., P. tecunumanii; P. occ., P. oocarpa).

Pine beetle species (Wood, 1982)	*Pinus* species (Farjon & Styles, 1997)						
	Finca Chuchyia Phase 1			**Finca Soccoro**	**Colonia Maria Tecun**	**Argueta**	**Barrenché**
	I	*II*	*III*	Phase 1	Phase 2	Phase 1	Phase 1
	P. ps.	*P. spp (P.ps., P. tec., P.occ.)*	*P. occ.*	*P.pseudostrobus*	*P. pseudostrobus*	*P. Tecunumaii*	*P. occarpa*
Dendroctonus approximatus							
Dendroctonus valens	9	52	10		2		
Dendroctonus vitei	59		144	55	79	2	12
Dendroctonus sp nov							
Dendroctonus frontalis							
Ips apache							
Ips cribricollis							
Pityophthorus confusus bellus			5				
Pseudips mexicanus	4						
Hylurgus imcomptus	2		1				
Hylurgops planirostris			1				
Gnathotrichus sulcatus	2						
Cossoninae ssp			4				

Tab. 6 Pine beetle species found in Guatemala, with pine species and sample.

Pine beetle species (Wood, 1982)	*Pinus* species (Farjon & Styles, 1997)				
	P. devoniana	*P. maximinoi*	*P. occarpa*	*P. pseudpstrobus*	*P. tecunumanii*
Lago Atitlan					
Dendroctonus approximatus					
Dendroctonus frontalis					
Dendroctonus sp. nov.				X	
Dendroctonus valens			X	X	X
Dendroctonus vitei			X	X	X
Ips apache					
Ips cribricollis				X	
Cossoninae ssp				X	
Gnathotrichus sulcatus				X	
Hylurgus imcomptus				X	
Hylurgops planirostris				X	
Pityophthorus confusus bellus				X	
Pseudips mexicanus				X	
Sierra de las Minas					
Dendroctonus approximates			1		
Dendroctonus sp.nov.			24		
Copan					
Dendroctonus frontalis		1			
Dendroctonus sp. nov.		211			
Pityophthorus confusus bellus		17			
Jocotán					
Dendroctonus frontalis					98
Ips apache					7
Lago el Pino					
Dendroctonus sp.nov.	2				

Tab. 7 Pine bark beetles collected in Honduras, location, host pine species and phase attack.

Pine beetle species (Wood, 1982)	*Pinus* species (Farjon & Styles, 1997)				
	Valle de Angles *P. ssp.* *(P. occarpa and P. maximinoi)* Phase 1	Yuscarán Finca Santa Clara *P. occarpa* Phase 1	San Juan Siguatepeque *P. maximinoi* Phase 1	Belen Santa Rosa de Copan *P. occarpa* Phase 2	La Colonia Olancho *P. caribea* Phase 1
Dendroctonus approximatus	4	4			
Dendroctonus valens	19				
Dendroctonus sp. nov.	2				
Dendroctonus frontalis					44
Ips apache	3	10	33		3
Ips cribricollis			65	23	

Tab. 8 Pine bark beetles collected by Fred Midtgaard in Belize and Guatemala, 2002-2003.

Pine beetle species (Wood, 1982)	*Pinus* species (Farjon & Styles, 1997)						
	Belize, MPR D`Silva *P. caribaea*	Belize, MPR Tower lodge *P. caribaea*	Belize Cow Trail *P. caribaea*	Guatemala Chimaltenango not indent.	Guatemala Chiquimula not indent.	Guaetamala Poptun *P. caribaea*	Guatemala Munic Fraijanes Finca Loma Linda not indent.
Dendroctonus sp. nov.			13				
Dendroctonus frontalis							
Ips apache	43	24	5	1	5	4	2
Ips cribricollis	7	7	1	1			

Tab. 9 Summary: Pine beetle species found on *Pinus* species in Guatemala and Honduras.

Pine beetle species (Wood, 1982)	*Pinus* species (Farjon & Styles, 1997)					
	P. occarpa	*P. pseudostrobus*	*P. tecunumanii*	*P. maximinoi*	*P. devoniana*	*P. caribaea*
Dendroctonus approximatus	X			X		
Dendroctonus valens		X		X		
Dendroctonus vitei	X	X	X			
Dendroctonus sp. nov.	X	X		X	X	
Dendroctonus frontalis			X	X		X
Ips apache	X		X	X		X
Ips cribricollis	X	X		X		
Pityophthorus confusus bellus		X		X		
Pseudips mexicanus		X				
Hylurgus imcomptus		X				
Hylurgops planirostris		X				
Gnathotrichus sulcatus		X				
Cossoninae ssp		X				

Sex composition

Identification of the sexes in both *Dendroctonus* and *Ips* species were done to determine any difference in sex distribution in the phase of attack. All collections were made at phase attack one, except collection taken in Guatemala, Colonia Maria Tecun and Piedra de Amolar. The data presentes only the main species collected at each location, *Dendroctonus* ssp (Fig. 23a) and *Ips* ssp (Fig. 23b).

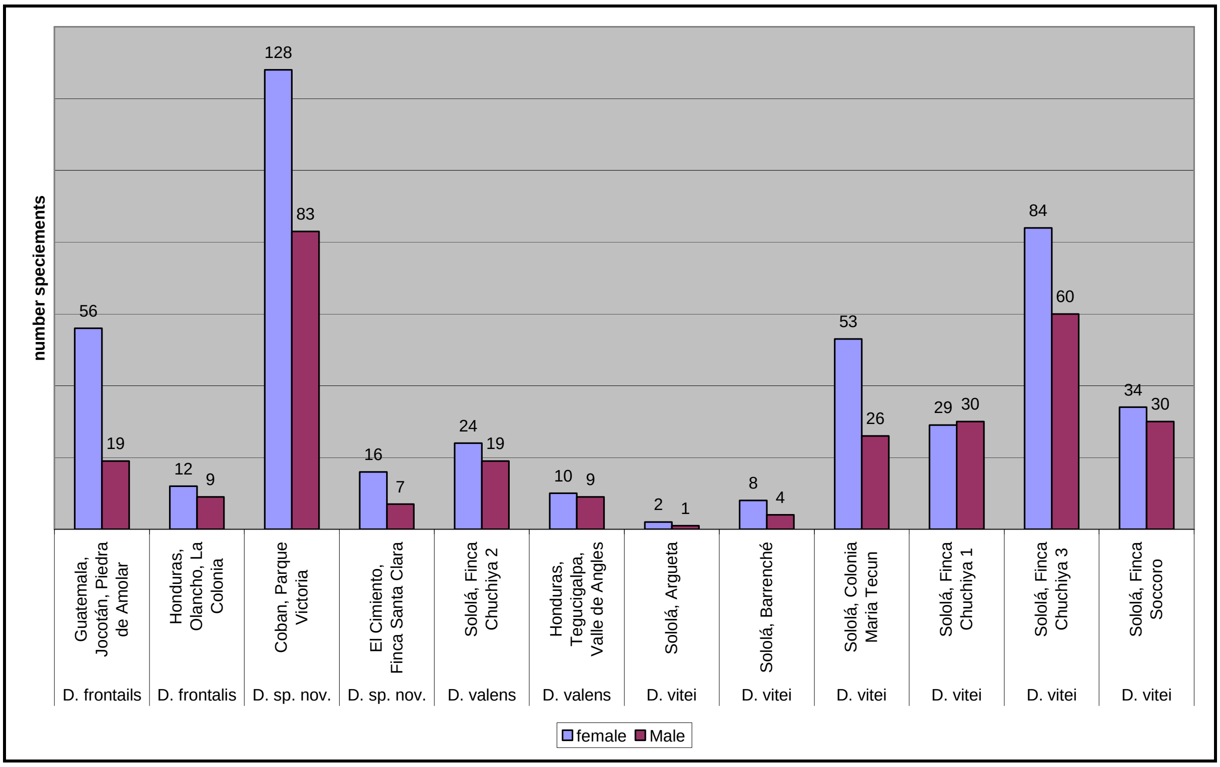


Fig. 23a Main species sex comparison, *Dendroctonus* spp.

With high sample number (> 65) at locations there is significant difference between sexes collected, with a greater number of females. But with lower sample number (< 65) the difference between the sexes is lower but still higher number of females. The only exception is samples from Sololá, Finca Chuchyia 1 where the females were outnumbered by males in one sample.

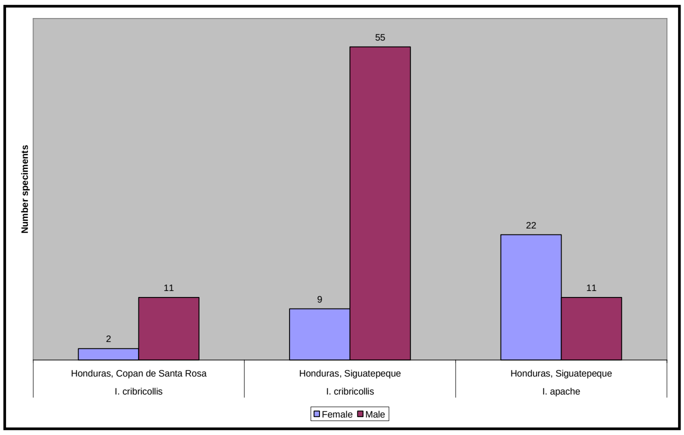


Fig. 23b Main species sex comparison, *Ips* spp.

The sample size of *Ips* ssp was lower than *Dendroctonus* ssp (< 65) and *Ips* ssp were collected at fewer locations, mainly as substitute species. The only locations *Ips* ssp were the main species are shown here (Fig. 23b) and only *Ips cribricollis* had significantly higher number of males. *Ips apache* had higher number of females.

Body size measurements

Normality test (Anderson-Darling)

Testing for normal distribution of body-size was performed for both elytra and pronotum among the species. The normality tests of elytra and pronotum shows the same distribution pattern, which indicates normal distribution of the data. Both elytra and pronotum of all species had P-value < 0,005, except elytra measurements of *D. valens* (P- value 0.385) and both elytra (P-value 0.037) and pronotum (P-value 0,054) of *Ips apache.* The distribution of the most extreme data of elytra and pronotum, the smallest and largest sizes, does not fit the estimated normal distribution line. It also seems to be a greater spread of the data plots for elytra than pronotum. This indicates that elytra vary more in size than pronotum (appendix II).

a) Body size difference with elevation

Tabel.10 The one-way ANOVA analysis: Elytra and pronotum length (mm) of *Dendroctonus* spp, compared with elevation (m).

Species	Location			Elytra			Pronotum		
		Elevation	n	Mean	StDev	P	Mean	StDev	P
D. frontalis	**La colonia**, Olancho, Honduras	700	44	2,0343	0,1051	**0,001**	0,80955	0,05759	**0,000**
	Piedra de Amolar, Jocotán, Guatemala	1000	98	1,9549	0,1456		0,75847	0,07209	
D. sp. nov.	**Cow Trail**, Belize	800	9	2,5856	0,1655	**0,374**	1,0444	0,0757	**0,155**
	Parque Victoria, Coban, Guatemala	1360	212	2,5646	0,2020		1,0371	0,0978	
	Finca Santa Clara, El Cimiento, Guatemala	1640	24	2,6242	0,1834		1,0775	0,0947	
D. valens (Honduras and Guatemal)	**Valle de Angeles**, Tegucigalpa, Honduras	1360	19	5,8189	0,3787	**0,086**	2,2816	0,1984	**0,064**
	Finca Chichiya 3, Sololá, Guatemala	2060	19	5,4784	0,3017		2,1211	0,1628	
	Finca Chuchiya 1, Sololá, Guatemala	2080	7	5,5914	0,5885		2,1357	0,2653	
	Finca Chuchiya 2, Sololá, Guatemala	2100	43	5,6142	0,4274		2,1865	0,1828	
D. valens (only Guatemala)	**Finca Chichiya 3**, Sololá, Guatemala	2060	19	5,4784	0,3017	**0,495**	2,1211	0,1628	**0,414**
	Finca Chuchiya 1, Sololá, Guatemala	2080	7	5,5914	0,5885		2,1357	0,2653	
	Finca Chuchiya 2, Sololá, Guatemala	2100	43	5,6142	0,4274		2,1865	0,1828	
D. vitei	**Finca Socorro**, Sololá, Guatemala	1880	62	2,8726	0,2007	**0,020**	1,1874	0,0912	**0,000**
	Finca Chichiya 3, Sololá, Guatemala	2060	144	2,7572	0,2177		1,1188	0,0979	
	Finca Chuchiya 1, Sololá, Guatemala	2080	59	2,7931	0,2531		1,1347	0,1147	
	Colonia Maria Tecun, Sololá, Guatemala	2340	79	2,7811	0,2242		1,1347	0,1031	
	Barrenché, Sololá, Guatemala	2460	11	2,8164	0,2464		1,1764	0,1218	

Dendroctonus frontalis

The analysis of *D. frontalis* is from two locations, Piedra de Amolar (Guatemala) and from La Colonia (Honduras). One sample is excluded from the analysis (Parque Victoria, Guatemala). Sample size and elevation varies between these to locations, elevation in La Colonia at approximately 700 m and Piedra de Amolar at 1360 m.

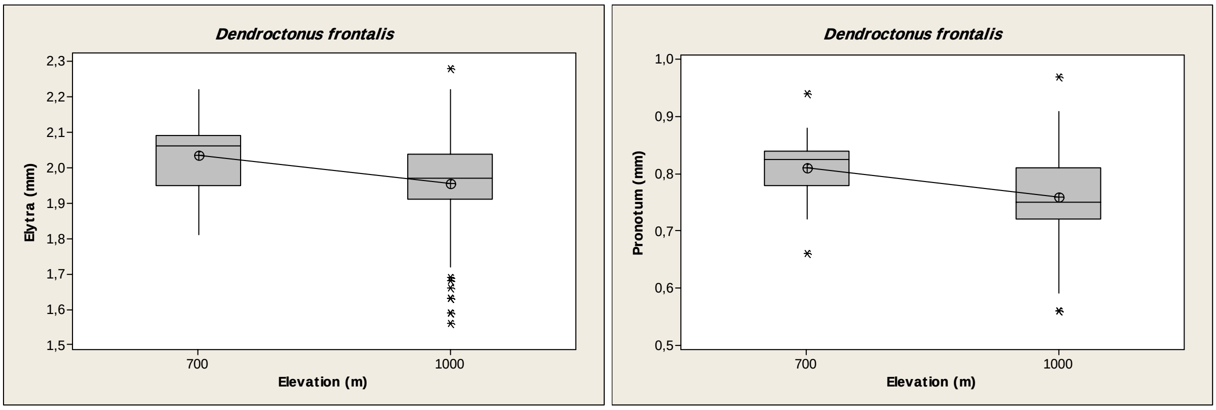


Fig. 24a **Fig. 24b**

Box plot of sample measurements of elytra (fig. 2a) and pronotum (fig. 2b) vs. elevation.
La Colonia (700m) and Piedra de Amolar (1360 m).

The box plots (fig. 24a and fig. 24b) show difference in body size at different elevation, with a greater body size at lower elevation. There is a bigger spread in size (both elytra and pronotum) at lower elevation, but the sample size is also larger. The one-way ANOVA analysis have low P-values (Tab. 10, P < 0,001 and tab. 10, P < 0,000) show that there is no significant difference in body size between these localities versus elevation. The samples from La Colonia have a significant larger size, with biggest difference on pronotum length.

Dendroctonus sp. nov.

The analysis of *D. sp. nov.* is from three locations, Cow Trail (Belize) and Parque Victoria (Guatemala) and Finca Santa Clara (Guatemala). Sample size varies between locations. One sample from Lago Atitlan is excluded from the analysis. Great elevation difference between locations, Cow trail, elevation (800 m), Parque Vitoria at (1360 m), and Finca Santa Clara at (1640 m).

The normality test of elytra and pronotum show the same distribution pattern, which indicates normal distribution of the data. Both have P-value < 0,005 (Appendix II).

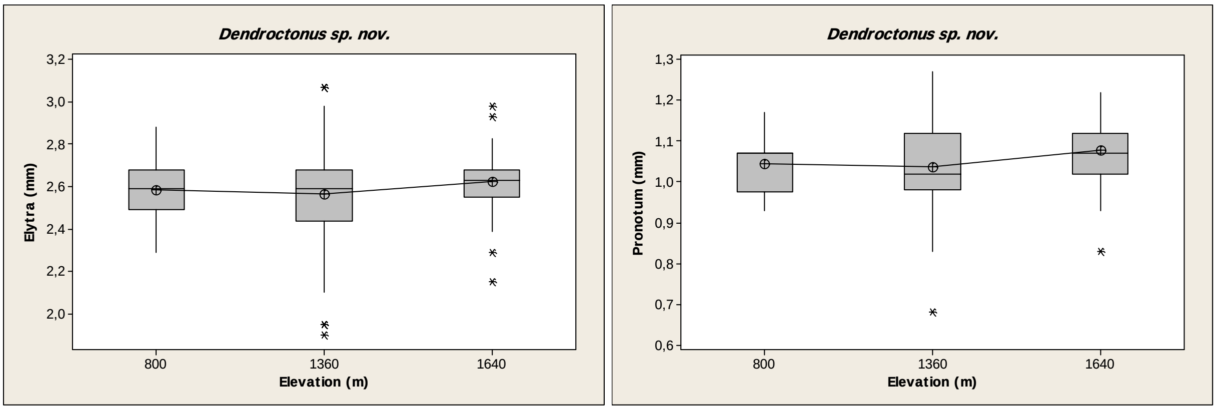


Fig. 25a **Fig. 25b**

Box plot of sample measurements of elytra (fig. 4a) and pronotum (fig. 4b) vs. elevation.

Cow Trail (800 m), Parque Victoria (1360 m) and Finca Santa Clara (1640 m).

The box plot of elytra (Fig. 25a) and pronotum (Fig. 25b) show difference in body size. High P-values (elytra, 0,374 and pronotum, 0,155) (Appendix III) from the one-way ANOVA analyses shows that there is no sigificant correlation between elevation and body size. Therefor there is significant difference in body size between elevation and support for the H1 hypothesis. But note that the samples from Belize, Cow Trail have bigger body size than expected from the elevation. In the 95% CIs there is ovelap between all three localities. Analysis of *D. sp. nov.* does support the hypothesis, but few samples from Cow Trail might influence the results.

Dendroctonus valens

Analysis of *D. valens* were done for 4 localities with big difference in elevation.Honduras, Valle de Angles (Honduras) (1360 m) and Finca Chuchiya 1 (2060 m), Finca Chuchiya 2 (2080 m) and Finca Chuchiya 3 (2100m) (Lago Atitlan, Guatemala). Samples from some locatlities were excluded (Lago Atitlan). Samples size and elevation varied between localcalities.

The normality test for pronotum fits (< 0,005) the estimated normal distribution line, while elytra was not normal distrinuted (0.385).

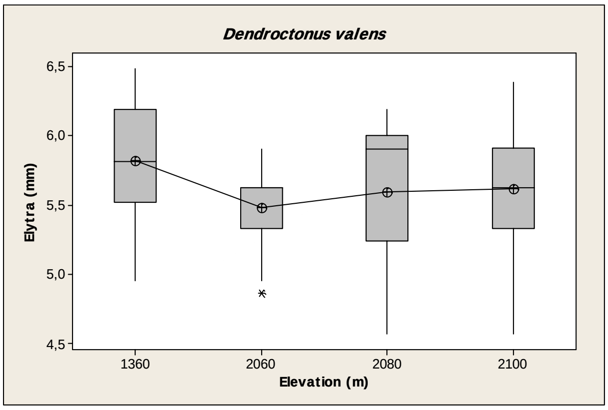


Fig. 26a

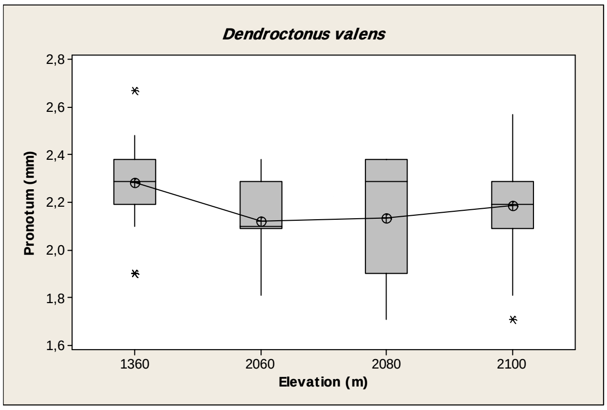
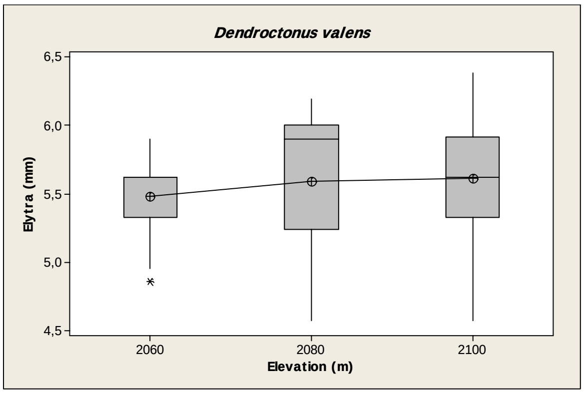


Fig. 26b

Box plot of sample measurements of elytra (fig. 9a) and pronotum (fig. 9b) vs. elevation.
Valle de Angeles (1360 m), Finca Chuchiya 3 (2060 m), Finca Chuchiya 1 (2080 m) and Finca Chichiya 2 (2100 m).

The box-plot of both elytra (fig. 26a) and pronotum (fig 26b) show difference in body-size. The one-way ANOVA analyses had high P-values (elytra, 0.086 and pronotum, 0,064) (Appendix III) which indicates no significant correlation between elevation and body size. Therefor is it support for the H1 hypothesis, and there is variation in body size between localities with different elevation. Difference in sample size disturbs the analyses negatively. There seem to be stronger support for the H1 hyposesis between the locations from Sololá, as the samples from Valle de Angeles had larger body size at its elevation than the other. An analysis for only the localities from Lago Atitlan was therefore conducted.



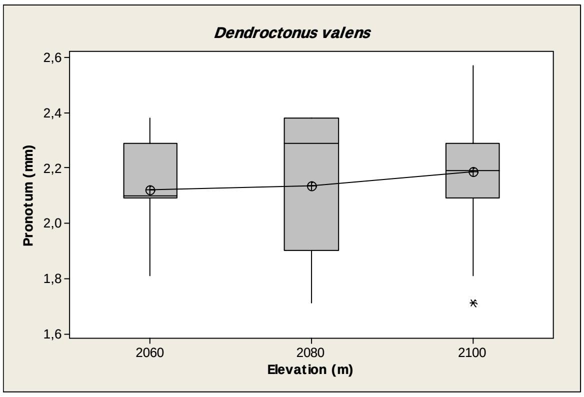


Fig. 27a **Fig. 27b**

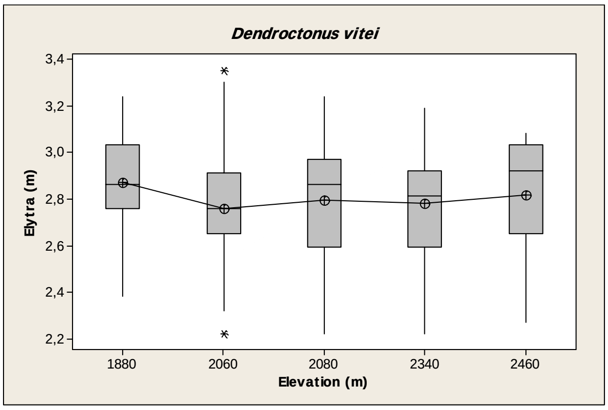
Box plot of sample measurements of elytra (fig. 2a) and pronotum (fig. 2b) vs. elevation.
Finca Chuchiya 3 (2060 m), Finca Chuchiya 1 (2080 m) and Finca Chichiya 2 (2100 m).

The one-way ANOVA analyses for the localities from Lago Atitlan had large P-values (Fig. 27a and Fig 27b) (elytra, 0,495 and pronotum, 0,414) (appendix III), which support for the H1 Hypothesis. There is variation in body size between the localities and elevation.

Dendroctonus vitei

Analysis of *D. vitei* are taken from 5 locations, all from Lago Atitlan, Finca Socorro (1880 m), Finca Chuchiya 3 (2060 m), Finca Chuchiya 1 (2080 m), Colonia Maria Tecun (2340 m) and Barrenché (2460 m). Samples and elevation varied between locations.

The normality test of elytra and pronotum fits the estimated normal distribution line with P-value of elytra (< 0,005) and pronotum (< 0,005) (Appendix II).There is a normal distribution of the body size for both elytra and pronotum.



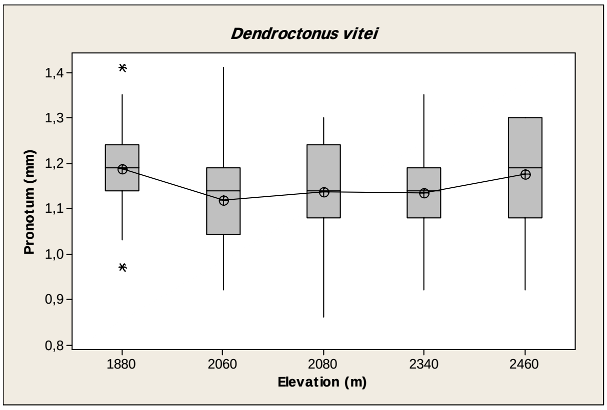


Fig. 28a **Fig. 28b**

Box plot of sample measurements of elytra (fig. 8a) and pronotum (fig. 8b) vs. elevation.
Finca Socorro (700 m), Finca Chuchiya 3 (2060 m), Finca Chuchiya 1 (2080 m), Colonia Maria Tecun (2340 m) and Barrenché (2460 m).

The box-plot of both elytra (fig. 28a) and pronotum (fig 28b) show little variation between body size and elevation. The one-way ANOVA analyses have low P- values (elytra, 0.020 and pronotum 0.000) (appendix III). There is therefore significant correlation between body size and elevation and no support for the H1 hypothesis. There is little variation in body size between localities with different elevation.

Ips apache

The analysis of *Ips apache* is taken from 4 locations, D`Silvas Forest Station (Mountain Pine Ridge, Belize) (800 m), Finca Santa Rosa (Honduras) (860 m), Piedra de Amolar (1000 m) (Guatemala) and San Juan (Honduras) (1105 m). Samples and elevation varies.
The normality test of elytra fits the estimated normal distribution line with P-value (0,037) but not for pronotum (0.054) (Appendix II). There is only normal distribution for elytra.

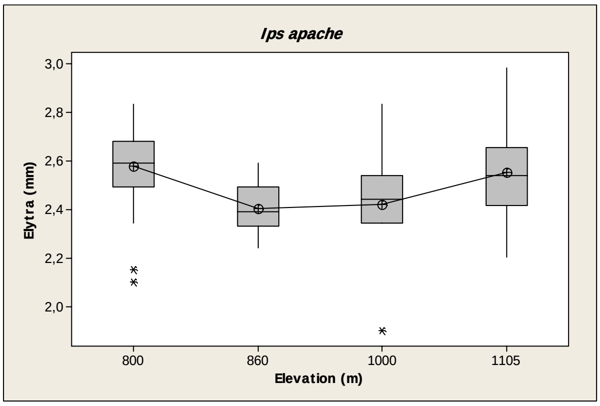


Fig. 29a

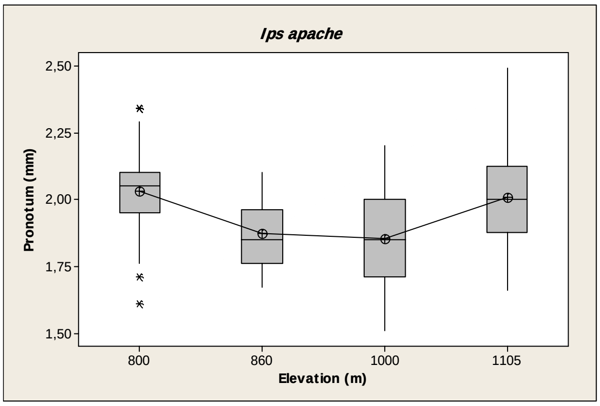


Fig. 29b

Box plot of sample measurements of elytra (fig. 11a) and pronotum (fig. 11b) vs. elevation.
D`Silva Forest Station (800 m), Finca Santa Rosa (860 m), Piedra de Amolar (1000 m) and San Juan (1105 m).

The boxplot of both elytra (fig. 29a) and Pronotum (fig. 29b) show no significant trend according to elevation. The one-way ANOVA analyses have low P-values for elytra (0,003) and pronotum, (0,002) (Appendix III). This indicates that there is no significant correlation between the body size and elevation. Analysis of *Ips apache* does support the H1 hypothesis, there is increase in body size with increasing elevation. The sample size for *Ips apache* was low which affects the analysis negatively and weakens the result.

Ips cricricollis

The analysis of *Ips cribricollis* is taken from 4 locations, Tower Lodge (Mountain Pine Ridge, Belize) (800 m), Finca Santa Rosa (Honduras) (860 m), Piedra de Amolar (Guatemala), (1000 m) and San Juan (Honduras) (1105 m). Samples and elevation varied.

The normality test of elytra and pronotum fits the estimated normal distribution line with P-value of elytra (< 0,005) and pronotum (< 0,005) (Appendix II). There is a normal distribution of the body-size range for both elytra and pronotum.

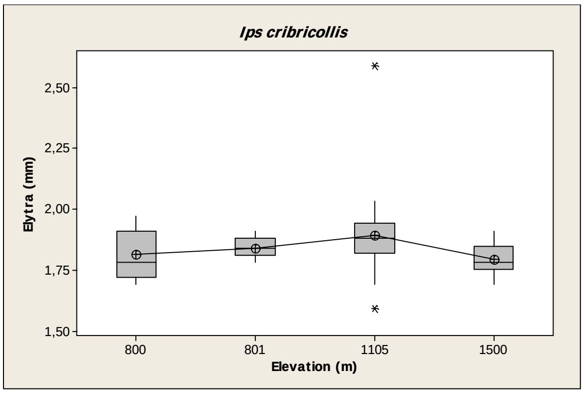


Fig. 30a

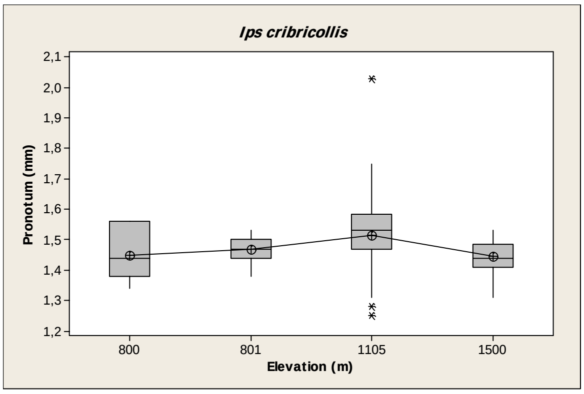


Fig. 30b

Box plot of sample measurements of elytra (fig. 11a) and pronotum (fig. 11b) vs. elevation.
D`Silva Forest Station (800 m), Finca Santa Rosa (860 m), San Juan (1105 m) and Belen (1500 m).

The boxplot of both elytra (fig. 30a) and Pronotum (fig. 30b) show no significant trend according to elevation. The one-way ANOVA analysis have low P-values, elytra (0,016) and pronotum (0,066). Only the values of elytra give support for the H1 hypothesis, this might be cause by low sample size from 2 of the locations (< 10).

b) The one-way analysis of body size difference between the sexes of the same species.

The mean difference in body size between female and male show that females are bigger (except for Ips apache were male are larger). The smallest species, Dendroctonus frontalis and Ips cribricollis had no significant difference, which might suggest that the size narrows the possibility to get significant answers. Elytra with greater variation in size, only *D. valens* and *D. vitei* had significant difference, but only the smallest species showed no significant difference for protonum measurements. This suggests that the use of pronotum in size measurements is more accurate and give best results (Tab. 11).

Tab. 11 Summary of the one-way ANOVA analysis: Body size difference between the sexes.

Species	**sex**	**Elytra**					**Pronotum**			
		n	**Mean difference**	**Mean**	**StDev**	**P**	**Mean difference**	**Mean**	**StDev**	**P**
D. frontalis	**Female**	68	0,0198	1,9725	0,1643	**0,450**	0.01081	0,76985	0,.08016	**0,416**
	Male	52		1,9527	0,1052			0,75904	0,05932	
D. sp. nov.	**Female**	151	0,0489	2,5881	0,2151	**0,054**	0,0477	1,0609	0,1044	**0,000**
	Male	102		2,5392	0,1682			1,0132	0.0773	
D. valens	**Female**	47	0,2509	5,7589	0,4084	**0,004**	0,1568	2,2679	0,1855	**0,000**
	Male	44		5,5080	0,4061			2,1111	0,1760	
D. vitei	**Female**	206	0,0701	2,8200	0,2345	**0,004**	0,037	1,1549	0,1062	**0,001**
	Male	151		2,7499	0,2065			1,1179	0,0971	
I. apache	**Female**	59	- 0,0479	2,5319	0,1727	**0.191**	- 0,1002	1,9641	0,1518	**0,004**
	Male	40		2,5798	0,1849			2,0643	0,1870	
I. cribricollis	**Female**	11	0,0695	1,9291	0,2362	**0,069**	0,0453	1,5373	0,1726	**0,189**
	Male	83		1,8596	0,0934			1,4920	0,0954	

Difference in body size between the sexes are shown in the figures under for both *Dendroctonus* and *Ips* species.

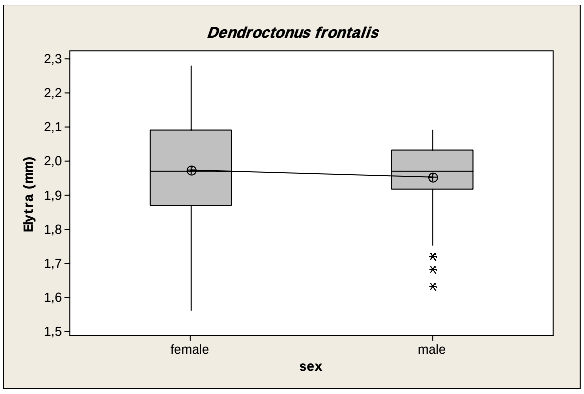


Fig. 31a

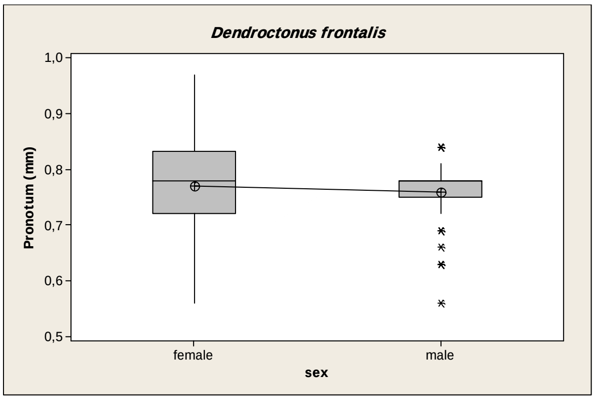
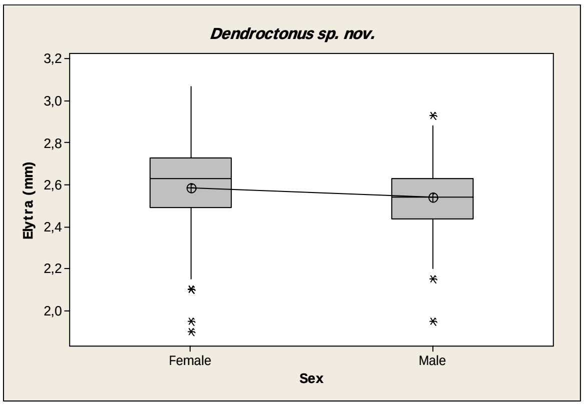


Fig. 31b



Fig, 32a

Fig.32b

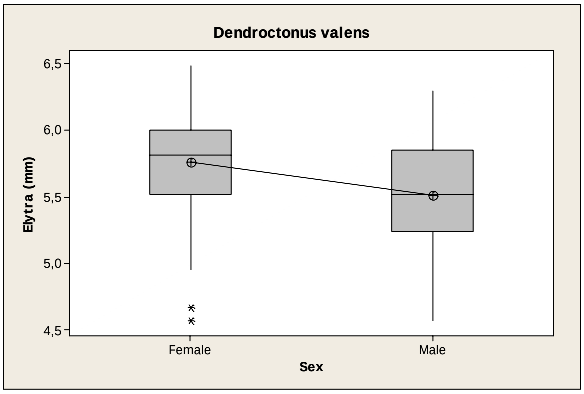


Fig. 33a

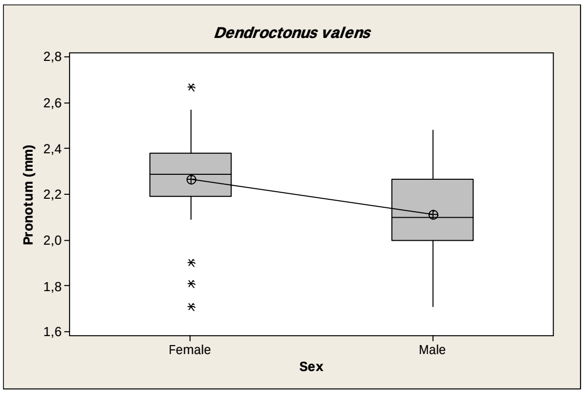


Fig. 33b

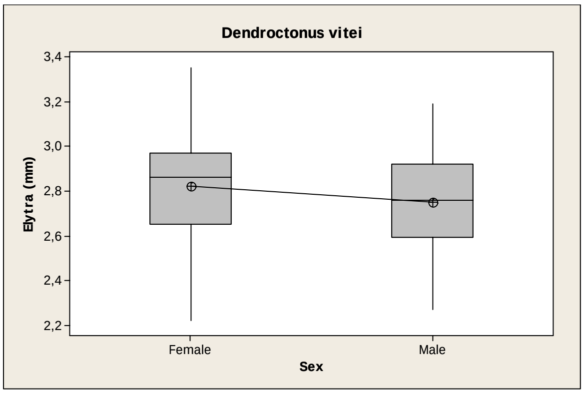


Fig. 34a

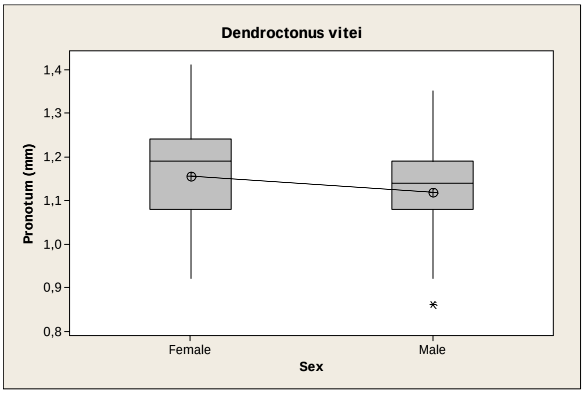


Fig. 34b

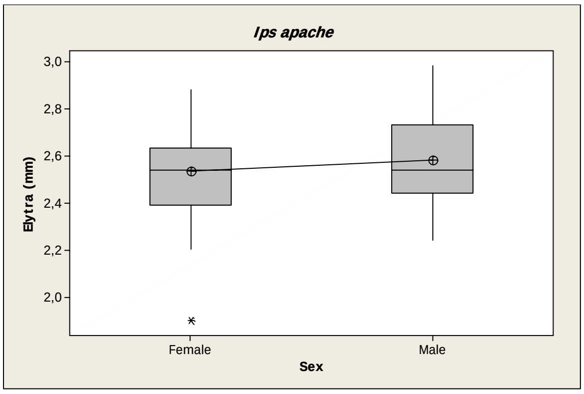


Fig. 35a

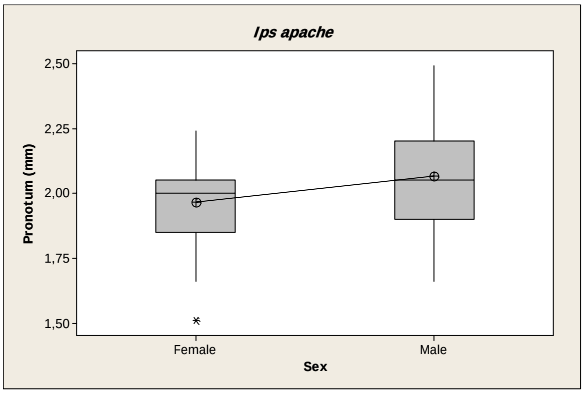


Fig. 35b

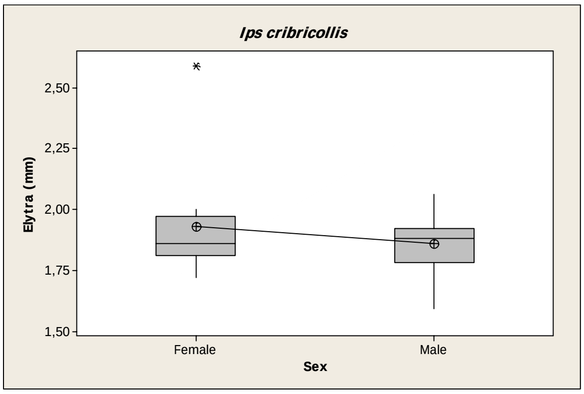


Fig. 36a

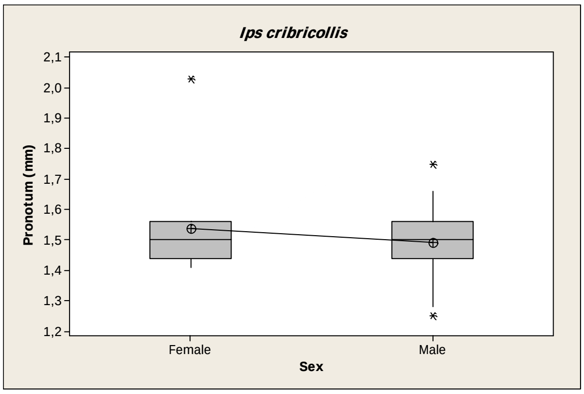


Fig. 36b

Figures show difference in body size between the sexes for the *Dendroctonus* and *Ips* species found.

Discussion

Guild structure

D. vitei was found on the northeastern and northern hills of Lago Atitlan, only known from this area in Guatemala (Patzún, Puente Tzantzir, Sololá (Wood, 1982), Quetzaltenango (Vité, 1975) In Mexico it has in addition been found an isolated province of Sierra Madre de Chiapas, Mexico (Salinas-Moreno *et. al.*, 2004). Little work has been done on this species since its acknowledgement as a new species in 1974 (Wood, 1982). Two samples that I collected in Parque Victoria, Coban might suggest a wider distribution in Guatemala. Because of the difficulties with classification of *Dendroctonus* species, this species may have been misidentified in earlier studies from Guatemala. From this study it is clear that *D. vitei* is the main aggressive pine bark beetle in area around Lago Atitlan. It attacks several pine species there, *P. occarpa, P. psedostrobus* and *P. tecunumanii* (in Coban also *P. maximinoi*). With attacks ranges from app. 1800 m to 2500 m (1350-1400 m, Parque Victoria, Coban) and observed attacks on several pine species, this species does not seem to be restricted by host or altitude, so other factors (tolerance, dispersal ability, behavior) could explain its narrow distribution. Climatic barriers might restrict this species from dispersial. As a species that prefer montainous areas and harsh climate, it would be difficult for this species to disperse over large distances if there is change in climatic conditions. This can be related to toporgaphy. But with the findings from Coban one can queation if the species distribution range is rigth. One can argue that *D. vitei* is also endemic to this area, further studies of this species are necessary to estimate its distribution range.

D. frontalis and *D.* sp.nov. are probably the most aggressive species with large overlapping distribution ranges in Central America. They were not found at same locations (except 1 sample of *D. frontalis*, Coban assosiated with a large attack of *D*. sp.nov). The elevation ranges overlaps and both species are found on the same host species. As *D. sp. nov.* just recently was distinguished from *D. frontalis* (Midtgaard and Thunes, 2002), these two species have formerly been classified as one. The difference between them are small, not only in morphological difference, but also host and habitat selection. As there is overlap in the results between *D. frontalis* and *D. sp. nov.*, it might indicate that these species uses different niches in the habitat (do not compete over the same resources in time and/or space). This can be explained by my sampling method, because samples were only taken from the ground and two meters up, and *D. frontalis* is know to utilize upper parts of the trunk in association of other species (Lanier *et.* al. 1988).This narrows the possibility to find other species that are found in the upper part of the tree.

The non-aggressive species *D. approximatus* and *D. valens* were found in small numbers at some of the location. These species are secondary species found in small number and rarely kill healty trees. *D. approximatus* and *D. valens* attacks trees only when other aggressive species of *Dendroctonus* have broken down the trees resistance, but occasionally *D. valens* attacks also seemingly healthy trees (Wood, 1982). At Finca Chuchiya 2 (Guatemala) active attacks of only *D. valens* was found, but this location had been attacked by aggressive pine bark beetles earlier and most of the trees had been cut down. The trees seemed unaffected by the infestations. In Valle de Angeles (Honduras), *Ips apache* was only found as secondary species on attacked trees. *Ips cribricollis* was found as primary pest in Belen, Santa Rosa de Copan (Honduras). This locality had unhealthy forest with fungal attacks. In San Juan, Siguatepeque (Honduras) trees had been cut down prior my visit; the trees contained only *Ips cribricollis* and *Ips apache*, and these two localities no other species were found. As secondary species and non-aggressive, it was not surprising to find these two species at localities with lots of slash (Wood, 1982). Also the *Ips* samples from Belize was taken after a large attack by *Dendroctonus sp. nov.*.

I have no indication that the secondary species, *Ips cribricollis, Ips apache, D. approximatus* and *D. valen* normally had any aggressive behavior in healthy forest. They were normally collected in small numbers in trees killed by aggressive species like *D. sp. nov.* or *D. frontalis.*.

Sample sizes of secondary and tertiary species were low or not present. As sampling were taken mainly at attack phase 1, it is not surprising that species compositions were not diverse. At phase 1 only the primary species attacks the host and produces pheromones that attracts larges number of conspecifics (*Dendroctonus* and *Ips*) and together creates a mass attack which break down the trees resistance and in turn kills it (Wood, 1982). Secondary species may also be attracted, but do enter the tree after its resistance is weakened or totally broken down. So as for phase 1 only the aggressive species would be the main species found together with small amount of non-aggressive species which they are known to be associated with (Wood, 1982). In my investigation, with one exception from Finca Chuchiya, Lago Atitlan (Guatemala), this is the general picture. This locality had several substitute species (low amount, <6 of each species) which indicates that the tree resistance was broken down, although the trees had symptoms of attack phase one. One can assume that the aggressive species kills the trees so fast that the symptoms for phase one had not yet disappeared. For this locality the definition for attack phase 1 does not fit.

From the other localities with attack phase one, only one aggressive species was found in large number, either associated with a small number of non-aggressive species or no other species at all.

As mentioned above, the sampling method narrows the likelyhood to finding several aggressive species. Specialication on different parts of the tree is assumed to be caused by interspecific resource competition. This segregation is influenced by phloem thickness and the body size of the attacking beetles. The *Dendroctonus* and *Ips* species have larges variation in size and the lower limit of colonization is affected by their body size. This means that these species do not attack parts of trees that have lower phloem thickness than their body size. On the other hand it is possible that species are able to attack were the phloem thickness is larger than their body size. But interspesific competition reduces this probability (Amezaga and Rodríguez, 1998).

The largest species, *D. approximatus* and *D. valens*, were only found on the lowest part of the tree (thickest phloem layer). *D. frontalis* and *D. sp.nov.* were found from the ground and up and I assume that they would be found higher than the sampling highth. *Ips apache* and *Ips cribricollis* were found all over the attacked trees as sampling of these species were taken from trees that had been cut down. My result did not show segregation between the different species because of the sampling method.

The majority of *Dendroctonus* species have low host specifity, attacking several different pine species (Salinas- Moreno *et. al.*, 2004). In the present study there was no specific host selection among the *Dendroctonus* and *Ips* species.They attacked different pine species either at the same (*D. vitei*), or at different locations. The geographic range was wide for all species (except *D. vitei*). It is possible that phloem thickness is an important factor for host selection. The difference in phloem thickness between pine species migth not differ significantly, but the difference within a tree varies considerably. I am not aware of any studies of phloem thickness variation in relation to altitude, but I suspect this could possibly be an important factor for separation the pine beetle species with increasing altitude.

Sex ratio

For monogamous species as *Dendroctonus*, the female is the first sex to attack tree and initiate boring of new galleries. As pheromones attract both sexes, males would search for holes made by the females. The males then enter holes with unaccompanied females to begin the mating process. The number of males entering the tree corresponds to the number of females that successfully bore into the tree (Bishir *et. al.*, 2004).

At the early stage of an attack (phase 1), a larger number of females would be found in the galleries. As the males arrive at an attacked tree later and uses time to search and locate an unaccompanied female, only a smaller number of males would be found in the galleries. The localities with *D. frontalis, D. sp. nov.* and *D. vitei* as primary species, there were a larger number of females at phase 1 as expected (one exception, Finca Chuchiya 1). The sex ratio can be used to estimate the attack phase because the number of both sexes will be equal at phase 2. As for the locality Finca Chuchiya 1 with 29 females and 30 males, I assume that the attack had been going on a bit time longer than at the other localities. This locality had also some tertiary species that support this assumption, but surprisingly the tree was in phase 1.

Ips apache and *Ips cribricollis* are polygamous, were the males attacks and penetrate the bark first. The females enter after the male have excavate the entrance tunnel to a mating chamber (Wood, 1982).

Only two locations from Honduras had *Ips apache* and *Ips cribricollis* as primary species and at these localities no other species was found. *Ips cribricollis* had a significant higher number of males, only *Ips apache* had higher number of females. An explanation might be that *Ips apache* attacked the tree first and the females have had time to enter the galleries, but to short time for this to happen for *Ips cribicollis*. Either way it does not give any consistent answer according to the attack phase.

Body size measurements

Body size compared with elevation

Variation in body size of imagines has been recorded for a number of beetle (Coleoptera) families, mainly with regard to mating, competition and female choice. The effect of environmental conditions on the body size of imagines has been less well studied (Krasnov *et. al.*, 1996). As for the mountain pine beetles (*D. frontalis*), body size is known to influence fitness, large females have more fat reserves, disperse father, survive extreme temperatures better and lay more eggs that small ones (Pureswaran and Borden, 2003). Variation in body size at different latitude for *D. frontalis* has also been reported (Lanier *et. al.*, 1988), but to my knowledge there has not been any research on body size according to elevation on mountain pine beetles.

Difference in climate (temperature and humidity) and host quality (phloem difference in host species) influences body size (Pureswaran and Borden, 2003). Increase in altitude tends to mimic altitudinal gradients; great difference in climatic conditions which leading to decreased population size and diversity. Studies of altitudinal variation in life history pattern in insects have linked life-history variation to soil or climatic, particularly temperature, as well as to changes in the biotic environment, such as competitors and recourse availability. Body size also changes across altitudinal and latitudinal gradients, but for insect species, the pattern seems less clear than for endotherm animals. Some larger at higher elevation, others are smaller or show no changes (Smith *et. al.*, 2000).

The present results do not show any significant trend for body size with increasing elevation for the *Dendroctonus* species as a whole. *D.* sp. nov. and *D. valens* supports the hypothesis, *D. frontalis* and *D. vitei* do not. This shows that there may be different prosesses involved for the different species of this genus. The greatest difference were between localities far apart. *D. frontalis* from Olancho (Honduras) was significantly larger than from higher elevation in Joctotan (Guatemala). Also *D. sp. nov.* from Cow Trail (Belize) had significant larger body size compared with what could be expected from similar elevation at other sites. Several explanatory models for the variation can be made.

1) Climatic differences between localities affect growth and body size. Large body size is directly linked to development speed. Low temperature leads to longer development time and larger size. Also harsh environment, with fluctuation temperature during development tends to increase body size (Smith *et. al.*, 2000).

2) Different pine species have different phloem thickness and there is correlation between body size of bark beetles and phloem thickness (Amezaga and Rodríguez, 1998). Bark beetles prefer host species with phloem thickness that correlates with their body size. Phloem thickness correlates with tree size and decreases with height of the pine. Segregation of bark beetle species in the same tree can be explained by the phloem thickness. Different species with different body size would utilize different host species or different part of the trees. Thus, if phloem thickness varies with altitude this could affect beetle size.

3) Size of the host tree might explain the body size difference. Even tough the size of the host trees were not measured, there were great difference in size of the host trees. As size in phloem thickness correlates with tree size, the size of bark beetles would also correlate to some degree with tree size.

4) Large body size is known to influence fitness in bark beetles, were females prefer to mate with large males. Higher fitness is known to produce lager offspring that abound the galleries earlier than smaller speciemence. There is a selection pressure for larger body size (Pureswaran and Borden, 2003). The majority of *Dendroctonus* species have low specifity toward its host (*Pinus*) in Mexico, which suggest that *Dendroctonus* behaves more as a oligophagous towards the genus *Pinus* (Salinas-Moreno *et. al.*, 2004). This seems to be true for the present study. Selection pressure for large body size should result in species separation over time, as different pine species have different phloem thickness. Dendroctonus species that attacks a pine species with phloem thickness larger than its body size, with up to 12 generations in one year, the selection pressure might generate maximum body size in relative short period of time. This might be true as the body size of the *Dendroctonus* species varies a lot (Wood, 1982).

Dendroctonus frontalis

The age and size of the pine species between the localities were very varied, as samples were taken from a young pine in Piedar de Amolar (Guatemala) (height app. 6 m, thickness app. 20-25 cm) which was approximately half the size of the tree collected from in La Colonia (Honduras) (height app.10 m, thickness 40-50 cm). It indicates that there should be larger body size of *D. sp. nov.* from the oldest and thickest trees. *D. sp. nov.* (*P.caribeae*) had larger body size compared with the other location, suggesting thicker phloem thickness. Although the age and size of the trees itself explains the body size difference for *D. frontalis*. Larger phloem thickness in *P. caribeae* might further increase the body size difference.

Dendroctonus sp. nov.

Samples were taken from three locations with elevation range from 800 m to 1640 m, with different pine species (*P. caribaea*, *P. maximinoi* and *P. oocarpa*) and distinct climatic differences (from dry and warm to cool and very humid). The significant difference in body size between these locations is primary linked to the climatic differences, especially temperature. At Cow Trail, (MPR, Belize) with the warmest and driest climate, the beetles were comparatively larger. At Finca Santa Clara (Guatemala), at highest elevation with cool, very humid, the beetles were small. I suspect increased development time to be the main cause for the significant body size difference *Dendroctonus sp.nov.*. Different phloem thickness could be another factor, but also tree age or size could be important factors. Note that *Dendroctonus sp.nov.* from Cow Trail (Belize) had a greater body size compared with similar elevations for other localities. This could be explained by the pine species (*P. caribeae*) that is a relative large and thick pine species. This correlates with phloem thickness and body size of the bark beetles. Also note that this was also found for *D. frontalis* from La Colonia (Honduras) compared with *D. frontalis* from Piedra de Amolar (Guatemala) (body size versus elevation was not significant).

Dendroctonus valens

D. valens from Valle de Angeles (Honduras) were larger compared with other localities that had higher elevation. A single analysis of the locations form Lago Atitlan had significant variation between body size and elevation (both elytra and pronotum), which indicates that body size does not only correlates with elevation or different host species. Samples taken from the same pine species (*P.occarpa*) in Finca Chuchiya (Guatemala) and Valle de Angeles (Honduras) showed opposite trends in body size versus elevation. The most obvious explanation is that the age and size of the trees were different. The trees in Valle de Angels were both old and at their maxuimum height and thickness, but *P. occarpa* in Finca Chuchiya was still in growth (lower height and thickness). I do not believe that climate can explain the body size difference as Valle de Angeles (Honduras) does not have any harsher weather compared to the locations in Lago Atitlan (Guatemala). As for the separated analysis from Finca Chuchiya, with the locations within 500 m² (no climatic difference), the analysis was significant. Differences in phloem thickness between the pine species seems to be the best possible answer why there is difference in body size within a small area as this.

Dendroctonus vitei

As *D. vitei* was only collected from localities in the northeastern and eastern hills by Lago Atitlan (Guatemala), one might think that body size would correlate with the elevation. The sampling area were quite small and the elevation differences were large (elevation from 1880 m to 2460 m). The analysis was not significant. The localities contained different pine species, samples were taken from *P. occarpa* or *P. pseudostrobus* at the different localities. The climatic variations between the localities are very small, only the temperature difference is large enough to affect growth and body size. The localities had forest of the same age, with a mix of different pine species. *P. occarpa* and *P.pseudostrobus* have the same estimated thickness range (80 -100 cm). With approximately the same thickness and height of both pine species from the localities, I assume that phloem thickness between the localities and pine species did not differ much. With little difference in phloem thickness this factor should cause little difference in body size, but temperature could still give body size differences between the locations as the elevation range is quite big. The mountain area around Lago Atitlan divide into to somewhat overlapping climatic region (the lowest ranges from 1500 to 2400 m with temperature between 15,0 and 23,0 in this region, the highest ranges from 1800 to 3000 m with temperature between 12,5 and 18,6, Mapa de Zonas de Vida de Holodrige, República de Guatemala, IGN, 2001). With the great variations in temperature there should be large differences in body size, as temperature has great influence in growth and body size. No such trend is found for *D. vitei* between the localities. There is no clear solution to the uniform body size pattern for *D. vitei.* But as *D. vitei* has a limited geographic range, one might expect that this mountain species well adapted to its habitat. The small difference in body size at different elevations supports this, as temperature have a major role in growth for the majority of *Dendroctonus* species but does not seem to affect *D. vitei*.

Sexual difference in body size

Little documentation on sexual difference in body size between the sexes on pine bark beetles was found. But there is a general rule that there often is sexual difference in body size, where females tend to be larger than males. This is also known to be true for pine bark beetles (Renwick *et. al.*, 1974; Pureswaran and Borden, 2003). Reproduction capacity is body size dependent and females have larger fat reserves to use in egg production. Pheromone production in pine bark beetles is important for aggregation. For many species this is crucial for survival, especially to overcome host resistance and thereby makes mating possible (Wood, 1982). Most of these pheromones produced by females are low cost associated with oxidation product of hosts resina. The opposite is true for the male as it produces pheromones with higher metabolic cost, this can be a secondary factor for body size difference in pine bark beetles (Pureswaran and Borden, 2003; Symmonds and Elgar, 2004). As for the analysis, there was a mean body size difference biase larger females within the species, but not all species showed significance for both elytra and pronotum. Only the two largest species, *D. valens* and *D. vitei*, had significant difference between the sexes for both elytra and pronotum. This indicates that even though female were larger, the sexual body size difference decreased with decreasing species size. As for the difference in elytra and pronotum measurements, greater variation in size of elytra than pronotum makes the measurements of pronotum more accurate and more trustworthy. But also difference in sample size of males and females and difference in body size between locations disturbs the analysis.

Conclusion

The diversity of species within phase of attack, host selection and distribution, fit with the assumptions of low species diversity at early phase of attack, and wide host selection within their distribution. The results shows low specifity towards it host (*Pinus*) and *Dendroctonus* and *Ips* behaves as a oligohagous generalist switching between pine host species. With wide host distribution, species richness would be a function of the range of its host, this explains the wide distribution of pine bark beetles in Central America. The sexual distribution can be seen as a function of the phase of attack, as the sexual distribution switches between phase 1 and 2. As most locations with phase 1, the sexual distribution was biased towards more females (*Dendroctonus*) or males (*Ips)*. One exception suggests that the defined phases of attack might not be uniform, and the symptoms of phase 1 could be delayed. This might have to do with the strength of the host, aggressiveness of attacking species and climatic variations. High variations in the body size at differents elevation with the same species, suggests that this kind of analysis need to consider using several other parameters to get good results. Climatic variations, phloem thickness, host and size of the tree are important features one has to take into consideration. Climatic variations, especially temperature, affects growth as lower temperature increases development time and body size. Host species can have different phloem thickness and the size of the host is correlated with the phloem thickness. The correlation in body size between the sexes showed that there is a bias toward larger females.

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Appendix I

Species, locations and coordinates for the Dendroctonus and Ips species found in Central America.

Dendroctonus ssp	Location	Lat./Long.
D. approximatus	Finca Santa Rosa, Yuscarán, Honduras	N 13º 58.08' W 86º 58.00'
	Finca Santa Clara, El Cimiento , Guatemala	N 14º 57.10' W 89º 52.05'
	Valle de Angeles, Tegucigalpa, Honduras	N 14º 09.09' W 87º 02.09'
D. frontalis	La Colonia, Olancho, Honduras	N 15º 11.54' W 85º 23.53'
	Parque Victoria, Coban, Guatemala	N 15º 28.30' W 90º 22.40'
	Piedra de Amolar, Jocotán, Guatemala	N 14º 41.10' W 89º 15.30'
D. sp. nov.	Colonia Maria Tecun, Sololá, Guatemala	N 14º 48.50' W 91º 12.20'
	Cow Trail, Mountain Pine Ridge, Belize	-
	Finca Santa Clara, El Cimiento , Guatemala	N 14º 57.10' W 89º 52.05'
	Laguna El Pino, Nuevo Santa Rosa, Guatemala	N 14º 20.05' W 90º 30.30'
	Parque Victoria, Coban, Guatemala	N 15º 28.30' W 90º 22.40'
	Piedra de Amolar, Jocotán, Guatemala	N 14º 41.10' W 89º 15.30'
	Valle de Angeles, Tegucigalpa, Honduras	N 14º 09.09' W 87º 02.09'
D. valens	Colonia Maria Tecun, Sololá, Guatemala	N 14º 48.50' W 91º 12.20'
	Finca Chuchiya, Sololá, Guatemala	N 14º 44.10' W 91º 07.40'
	Finca Chuchiya, Sololá, Guatemala	N 14º 43.90' W 91º 07.50'
	Finca Chuchiya, Sololá, Guatemala	N 14º 44.00' W 91º 07.50'
	Valle de Angeles, Tegucigalpa, Honduras	N 14º 09.09' W 87º 02.09'
D. vitei	Argueta, Sololá, Guatemala	N 14º 48.30' W 89º 13.10'
	Barrenché, Sololá, Guatemala	N 14º 49.30' W 91º 12.40'
	Colonia Maria Tecun, Sololá, Guatemala	N 14º 48.50' W 91º 12.20'
	Finca Chuchiya, Sololá, Guatemala	N 14º 44.10' W 91º 07.40'
	Finca Chuchiya, Sololá, Guatemala	N 14º 44.00' W 91º 07.50'
	Finca Santa Clara, El Cimiento , Guatemala	N 14º 07.10' W 89º 52.05'
	Finca Socorro, Sololá, Guatemala	N 14º 45.10' W 91º 08.20'

Ips ssp.		
Ips apache	Belen, Copán, Honduras	-
	Chimaltenango, Guatemala	-
	Chiquimula, Guatemala	-
	Cow Trail, Mountain Pine Ridge, Belize	-
	D`Silva Forest Station, Mountain Pine Ridge, Belize	-
	Finca Loma Linda, Munic Frajianes, Guatemala ??	-
	Finca Santa Rosa, Yuscarán, Honduras	N 13º 58.08' W 86º 58.00'
	La Colonia, Olancho, Honduras	N 15º 11.54' W 85º 23.53'
	Piedra de Amolar, Jocotán, Guatemala	N 14º 41.10' W 89º 15.30'
	Poptun, Guatemala	-
	San Juan, Siguatepeque, Honduras	N 14º 35.177' W 87º 49.808'
	Tower Lodge, Mountain Pine Ridge, Belize	-
	Valle de Angeles, Tegucigalpa, Honduras	N 14º 09.09' W 87º 02.09'
Ips cribricollis	Belen, Copán, Honduras	-
	Valle de Angeles, Tegucigalpa, Honduras	N 14º 09.09' W 87º 02.09'
	San Juan, Siguatepeque, Honduras	N 14º 35.177' W 87º 49.808'

Appenix II

Normality test (Anderson-Darling) with probability plot. Tested for all *Dendroctonus spp* and *Ips spp*.

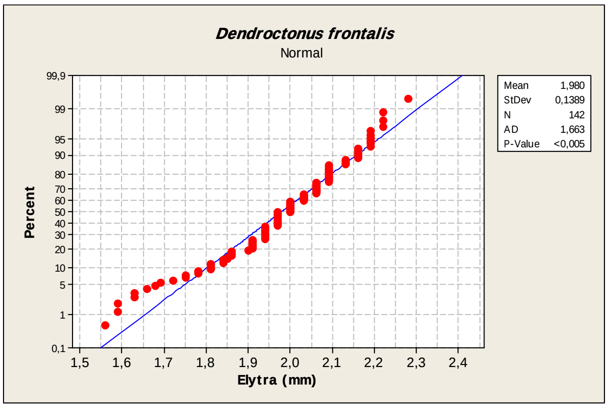

Fig. 1a Probability plot, elytra.

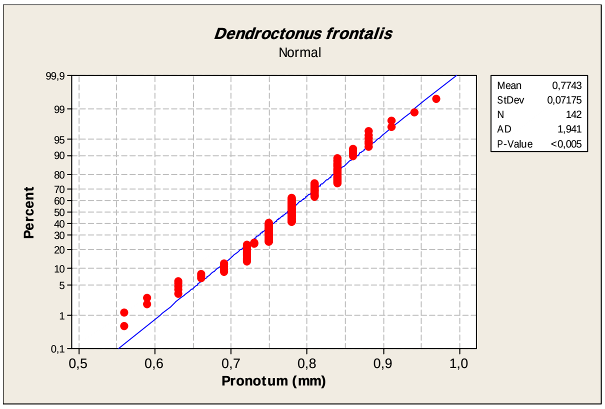

Fig. 1b Probability plot, pronotum.

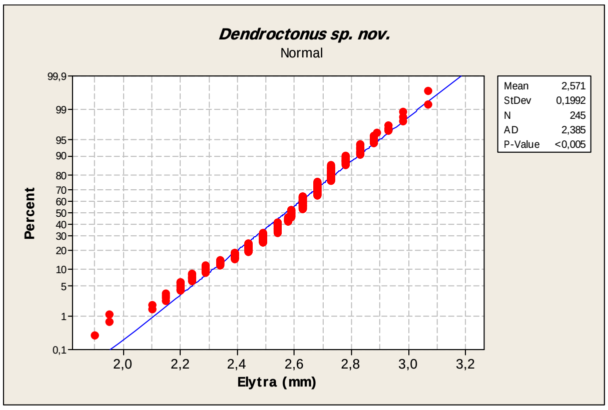

Fig. 2a Probability plot, elytra.

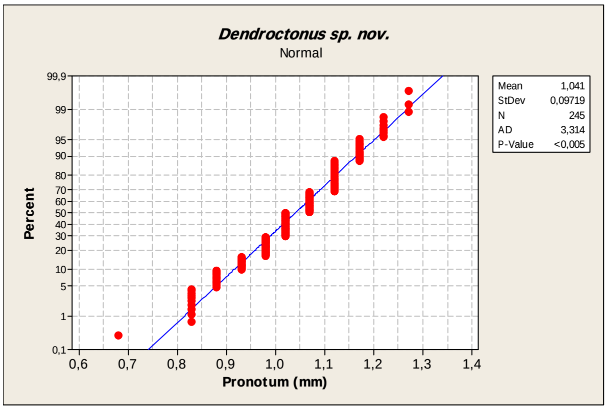

Fig. 2b Probability plot, pronotum.

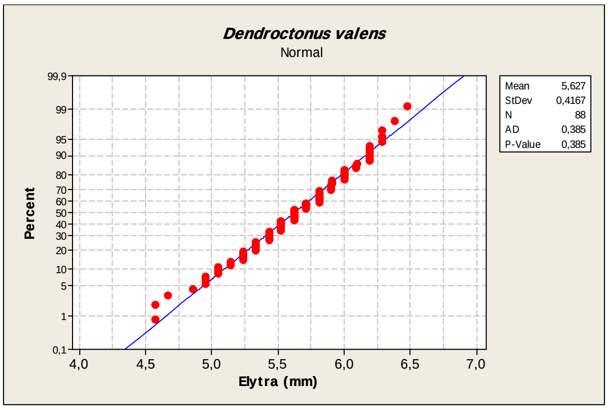

Fig. 3a Probability plot, elytra.

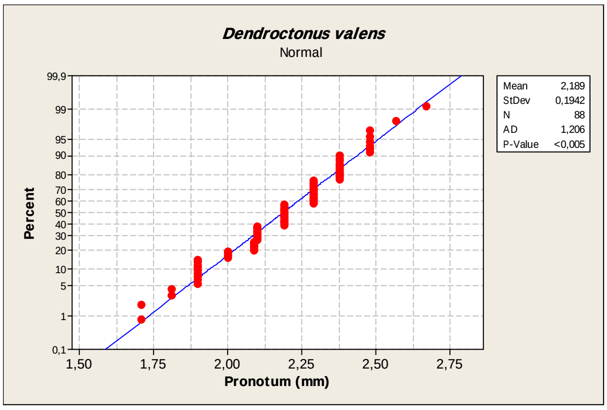

Fig. 3b Probability plot, pronotum.

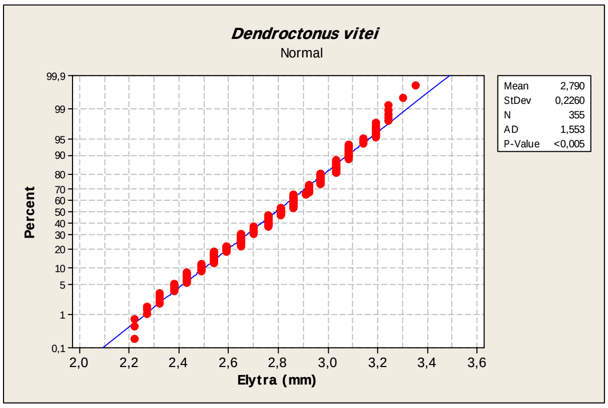

Fig.4a Probability plot, elytra.

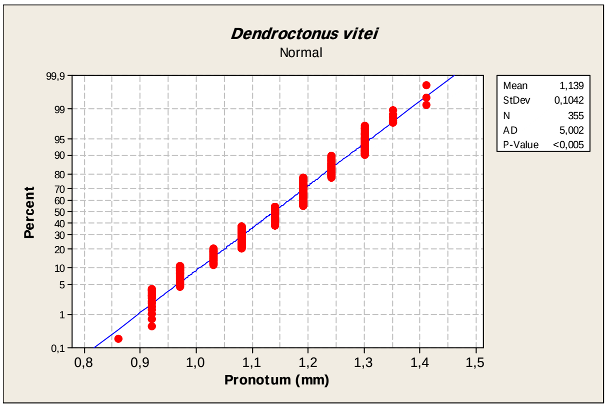

Fig. 4b Probability plot, pronotum.

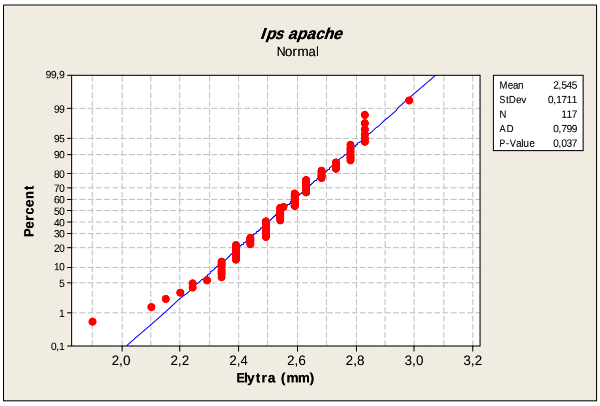

Fig. 5a Probability plot, elytra**.**

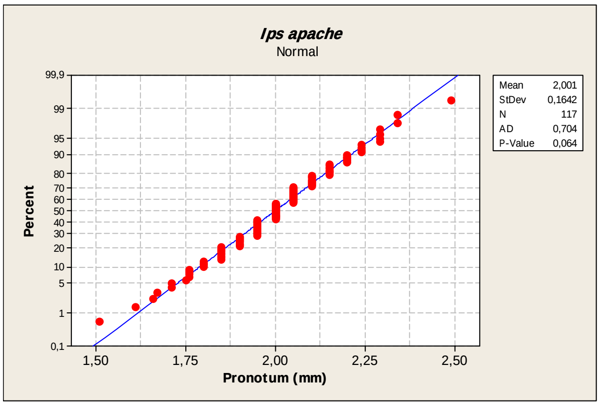

Fig. 5b Probability plot, pronotum.

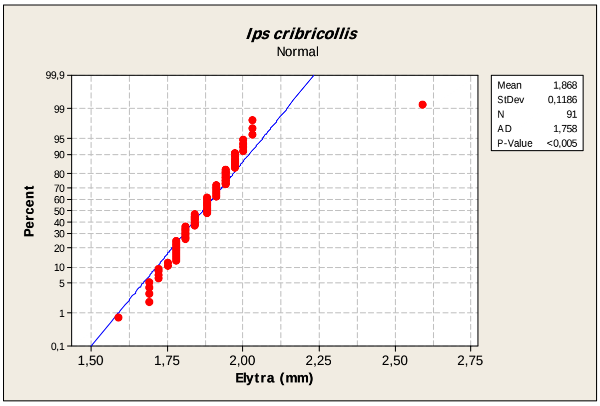

Fig. 6a Probability plot, elytra**.**

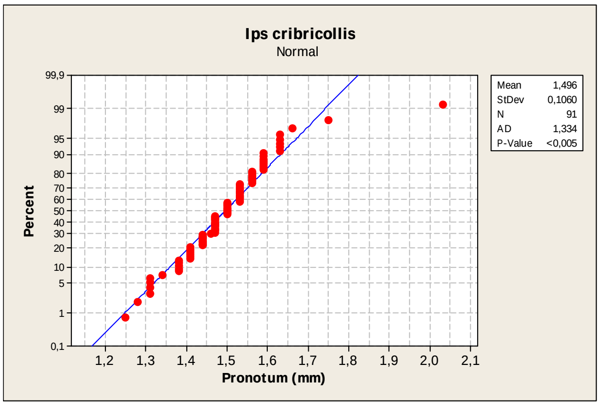

Fig. 6b Probability plot, pronotum.

Appendix III

One-way ANOVA analysis: Elytra (mm) versus elevation (m) and pronotum (mm) versus elevation (m) of all *Dendroctonus spp* and *Ips spp*, except *Dendroctonus approximatus*.

Dendroctonus frontalis

Tab. 1a
One-way ANOVA: Elytra versus Elevation

```
Source      DF      SS      MS      F      P
Elevation    1  0,1915  0,1915  10,60  0,001
Error      140  2,5299  0,0181
Total      141  2,7215

S = 0,1344   R-Sq = 7,04%   R-Sq(adj) = 6,37%


Individual 95% CIs For Mean Based on
Pooled StDev
Level   N    Mean   StDev  --------+---------+---------+---------+-
700    44  2,0343  0,1051                  (---------*---------)
1000   98  1,9549  0,1456  (------*-----)
                           --------+---------+---------+---------+-
                                 1,960     2,000     2,040     2,080

Pooled StDev = 0,1344
```

Tab. 1b
One-way ANOVA: Pronotum versus Elevation

```
Source      DF       SS       MS      F      P
Elevation    1  0,07922  0,07922  17,15  0,000
Error      140  0,64666  0,00462
Total      141  0,72588

S = 0,06796   R-Sq = 10,91%   R-Sq(adj) = 10,28%


Individual 95% CIs For Mean Based on
Pooled StDev
Level   N     Mean    StDev  --+---------+---------+---------+-------
700    44  0,80955  0,05759                    (-------*-------)
1000   98  0,75847  0,07209  (----*-----)
                             --+---------+---------+---------+-------
                             0,750     0,775     0,800     0,825

Pooled StDev = 0,06796
```

Tab. 2a
One-way ANOVA: Elytra versus Elevation

```
Source      DF      SS      MS     F      P
Elevation    2  0,0784  0,0392  0,99  0,374
Error      242  9,6017  0,0397
Total      244  9,6800

S = 0,1992   R-Sq = 0,81%   R-Sq(adj) = 0,00%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  ---------+---------+---------+---------+
 800     9  2,5856  0,1655  (-----------------*------------------)
1360   212  2,5646  0,2020              (--*---)
1640    24  2,6242  0,1834              (-----------*----------)
                            ---------+---------+---------+---------+
                                   2,520     2,590     2,660     2,730

Pooled StDev = 0,1992
```

Tab. 2b
One-way ANOVA: Pronotum versus Elevation

```
Source      DF       SS       MS     F      P
Elevation    2  0,03524  0,01762  1,88  0,155
Error      242  2,26942  0,00938
Total      244  2,30466

S = 0,09684   R-Sq = 1,53%   R-Sq(adj) = 0,72%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev    +---------+---------+---------+---------
 800     9  1,0444  0,0757    (-----------------*------------------)
1360   212  1,0371  0,0978                 (--*---)
1640    24  1,0775  0,0947                     (----------*----------)
                              +---------+---------+---------+---------
                            0,980     1,015     1,050     1,085

Pooled StDev = 0,0968
```

Dendroctonus valens (all locations)

Tab. 3a
One-way ANOVA: Elytra versus Elevation

```
Source     DF      SS     MS     F      P
Elevation   3   1,135  0,378  2,28  0,086
Error      84  13,970  0,166
Total      87  15,105

S = 0,4078   R-Sq = 7,52%   R-Sq(adj) = 4,21%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev  ------+---------+---------+---------+---
1360   19  5,8189  0,3787                    (--------*--------)
2060   19  5,4784  0,3017   (--------*--------)
2080    7  5,5914  0,5885  (---------------*--------------)
2100   43  5,6142  0,4274             (-----*-----)
                           ------+---------+---------+---------+---
                               5,40      5,60      5,80      6,00

Pooled StDev = 0,4078
```

Tab. 3b
One-way ANOVA: Pronotum versus Elevation

```
Source     DF      SS      MS     F      P
Elevation   3  0,2707  0,0902  2,52  0,064
Error      84  3,0118  0,0359
Total      87  3,2825

S = 0,1894   R-Sq = 8,25%   R-Sq(adj) = 4,97%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev   -+---------+---------+---------+--------
1360   19  2,2816  0,1984                        (-------*--------)
2060   19  2,1211  0,1628       (--------*--------)
2080    7  2,1357  0,2653   (--------------*-------------)
2100   43  2,1865  0,1828                 (-----*----)
                            -+---------+---------+---------+--------
                           2,00      2,10      2,20      2,30

Pooled StDev = 0,1894
```

Dendroctonus valens (Guatemala)

Tab. 4a
One-way ANOVA: Elytra versus Elevation

```
Source     DF      SS     MS     F      P
Elevation   2   0,245  0,123  0,71  0,495
Error      66  11,388  0,173
Total      68  11,633

S = 0,4154   R-Sq = 2,11%   R-Sq(adj) = 0,00%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev    +---------+---------+---------+---------
2060   19  5,4784  0,3017     (----------*-----------)
2080    7  5,5914  0,5885    (------------------*-------------------)
2100   43  5,6142  0,4274                 (-------*-------)
                             +---------+---------+---------+---------
                           5,28      5,44      5,60      5,76

Pooled StDev = 0,4154
```

Tab. 4b
One-way ANOVA: Pronotum versus Elevation

```
Source     DF      SS      MS     F      P
Elevation   2  0,0624  0,0312  0,89  0,414
Error      66  2,3035  0,0349
Total      68  2,3659

S = 0,1868   R-Sq = 2,64%   R-Sq(adj) = 0,00%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev   -+---------+---------+---------+--------
2060   19  2,1211  0,1628        (----------*----------)
2080    7  2,1357  0,2653   (-----------------*-----------------)
2100   43  2,1865  0,1828                    (------*------)
                            -+---------+---------+---------+--------
                           2,000     2,080     2,160     2,240

Pooled StDev = 0,1868
```

Tab. 5a
One-way ANOVA: Elytra versus Elevation

```
Source      DF       SS      MS     F      P
Elevation    4   0,5925  0,1481  2,96  0,020
Error      350  17,4936  0,0500
Total      354  18,0861

S = 0,2236   R-Sq = 3,28%   R-Sq(adj) = 2,17%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  -------+---------+---------+---------+--
1880    62  2,8726  0,2007                     (-------*-------)
2060   144  2,7572  0,2177        (----*----)
2080    59  2,7931  0,2531          (-------*-------)
2340    79  2,7811  0,2242         (------*------)
2460    11  2,8164  0,2494  (------------------*------------------)
                            -------+---------+---------+---------+--
                                 2,730     2,800     2,870     2,940

Pooled StDev = 0,2236
```

Tab. 5b
One-way ANOVA: Pronotum versus Elevation

```
Source      DF      SS      MS     F      P
Elevation    4  0,2211  0,0553  5,34  0,000
Error      350  3,6194  0,0103
Total      354  3,8404

S = 0,1017   R-Sq = 5,76%   R-Sq(adj) = 4,68%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  -----+---------+---------+---------+----
1880    62  1,1874  0,0912                     (------*-------)
2060   144  1,1188  0,0979  (----*---)
2080    59  1,1369  0,1147    (-------*------)
2340    79  1,1347  0,1031     (-----*------)
2460    11  1,1764  0,1218      (----------------*----------------)
                            -----+---------+---------+---------+----
                               1,120     1,155     1,190     1,225

Pooled StDev = 0,1017
```

Ips apache

Tab. 6a

One-way ANOVA: Elytra versus Elevation

```
Source      DF      SS      MS     F      P
Elevation    3  0,3931  0,1310  4,93  0,003
Error      113  3,0018  0,0266
Total      116  3,3949

S = 0,1630   R-Sq = 11,58%   R-Sq(adj) = 9,23%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev    +---------+---------+---------+---------
 800   67  2,5773  0,1483                            (---*---)
 860   10  2,4000  0,1049    (---------*---------)
1000    7  2,4186  0,2785    (-----------*-----------)
1105   33  2,5506  0,1755                       (-----*-----)
                             +---------+---------+---------+---------
                           2,30      2,40      2,50      2,60

Pooled StDev = 0,1630
```

Tab. 6b

One-way ANOVA: Pronotum versus Elevation

```
Source      DF      SS      MS     F      P
Elevation    3  0,3800  0,1267  5,21  0,002
Error      113  2,7483  0,0243
Total      116  3,1283

S = 0,1560   R-Sq = 12,15%   R-Sq(adj) = 9,81%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev  ------+---------+---------+---------+---
 800   67  2,0318  0,1404                             (---*---)
 860   10  1,8740  0,1282      (--------*---------)
1000    7  1,8529  0,2180  (----------*-----------)
1105   33  2,0079  0,1781                       (-----*----)
                           ------+---------+---------+---------+---
                               1,80      1,90      2,00      2,10

Pooled StDev = 0,1560
```

Ips cribricollis

Tab. 7a

One-way ANOVA: Elytra versus Elevation

```
Source     DF      SS      MS     F      P
Elevation   3  0,1418  0,0473  3,66  0,016
Error      87  1,1244  0,0129
Total      90  1,2662

S = 0,1137   R-Sq = 11,20%   R-Sq(adj) = 8,13%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev  -----+---------+---------+---------+----
 800    7  1,8129  0,1006  (-----------------*----------------)
 801    7  1,8386  0,0445        (----------------*----------------)
1105   64  1,8925  0,1261                              (----*-----)
1500   13  1,7915  0,0643   (-----------*------------)
                           -----+---------+---------+---------+----
                              1,750     1,800     1,850     1,900

Pooled StDev = 0,1137
```

Tab. 7b

One-way ANOVA: Pronotum versus Elevation

```
Source     DF      SS      MS     F      P
Elevation   3  0,0799  0,0266  2,49  0,066
Error      87  0,9311  0,0107
Total      90  1,0110

S = 0,1034   R-Sq = 7,90%   R-Sq(adj) = 4,73%


                           Individual 95% CIs For Mean Based on
                           Pooled StDev
Level   N    Mean   StDev  ------+---------+---------+---------+---
 800    7  1,4471  0,0881  (--------------*---------------)
 801    7  1,4700  0,0490      (---------------*---------------)
1105   64  1,5150  0,1149                          (----*----)
1500   13  1,4438  0,0565     (-----------*----------)
                           ------+---------+---------+---------+---
                               1,400     1,450     1,500     1,550

Pooled StDev = 0,1034
```

Appenix IV

One-way ANOVA analysis: Body size comparison between the sexes. Elytra (mm) versus sex and pronotum (mm) versus sex.

Dendroctonus frontalis

Tab. 8a

One-way ANOVA: Elytra versus sex

```
Source   DF      SS      MS     F      P
sex       1  0,0116  0,0116  0,57  0,450
Error   118  2,3743  0,0201
Total   119  2,3859

S = 0,1418   R-Sq = 0,48%   R-Sq(adj) = 0,00%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  -----+---------+---------+---------+----
female  68  1,9725  0,1643            (-------------*-------------)
male    52  1,9527  0,1052  (---------------*---------------)
                            -----+---------+---------+---------+----
                               1,925     1,950     1,975     2,000

Pooled StDev = 0,1418
```

Tab. 8b

One-way ANOVA: Pronotum versus sex

```
Source   DF       SS       MS     F      P
sex       1  0,00345  0,00345  0,67  0,416
Error   118  0,60995  0,00517
Total   119  0,61340

S = 0,07190   R-Sq = 0,56%   R-Sq(adj) = 0,00%


                              Individual 95% CIs For Mean Based on
                              Pooled StDev
Level    N     Mean    StDev  ----+---------+---------+---------+-----
female  68  0,76985  0,08016             (--------------*-------------)
male    52  0,75904  0,05932  (----------------*---------------)
                              ----+---------+---------+---------+-----
                                0,744     0,756     0,768     0,780

Pooled StDev = 0,07190
```

Tab. 8a
One-way ANOVA: Elytra versus Sex

```
Source   DF      SS      MS     F      P
Sex       1  0,1457  0,1457  3,73  0,054
Error   251  9,7976  0,0390
Total   252  9,9434

S = 0,1976   R-Sq = 1,47%   R-Sq(adj) = 1,07%


                             Individual 95% CIs For Mean Based on
                             Pooled StDev
Level     N    Mean   StDev  ------+---------+---------+---------+---
Female  151  2,5881  0,2151                    (----------*---------)
Male    102  2,5392  0,1682  (-----------*------------)
                             ------+---------+---------+---------+---
                                 2,520     2,550     2,580     2,610

Pooled StDev = 0,1976
```

Tab. 8a
One-way ANOVA: Pronotum versus Sex

```
Source   DF       SS       MS      F      P
Sex       1  0,13847  0,13847  15,52  0,000
Error   251  2,23990  0,00892
Total   252  2,37837

S = 0,09447   R-Sq = 5,82%   R-Sq(adj) = 5,45%


                             Individual 95% CIs For Mean Based on
                             Pooled StDev
Level     N    Mean   StDev  --+---------+---------+---------+-------
Female  151  1,0609  0,1044                      (-----*-----)
Male    102  1,0132  0,0773  (------*-------)
                             --+---------+---------+---------+-------
                             1,000     1,025     1,050     1,075

Pooled StDev = 0,0945
```

Dendroctonus valens

Tab. 9a
One-way ANOVA: Elytra versus Sex

```
Source  DF      SS     MS     F      P
Sex      1   1,432  1,432  8,63  0,004
Error   89  14,765  0,166
Total   90  16,196

S = 0,4073   R-Sq = 8,84%   R-Sq(adj) = 7,81%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev   -+---------+---------+---------+--------
Female  47  5,7589  0,4084                    (-------*-------)
Male    44  5,5080  0,4061   (-------*-------)
                             -+---------+---------+---------+--------
                            5,40      5,55      5,70      5,85

Pooled StDev = 0,4073
```

Tab. 9b
One-way ANOVA: Pronotum versus Sex

```
Source  DF      SS      MS      F      P
Sex      1  0,5583  0,5583  17,05  0,000
Error   89  2,9144  0,0327
Total   90  3,4727

S = 0,1810   R-Sq = 16,08%   R-Sq(adj) = 15,13%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  ------+---------+---------+---------+---
Female  47  2,2679  0,1855                        (-------*------)
Male    44  2,1111  0,1760  (-------*------)
                            ------+---------+---------+---------+---
                                2,100     2,170     2,240     2,310

Pooled StDev = 0,1810
```

Dendroctonus vitei

Tab. 10a

One-way ANOVA: Elytra versus Sex

```
Source   DF       SS      MS     F      P
Sex       1   0,4283  0,4283  8,61  0,004
Error   355  17,6708  0,0498
Total   356  18,0991

S = 0,2231   R-Sq = 2,37%   R-Sq(adj) = 2,09%


                             Individual 95% CIs For Mean Based on
                             Pooled StDev
Level     N    Mean   StDev  -----+---------+---------+---------+----
Female  206  2,8200  0,2345                        (--------*-------)
Male    151  2,7499  0,2065  (----------*---------)
                             -----+---------+---------+---------+----
                                2,730     2,765     2,800     2,835

Pooled StDev = 0,2231
```

Tab. 10b

One-way ANOVA: Pronotum versus Sex

```
Source   DF      SS      MS      F      P
Sex       1  0,1190  0,1190  11,34  0,001
Error   355  3,7240  0,0105
Total   356  3,8430

S = 0,1024   R-Sq = 3,10%   R-Sq(adj) = 2,82%


                             Individual 95% CIs For Mean Based on
                             Pooled StDev
Level     N    Mean   StDev  ---------+---------+---------+---------+
Female  206  1,1549  0,1062                     (------*------)
Male    151  1,1179  0,0971  (-------*-------)
                             ---------+---------+---------+---------+
                                    1,120     1,140     1,160     1,180

Pooled StDev = 0,1024
```

Ips apache

Tab. 11a
One-way ANOVA: Elytra versus Sex

```
Source  DF      SS      MS     F      P
Sex      1  0,0547  0,0547  1,73  0,191
Error   97  3,0628  0,0316
Total   98  3,1175

S = 0,1777   R-Sq = 1,75%   R-Sq(adj) = 0,74%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  ---------+---------+---------+---------+
Female  59  2,5319  0,1727  (-----------*----------)
Male    40  2,5798  0,1849            (-------------*-------------)
                            ---------+---------+---------+---------+
                                   2,520     2,560     2,600     2,640

Pooled StDev = 0,1777
```

Tab. 11b
One-way ANOVA: Pronotum versus Sex

```
Source  DF      SS      MS     F      P
Sex      1  0,2393  0,2393  8,59  0,004
Error   97  2,7012  0,0278
Total   98  2,9405

S = 0,1669   R-Sq = 8,14%   R-Sq(adj) = 7,19%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  ------+---------+---------+---------+---
Female  59  1,9641  0,1518  (--------*-------)
Male    40  2,0643  0,1870                    (----------*---------)
                            ------+---------+---------+---------+---
                                1,950     2,000     2,050     2,100

Pooled StDev = 0,1669
```

Ips cribricollis

Tab. 12a
One-way ANOVA: Elytra versus Sex

```
Source  DF      SS      MS     F      P
Sex      1  0,0469  0,0469  3,39  0,069
Error   92  1,2732  0,0138
Total   93  1,3200

S = 0,1176   R-Sq = 3,55%   R-Sq(adj) = 2,50%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev  ---+---------+---------+---------+------
Female  11  1,9291  0,2362       (-------------*-------------)
Male    83  1,8596  0,0934  (----*----)
                            ---+---------+---------+---------+------
                             1,850     1,900     1,950     2,000

Pooled StDev = 0,1176
```

Tab. 12b
One-way ANOVA: Pronotum versus Sex

```
Source  DF      SS      MS     F      P
Sex      1  0,0199  0,0199  1,75  0,189
Error   92  1,0450  0,0114
Total   93  1,0648

S = 0,1066   R-Sq = 1,87%   R-Sq(adj) = 0,80%


                            Individual 95% CIs For Mean Based on
                            Pooled StDev
Level    N    Mean   StDev    +---------+---------+---------+---------
Female  11  1,5373  0,1726     (-----------------*-----------------)
Male    83  1,4920  0,0954    (-----*------)
                              +---------+---------+---------+---------
                            1,470     1,505     1,540     1,575

Pooled StDev = 0,1066
```

The photographic figures are taken from www.forestryimages.org.