N° d'ordre : 4176

THÈSE

PRÉSENTÉE A

L'UNIVERSITÉ BORDEAUX 1

ÉCOLE DOCTORALE SCIENCES ET ENVIRONNEMENTS

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POUR OBTENIR LE GRADE DE DOCTEUR

SPÉCIALITÉ : ÉCOLOGIE EVOLUTIVE,
FONCTIONNELLE ET DES COMMUNAUTÉS

Effet de la diversité des essences forestières sur les niveaux de population de la processionnaire du pin (*Thaumetopoea pityocampa*), à différentes échelles spatiales, dans la forêt des Landes de Gascogne

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Soutenue le 10 décembre 2010

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Les peuplements forestiers mélangés subissent moins de dégâts d'insectes herbivores que les peuplements purs, du fait d'une diminution de l'accessibilité à la ressource ou/et d'une amélioration des conditions de survie de leurs ennemis naturels. Pour vérifier ces hypothèses, nous avons étudié un insecte ravageur, la processionnaire du pin (***Thaumetopoea pityocampa***), et ses insectes parasitoïdes dans le contexte de monoculture de pin maritime (***Pinus pinaster***) de la forêt des Landes de Gascogne, où persistent localement des zones de milieu ouvert (pare feux, coupes rases) et des boisements d'essences feuillues (haies en bordure de peuplement de pin, ripisylves, îlots). Nous avons pu démontrer que :

(1) La colonisation des parcelles de pin par la processionnaire est limitée par la présence de haies de feuillus en lisière de parcelle. En effet, les feuillus jouent un rôle de barrière physique, entravant la détection visuelle des pins par la femelle de processionnaire lorsqu'elle recherche un site d'oviposition.

(2) La longévité des principaux parasitoïdes, spécialiste et généraliste, des œufs de processionnaire est favorisée par la consommation de miellat produit par des pucerons du chêne. Cela permet notamment à l'espèce généraliste, qui émerge deux mois avant la processionnaire, de prolonger sa présence dans le milieu et donc d'augmenter sa probabilité de parasiter des pontes de processionnaire.

(3) Les chrysalides de processionnaire du pin survivent mieux dans le sol des milieux ouverts que sous couvert forestier (de pin ou de feuillus), du fait d'une température et d'une humidité plus élevées. L'association de pins et de milieux ouverts favorise la processionnaire par complémentation des habitats, tandis que la présence de feuillus peut représenter un piège écologique pour les chenilles au moment de l'enfouissement.

(4) À l'échelle du paysage, les peuplements de pin maritime au centre de paysages hétérogènes sont moins infestés que dans les paysages de monoculture. De plus, les niveaux d'infestation de la processionnaire diminuent lorsque la proportion de feuillus dans le paysage environnant augmente.

Ces résultats sont interprétés en fonction des mécanismes écologiques expliquant la relation entre diversité et herbivorie. Des possibilités de transfert vers la gestion forestière de la forêt des Landes de Gascogne sont proposées, ainsi que des perspectives en termes de recherche scientifique.

Effect of tree species diversity on population levels of the pine processionary moth (***Thaumetopoea pityocampa***), at different spatial scales, in the Landes de Gascogne forest

Mixed forests are less prone to insect damage than pure forests because of reduced host accessibility and/or improved control by natural enemies. To test these hypotheses, we have studied the ecology of the pine processionary moth (PPM) (***Thaumetopoea pityocampa***) and its parasitoid, in a monoculture of maritime pine (***Pinus pinaster***) plantations, the Landes de Gascogne forest. There, open areas (firebreaks, clear cuts) and patches of broadleaved woodlands (hedgerows, riparian forest, natural forest remnants) still persist locally. In this study we have shown that:

(1) Pine stand colonization by PPM was limited by the presence of broadleaved hedgerows at stand edge. Broadleaved trees formed physical barriers disrupting the visual detection of pine trees by PPM females when searching for an oviposition site.

(2) The longevity of the two main PPM egg parasitoids increased when specimen were fed with honeydew produced by oak aphids. The generalist species, which emerges two months before PPM, could benefit from this longer lifespan to overlap its host emergence.

(3) PPM pupae survived better in the soil of open areas than under forest covers (pine or broadleaved trees), because of higher temperature and humidity. The association between pine stands and open areas benefits PPM through habitat complementation, whereas the presence of broadleaved trees may act as an ecological trap for PPM caterpillars.

(4) Maritime pine stands within heterogeneous landscapes exhibited lower PPM infestations than similar stands within pine monocultures. PPM infestation levels decreased with increasing percent broadleaved area in the surrounding landscape.

These results are discussed according to the ecological mechanisms which may explain the relationship between insect herbivory and tree species diversity. Perspectives for improved PPM management in the Landes de Gascogne forest, and for further scientific research are proposed.

Voici déjà cinq ans que je suis arrivée à Pierroton. Durant ces années, j'ai souvent pensé à cette page que j'écrirai quand j'aurai terminé ma thèse. L'idée de pouvoir remercier ainsi toutes les personnes qui m'ont apporté leur soutien m'a donné du courage lorsque la motivation me manquait. En bonne scientifique que j'espère être devenue, j'ai agrémenté mon discours de diverses références bibliographiques…

« **C'est le rôle essentiel du professeur d'éveiller la joie de travailler et de connaître** » (Einstein, 1934)
En premier lieu, j'aimerais te remercier, Hervé, de m'avoir proposé ce sujet passionnant, et de m'avoir soutenue dans toutes mes décisions. Merci aussi et surtout pour la compréhension dont tu as toujours fait preuve à mon égard.

« **I get by with a little help from my friends** » (The Beatles, 1967)
Merci à toi, Annabel, pour m'avoir maintes fois remonté le moral et fait envisager les choses sous un angle nouveau. Tu as su faire des statistiques un sujet de conversation agréable, ce qui n'est pas peu dire !

Un grand merci à Didier Alard, pour ses encouragements lors de mon tout premier colloque scientifique ; à Andrea Battisti, pour ses nombreux conseils sur les parasitoïdes de la processionnaire ; à Manuela Branco, pour m'avoir si gentiment accueillie dans ses locaux et fait découvrir la région de Lisbonne ; et à Alain Roques pour sa participation active à mon comité de thèse.

« **Et bras dessus bras dessous, vers les frais bocages, ils vont à la chasse aux papillons** » (Brassens, 1952)
Je tiens particulièrement à remercier toute l'équipe d'entomologie, Pierre, Inge, Fabrice, Dominique, Luc et Amélie, de m'avoir si souvent aidée sur le terrain comme au bureau, physiquement comme moralement. J'espère retrouver un jour une aussi bonne ambiance de travail qu'avec vous.

« **When you're in need of love, they give you care and attention**» (Queen, 1986)
Il est bien évident que je n'aurais jamais pu venir à bout de ce travail sans l'aide des collègues qui ont eu le courage de partager mon bureau, JC, Brice, Bastien, JS et Guillaume. Qu'ils aient été conseillers artistiques, psy, relecteurs, scénaristes des aventures de M. Patate ou adeptes du beer o'clock, ils ont représenté une aide inestimable.

« **Les copains d'abord** » (Brassens, 1964)
De nombreuses personnes ont contribué à ce travail, plus ou moins directement, et elles méritent toutes d'en être remerciées. J'espère n'oublier personne… MERCI À : Marion (après avoir partagé les aléas de la thèse, nous voilà prêtes à partager notre belle-famille ^^), Cathy (ton bureau restera ma planque favorite), Michel (ma Belle ♫) & Alex d'Ephyse ; Lilou & Michel (ma Belle ♪, bis)

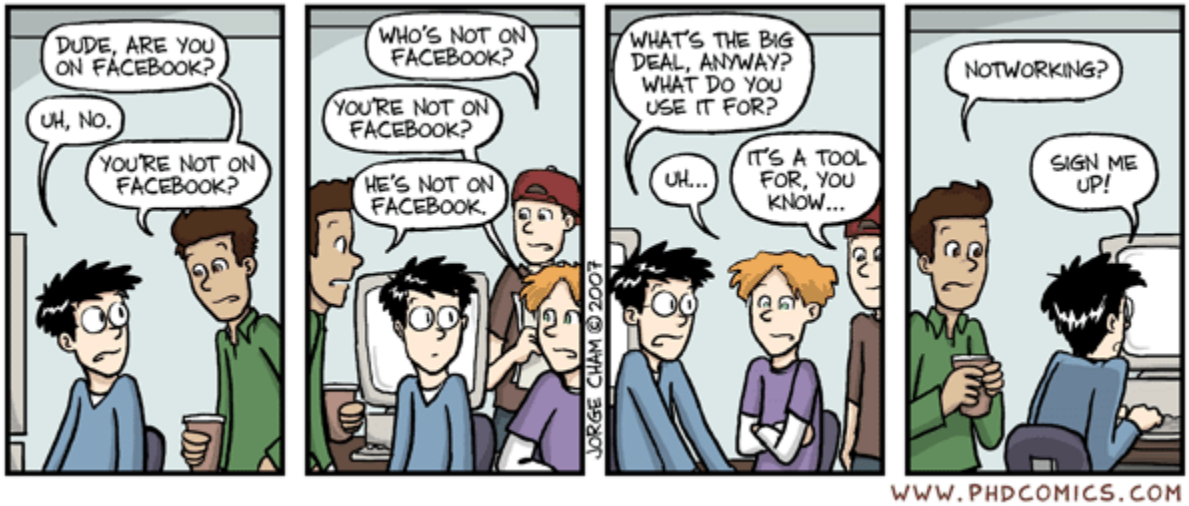
d'avoir corrigé mon anglais (gros boulot !) ; Caro d'avoir toujours su qu'il était impossible de nous changer ; (Martine)² pour ta bonne humeur quotidienne ; Frédo pour ta gentillesse et tes regards pleins de sympathie☺ ; les équipes de l'URZF d'Orléans et de l'UEFM d'Avignon (et plus particulièrement Jean-Claude et Cathy) d'avoir partagé vos connaissances sur la processionnaire ; Les profs de l'ENITAB Lionel et Thomas de m'avoir confié vos élèves, Sylvie et Coralie de m'avoir fait découvrir la recherche, Mark de m'avoir souvent relue et conseillée ; Helena, Iñaki et Jorge, Rozenn, Lélia et François pour votre gentillesse et votre amitié ; et bien sûr… mes très chers Dadou & Gérald qui avez su, par votre soutien sans faille qui dépasse largement le cadre professionnel, m'empêcher de broyer du noir… ☺

« **Si tu m'apprivoises, nous aurons besoin l'un de l'autre** » (St Exupéry, 1943)
De nombreux animaux ont contribué à cette thèse. Toutes les processionnaires et parasitoïdes que j'ai cruellement sacrifiés, déjà, mais aussi et surtout Copernic, Collyre et Indy, qui étaient toujours les premiers lorsqu'il s'agissait de partir sur le terrain !

« **Keep on with the force, don't stop **** » (Michael Jackson, 1979)
Un grand merci à ma belle famille, Cathy & Patou, Éliane & Yves, Aurore & Super Jéjé & la petite Saria, Marion (bis) & Lolo aka Koopa, ma Chouchou ainsi qu'Emeline et Guillaume, pour tout le temps passé ensemble, les soirées entre filles, les arrivées surprises, les nombreux repas partagés, les soirées au ciné ou simplement à ne rien faire… mais ensemble ! Vous représentez un soutien de tous les instants !

« **Love is our resistance** » (Muse, 2009)
Les mots me manquent pour exprimer tout mon amour à ma famille, Maman & Papa, Noémie & Erwan, Alice & Thomas & la petite Ondine. Rien de tout cela n'aurait été possible sans vous… Un nouveau Dr. Dulaurent sera bientôt dans la place !

« **La gravité ne peut être tenue responsable pour ceux qui tombent… amoureux** » (Einstein)
Pour finir, je souhaiterais exprimer toute ma tendresse à mon Juju. Je t'aime.



CHAPITRE 1

Introduction Générale

1. Le rôle fonctionnel de la biodiversité

La biodiversité est la diversité naturelle des organismes vivants. Elle s'apprécie en considérant la diversité des écosystèmes, des espèces, des populations et des gènes dans l'espace et dans le temps. Les activités anthropiques sont à l'origine d'une érosion de la biodiversité dans le monde à un rythme sans précédent (Thomas et al. 2004, Thuiller et al. 2005), probablement plus de 100 à 1000 fois plus rapide que lors des extinctions massives ayant marqué les changements d'ères géologiques (Millennium Ecosystem Assessment 2005). Trois raisons majeures peuvent expliquer cette érosion accélérée : l'altération, voire la destruction, des habitats, les invasions biologiques et le réchauffement climatique (Pimm et al. 1995, Ricciardi et Rasmussen 1999). L'appauvrissement de la biodiversité et du patrimoine naturel pose des problèmes éthiques et esthétiques mais il représente également un risque de dégradation des services assurés par les écosystèmes (Figure 1).

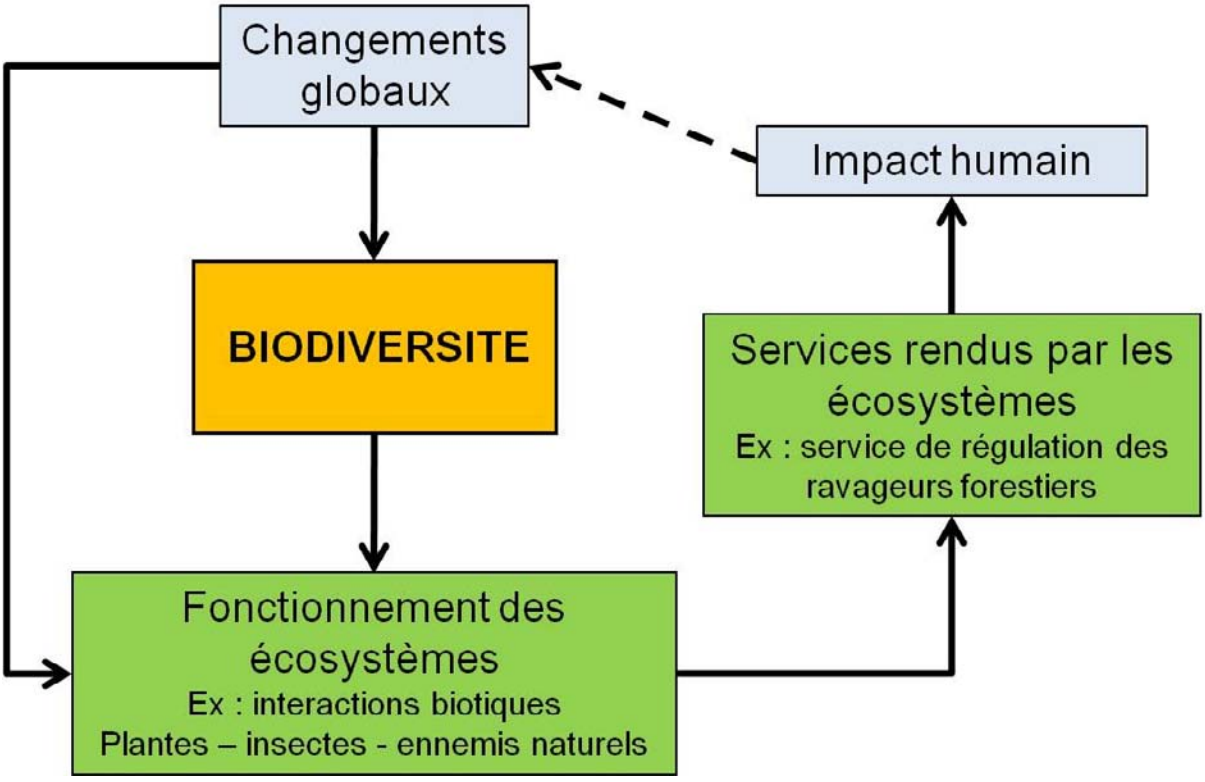


Figure 1 : Fonctionnement des écosystèmes et interaction avec les sociétés humaines (Figure adaptée du Millennium Ecosystem Assessment 2005)

Les écologues s'accordent en effet à penser que la diminution du nombre d'espèces devrait conduire à une altération du fonctionnement des écosystèmes (McCann 2000, Chapin et al. 2000, Hughes et Petchey 2001, Loreau et al. 2001, Pfisterer et Schmid 2002, Jonsson et Malmqvist 2003). Trois mécanismes ont été proposés pour expliquer la relation positive entre diversité des espèces et le fonctionnement primaire (production de biomasse) des écosystèmes : 1) l'effet

d'échantillonnage, qui suppose que les écosystèmes riches en espèces ont une plus grande probabilité de contenir des espèces très productives (Wardle 2001) ; 2) la complémentation de niches (Leibold 1995), qui explique que la diversité des espèces s'accompagne d'une diversité de leurs traits fonctionnels et donc de leur capacité à utiliser de façon complémentaire les différentes ressources disponibles (eau, lumière, nutriment) pour assurer leur croissance et enfin 3) la facilitation qui est définie comme une interaction positive entre espèces, une espèce offrant de meilleures conditions de développement à ses voisines (ex. ombrage pour les plantes sciaphiles) (Bertness et Callaway 1994).

La majorité des études sur la relation entre biodiversité et fonctionnement des écosystèmes s'est concentrée sur le rôle de la richesse spécifique ou de la diversité fonctionnelle de producteurs primaires (plantes), dans le fonctionnement primaire (production de biomasse) d'écosystèmes assez simples : systèmes prairiaux (Yamamura 2002), microcosmes bactériens (Fox et McGrady-Steed 2002), mésocosmes aquatiques (Cardinale et al. 2002). Du fait des difficultés de manipulation ou de suivi sur le long terme, peu d'expérimentations ont été menées sur l'effet de la biodiversité sur le fonctionnement de systèmes dominés par des espèces pérennes comme les forêts (Scherer-Lorenzen et al. 2005, Carnus et al. 2006, Firn et al. 2007, Loreau 2010). Cependant de récentes études démontrent l'existence d'une relation positive entre diversité et productivité des forêts (Vila et al. 2007, Paquette et Messier 2010).

Les effets de la diversité sur le fonctionnement primaire des communautés, au travers de plusieurs niveaux trophiques (producteurs, consommateurs, prédateurs), sont encore peu connus (Steiner et al. 2005, Petermann et al. 2010). Or la diversité des insectes herbivores est connue pour être positivement corrélée avec celle des plantes (Siemann et al. 1998, Haddad et al. 2001). Aussi, si l'on applique le même raisonnement que pour les producteurs, on devrait s'attendre à ce qu'une plus grande richesse d'herbivores se traduise par une meilleure utilisation des ressources, et donc une plus grande exploitation des plantes par herbivorie, conduisant ***in fine*** à une diminution de la biomasse végétale. Cela viendrait donc contredire les observations d'une augmentation de la productivité des plantes dans les communautés végétales riches en espèces (Kelty 2006, Piotto 2008). Un moyen d'analyser ce paradoxe est de considérer les études portant sur l'impact des insectes herbivores, en particulier les insectes ravageurs des cultures, dans des agrosystèmes plus ou moins diversifiés. Tonhasca et Byrne (1994) ont comparé les résultats de 31 articles publiés sur 10 ans, afin de tester l'hypothèse que les cultures diversifiées subissent moins d'attaques d'insectes ravageurs que les monocultures. Dans plus de 70 % des cas, ils ont montré des effets positifs de la diversité. Une autre méta-analyse, reprenant la même hypothèse avec 119 études menées en milieu forestier, a également démontré que les dégâts d'insectes herbivores sont significativement plus élevés dans les peuplements purs d'une essence forestière que dans les peuplements où cette essence est associée à d'autres espèces d'arbres (Jactel et Brockerhoff 2007). Ces résultats suggèrent que d'autres mécanismes que pour les plantes expliquent la relation entre diversité et fonctionnement des populations d'herbivores. Plusieurs mécanismes écologiques, développés ci-dessous, ont été en effet proposés pour expliquer l'effet négatif de la diversité des espèces végétales sur l'herbivorie (Barbosa et al. 2009).

2. Mécanismes écologiques expliquant la relation diversité-résistance

L'association de plusieurs espèces végétales peut permettre de diminuer leur détection et / ou leur exploitation par les insectes herbivores (« ***associational resistance*** »). Ce phénomène peut s'expliquer par les mécanismes suivants.

2.1. Accès à la ressource

L'hypothèse de la concentration de la ressource proposée par Root (1973) et vérifiée par Risch (1981) suggère que l'accessibilité à la plante pour les herbivores diminue lorsque la proportion de plantes non hôtes augmente. L'accessibilité à la plante hôte peut en fait être altérée par la présence de différents types de barrière : quantitative, physique ou chimique (Jactel et al. 2008).

La première raison qui explique que les mélanges d'espèces soient moins attaqués par les herbivores que les monocultures tient au fait que la ressource y est moins concentrée, et donc plus difficile à détecter (Root 1973). Kareiva (1983) a en effet démontré que la proportion d'insectes herbivores augmentait avec la taille des patchs de leur plante hôte. A l'inverse, quand plusieurs espèces sont en mélange, une ***barrière quantitative*** s'applique, limitant la quantité de nourriture disponible pour les herbivores, et entravant leur détection. D'autre part, plusieurs études ont démontré que les insectes détectaient mieux leur ressource quand elle était plus concentrée (Baliddawa 1985). Les insectes se dispersant de manière ***passive*** sont particulièrement sensibles au mélange d'espèces. Par exemple, les larves de la tordeuse des bourgeons ***Choristoneura fumiferana*** (un défoliateur majeur de l'épicéa et du sapin au Canada) ou du Bombyx disparate ***Lymantria dispar*** (un défoliateur majeur des chênaies dans l'ensemble de l'hémisphère nord) sont transportées par le vent durant leurs premiers stades larvaires. La probabilité d'atterrir sur un arbre hôte lors de la dispersion de ces jeunes chenilles diminue en fonction de la présence d'arbres non hôtes dans le voisinage, et les niveaux d'infestation peuvent ainsi être réduits (Cappuccino et al. 1998).

Un mélange d'essences peut également jouer un rôle de ***barrière physique*** à la dispersion ***active*** des herbivores lorsque l'hôte est physiquement caché par d'autres plantes (Watt 1992). Plusieurs études se sont penchées sur l'effet de la végétation environnante sur les niveaux d'infestation de jeunes plants d'arbre. Les niveaux d'infestation de ***Rhyacionia frustrana*** sur des jeunes plants de pin Taeda (***Pinus taeda)*** sont notamment limités par la présence de végétation haute et dense alentours (Sun et al. 1998), de même que les infestations de ***Pissodes strobi*** sur pin Gris (***Pinus banksiana)*** (Bellocq et Smith 1995). La notion de barrière physique concerne également les insectes utilisant activement des stimuli visuels pour détecter leur hôte (Prokopy 1983). Ces insectes peuvent être perturbés par la présence de plantes non hôtes ayant une forme ou une couleur différente, qui limiterait l'apparence des arbres hôtes (Moore et al. 1991). Ainsi, le papillon femelle de la processionnaire ***Ochrogaster lunifer*** oriente son vol de ponte vers des silhouettes d'arbre se détachant sur fond clair. La présence d'une végétation

massive cachant l'arbre hôte se traduit par une réduction de ses niveaux d'infestation (Floater et Zalucki 2000).

Enfin, l'hypothèse d'une ***barrière chimique*** à la colonisation de l'arbre hôte suggère que les insectes qui repèrent leur hôte par certains composés volatiles qu'il émet (« Volatile organic compound ») sont perturbés par la présence de composés émis par d'autres essences non hôtes (Visser 1986). En effet, les composés volatiles diffèrent entre les espèces d'arbres. Dans les peuplements mixtes, le signal olfactif émis est donc plus complexe que dans les peuplements purs, rendant plus difficile le repérage de l'essence hôte par un insecte herbivore (Zhang 2001). D'après Risch (1981), la perturbation de la reconnaissance olfactive de l'hôte pourrait également réduire le temps passé dans un habitat et perturber le comportement de reproduction de certains insectes, limitant ainsi leur niveau de population dans les peuplements mélangés. En particulier, les coléoptères saproxyliques des conifères sont connus pour être attirés par les composés volatiles émis par leur hôte (Wood 1982). Certains composés émis par des essences feuillues non hôtes sont connus pour avoir des effets répulsifs sur différentes espèces de coléoptères saproxyliques (Schlyter et al. 2000). Une réduction des infestations de rondins de pin par ***Ips sexdentatus*** a notamment été démontrée quand ces piles étaient entourées de branches de bouleau (Jactel et al. 2001).

2.2. Rôle des ennemis naturels

L'hypothèse du rôle des ennemis naturels, proposée par Root (1973) et revue par Russel (1989), suggère que la diversité des essences végétales peut favoriser les ennemis naturels en leur apportant un abri, des sites d'oviposition ou d'hibernation, des hôtes ou proies alternatifs, ou encore une alimentation complémentaire pouvant améliorer leur fitness. Cette hypothèse a partiellement été confirmée par Siemann et al. (1999) qui a démontré que la diversité des espèces végétales pouvait effectivement engendrer une augmentation de la proportion de certains prédateurs ou parasitoïdes.

Les communautés de plantes les plus riches en espèces offrent des microhabitats et microclimats différents (Porté et al. 2004), offrant ainsi plus de possibilités d'abris aux ennemis naturels pour résister aux conditions défavorables. D'après Landis et al. (2000), dans un contexte d'agroécosystème, la présence d'une végétation en bordure de champ permettrait aux ennemis naturels (1) d'hiverner et ainsi d'assurer un contrôle biologique efficace l'année suivante (Thomas et al. 1991), (2) d'échapper aux températures élevées et aux faibles humidités en été (Orr et al. 1997), et (3) de trouver des sites stables où déposer leurs œufs (Lundgren et al. 2009). Dans un contexte forestier, certains oiseaux ont besoin d'habitats favorables pour nicher. Ainsi, dans les forêts de conifères à courte rotation, la présence d'arbres âgés d'essences feuillues peut favoriser certains oiseaux insectivores en leur fournissant des cavités pour nicher, améliorant ainsi leur impact sur les populations d'insectes (Dickson et Segelquist 1979).

Par ailleurs les mélanges d'essences végétales abritent davantage d'espèces herbivores (Siemann et al. 1998, Haddad et al. 2001), qui peuvent constituer une réserve élargie de proies et d'hôtes alternatifs pour les prédateurs et parasitoïdes généralistes. Ainsi, leur niveau de population peut être maintenu à un niveau stable

pendant la période durant laquelle leur proie ou hôte cible n'est pas disponible dans l'habitat (Landis et al. 2000). Dans une étude sur le prédateur généraliste ***Coccinella septempunctata***, Bianchi et al. (2004) ont mis en évidence que lorsque l'infestation de leur proie principale, un puceron ravageur du blé, était retardée, ce prédateur pouvait maintenir ses niveaux de population à un degré suffisant pour être efficace grâce à la consommation d'autres pucerons infestant des plantes non cultivées. De même, l'un des parasitoïdes de ***Choristoneura fumiferana*** (défoliateur des résineux), est capable de parasiter des insectes défoliateurs des essences feuillues (Cappuccino et al. 1998), ce qui lui permet de maintenir ses populations lorsque l'hôte principal n'est pas disponible dans le milieu.

Enfin, les communautés végétales diversifiées peuvent fournir des ressources alimentaires complémentaires aux ennemis naturels (Russel 1989). Des substances riches en sucre sont produites par certaines espèces végétales (ex. nectar) ou par certains insectes associés à ces espèces (ex. miellat de puceron). Ces substances peuvent devenir une nourriture complémentaire essentielle, notamment pour les parasitoïdes qui sont dépendants des ressources en hydrates de carbone fournies par leur milieu (Lewis et al. 1998). En effet, la consommation de sucre permet d'augmenter leur durée de vie (Hogervorst et al. 2007), leur fécondité (Sood et Pajni 2006), leur activité de vol (Casas et al. 2003), ou une combinaison de ces éléments (Wäckers 2003). Ainsi, Zoebelein (1957) a démontré que les mélanges d'essences forestières fournissait un meilleur apport en miellat de puceron que les monocultures, car différentes essences d'arbres abritent différentes espèces de pucerons actives à différentes saisons au cours de l'année, et qui peuvent donc se complémenter.

2.3. Modification des conditions abiotiques

Dans un contexte forestier, les conditions microclimatiques sous couvert peuvent varier spatialement entre la lisière et l'intérieur, et d'autre part en fonction de la diversité des essences végétales.

A l'échelle d'un peuplement, la diversité des arbres peut altérer les conditions microclimatiques de l'air et les conditions édaphiques du sol. Les températures de l'air et du sol sont ainsi plus élevées dans des peuplements mixtes de conifères et de feuillus (***Pinus nigra*** et ***Fagus silvatica***) que dans des monocultures de pin (Porté et al. 2004). Ces différences de conditions microclimatiques sous différents types de couvert peuvent influencer et modifier le comportement de ponte et la survie des insectes (Barbosa et al. 2009).

2.4. Quand la diversité favorise l'herbivorie

2.4.1. Phénomènes de contagion

L'association de plusieurs espèces d'hôte peut parfois engendrer une augmentation du niveau d'herbivorie (Barbosa et al. 2009). Ce mécanisme appelé susceptibilité par association (”associational susceptibility”) apparaît lorsque trois facteurs sont réunis : (1) la présence d'un insecte herbivore polyphage capable de consommer plusieurs essences en mélange, (2) une plus grande appétence d'une des plantes hôtes et (3) une densité élevée de l'insecte herbivore, qui consomme

entièrement la ressource fournie par la première plante hôte, développe ses populations et opère alors un transfert sur d'autres espèces de plantes voisines (phénomène de contagion) qui n'auraient pas été consommées sans la présence de l'hôte favorable (White et Whitham 2000). Par exemple, le bombyx disparate ***Lymantria dispar***, dont les principales essences hôtes sont feuillues (chêne, peuplier, bouleau), peut également se nourrir de conifères quand la ressource en feuillues est épuisée (Montgomery et al. 1989). Ainsi, les pins blancs ***Pinus strobus*** plantés en association avec des chênes subissent de plus fortes défoliations par le bombyx que lorsqu'ils sont plantés en monoculture (Brown et al. 1988).

2.4.2. Réponse différente des insectes généralistes et spécialistes

La réponse des insectes généralistes à la diversité des essences est beaucoup plus variable que celle des spécialistes (Jactel et al. 2005, 2007). En effet, lorsqu'aucune autre essence du mélange que l'espèce hôte principale n'est appétente pour le généraliste, la diversité induit bien une diminution des risques de dégâts par l'insecte. Cependant, lorsque les essences en mélange sont toutes des hôtes potentiels d'un herbivore généraliste, la diversité n'induit pas de diminution de l'herbivorie. Elle peut même induire une augmentation des dégâts lorsqu'une essence plus sensible à l'insecte est présente en association avec l'essence principale. Dans ce cas, si le niveau de population de l'insecte généraliste est élevé, un phénomène de contagion aux essences secondaires peut intervenir, induisant une augmentation globale des dégâts d'herbivorie.

3. La relation diversité-stabilité à différentes échelles spatiales

L'ensemble des études évoquées précédemment traite de la diversité végétale à l'échelle de la parcelle ou du peuplement. Or, les capacités de dispersion des insectes herbivores, qui peut atteindre plusieurs kilomètres, indiquent que leur territoire peut s'étendre à des surfaces bien plus importantes. Par ailleurs, la diversité des plantes est aussi distribuée à l'échelle du paysage, notamment quand celui-ci est composé d'une mosaïque de parcelles de compositions végétales différentes. Enfin, bien que la conversion de peuplements purs en peuplements mélangés soit une stratégie prometteuse (Hartley 2002, Kelty 2006) et de plus en plus pratiquée en Europe centrale (Jäkel et Roth 2004, Kint et al. 2009), elle pose trop de problèmes techniques pour être étendue à l'ensemble des monocultures forestières. Or des travaux ont montré que la biodiversité peut être conservée ou restaurée en modifiant la composition des paysages forestiers (Brockerhoff et al. 2008). Il apparaît donc intéressant et utile de considérer la relation entre diversité et résistance des écosystèmes aux insectes herbivores à l'échelle du paysage.

La diversité des paysages est définie par différentes caractéristiques spatiales notamment rapportées par Burel et Baudry (1999). Généralement, le paysage est considéré comme une mosaïque de polygones, ou patchs, auxquels un type d'occupation du sol est affecté (agricole, urbain, forestier etc.). Le paysage peut alors être caractérisé par trois métriques : son ***hétérogénéité***, qui concerne la diversité et l'équitabilité des types de patchs ; sa ***connectivité***, qui traduit la moyenne des distances entre patchs de même type et sa ***fragmentation***, qui représente le nombre de patchs par unité de surface. En considérant que les patchs qui composent un

paysage représentent des taches d'habitat (ou de non habitat) plus ou moins favorables à la survie des populations, l'écologie des espèces peut alors être considérée à l'échelle du paysage. Ainsi, l'hétérogénéité d'un paysage peut être associée aux concepts de complémentation d'habitat (lorsque des taches d'habitats favorables de différente nature permettent aux espèces de satisfaire des besoins complémentaires tels que la reproduction et l'alimentation) et de supplémentation d'habitat (lorsque plusieurs taches d'un habitat en particulier sont nécessaires pour répondre à un besoin important de ressources) (Dunning et al. 1992). De même la notion de connectivité des taches d'habitats favorables à une espèce peut être associée aux besoins de dispersion des individus de cette espèce, qui doivent explorer le paysage à la recherche de nourriture, de partenaires pour la reproduction, ou de sites d'abri ou de ponte (With et al. 1997). Enfin la fragmentation peut avoir des effets contradictoires, limitant la taille des taches d'habitats et donc la probabilité de survie d'un certain nombre d'espèces, mais augmentant aussi les interfaces entre habitats de différents types et favorisant donc les espèces associées aux écotones (Fortin et Maufette 2001, Fahrig 2003).

Il apparaît donc possible de tester, à l'échelle du paysage, la validité des hypothèses écologiques émises à l'échelle du peuplement entre diversité des forêts et résistance à l'herbivorie. Par exemple, le développement des populations d'herbivores dépend de la taille, du nombre et de la distribution dans l'espace des taches d'habitat favorable. Ainsi, l'hypothèse écologique concernant la concentration de la ressource pourrait être associée aux notions de fragmentation et d'absence de connectivité du paysage. De la même manière, les barrières à la colonisation pourraient être traduites en termes d'obstacles que la fragmentation et l'absence de connectivité des paysages opposent au déplacement des individus. Par ailleurs, les caractéristiques des peuplements mélangés favorisant le maintien et l'efficacité des ennemis naturels pourraient être transposées à l'échelle du paysage. Leurs besoins d'abri, de site d'oviposition ou d'alimentation complémentaire pourraient en effet être satisfaits par l'hétérogénéité du paysage. Enfin, l'hétérogénéité des occupations du sol peut être à l'origine d'une hétérogénéité des conditions climatiques auxquelles seraient sensibles les insectes herbivores.

Quelques études ont déjà mis en évidence l'effet négatif de l'hétérogénéité des mosaïques paysagères sur les niveaux d'infestation d'insectes herbivores. Par exemple, les dommages associés au méligèthe du colza (***Meligethes aeneus***) sont en moyenne moins élevés dans les parcelles entourées d'un paysage hétérogène (Thies et Tscharntke 1999, Thies et al. 2003). Plus généralement, Bianchi et al. (2006) ont synthétisé les résultats d'études menées en milieu agricole. Dans 74 % et 45 % des cas respectivement, les populations d'ennemis naturels étaient plus importantes, et les dégâts d'herbivore moins élevés, au sein de paysages hétérogènes qu'au sein de paysages agricoles simplifiés. Des études conduites en milieu forestier sur la tordeuse des bourgeons de l'épinette (***Choristoneura fumiferana***), ont abouti au même constat. Les taux d'attaque de cet insecte dans les parcelles de certaines essences de conifères peuvent être limités par la présence alentours de forêts mélangées comprenant des essences feuillues (Cappuccino et al. 1998, Mackinnon et MacLean 2003, Campbell et al. 2008). A notre connaissance, il existe très peu d'autres études traitant du rôle de la composition des paysages forestiers sur les niveaux d'infestation par les insectes ravageurs.

L'ensemble des mécanismes écologiques présentés ici, reliant diversité et santé des forêts, est issu d'études éparses menées sur des modèles différents, dans des contextes variés. Il serait donc intéressant de tester ces hypothèses sur un unique modèle afin d'évaluer le poids respectif des différents mécanismes proposés pour expliquer la diminution de l'herbivorie dans les forêts mélangées.

4. Modèle étudié

4.1. La processionnaire du pin

La processionnaire du pin ***Thaumetopoea pityocampa*** (Denis & Schiffermüller) (Lepidoptera, Notodontidae) est un insecte ravageur majeur du Sud de l'Europe et du Nord de l'Afrique (FAO 2010). La chenille s'attaque à toutes les essences de pin présentes en France, ainsi qu'aux cèdres (Démolin 1969). La consommation des aiguilles par les chenilles induit une diminution de la croissance de l'arbre, qui peut le rendre sensible aux attaques d'autres ravageurs comme les scolytes ou le pissode (Lemoine 1977, Graf et Mzibri 1995, Markalas 1998). L'aire de répartition de cet insecte s'étend sur une grande partie du territoire français, et atteint actuellement sa limite Nord aux portes de Paris (Robinet et al. 2007). Cette limite est en expansion aussi bien en latitude qu'en altitude du fait du réchauffement climatique qui, en augmentant les températures hivernales, permet un meilleur taux de survie des chenilles en zone de front (Battisti et al. 2005). Les niveaux d'infestation de la processionnaire connaissent des phases de pullulation suivies de périodes de faible niveau d'infestation, selon une dynamique de population cyclique qui s'étend sur 6 à 8 ans (Robinet 2006). Les chenilles de processionnaire sont également connues pour leurs propriétés urticantes qui posent de nombreux problèmes sanitaires pour les humains et les animaux (Ducombs et al. 1981).

4.1.1. Cycle de développement (Figure 2)

Le cycle de vie de la processionnaire est généralement annuel mais peut s'étendre sur plusieurs années selon les conditions du milieu, montrant une forte variabilité de la phénologie de l'espèce en fonction de la latitude et de l'altitude (Démolin 1974). Ainsi, les indications temporelles indiquées plus loin dans ce paragraphe concernent la phénologie de l'espèce dans le Sud Ouest de la France.

La phase adulte du cycle de vie de la processionnaire a été précisément décrite par Démolin (1969). L'émergence des adultes a lieu au cours de l'été, entre la fin du mois de juin et la fin du mois d'août, au coucher du soleil. Les adultes mâles sont plus petits que les femelles, et le sexe ratio est généralement proche de 1. Sitôt après sa sortie de terre, le papillon gagne un emplacement surélevé proche (tige, herbe, branche) pour y déployer ses ailes. A la tombée de la nuit, les femelles émettent une phéromone sexuelle pour orienter le vol des mâles. Le mâle meurt dans les heures qui suivent l'accouplement. La femelle, quant à elle, recherche alors un hôte par sa silhouette (Démolin 1969) ou les composés volatiles qu'il émet (Zhang et al. 2003, Paiva et al. 2010), et y dépose ses œufs, généralement autour de deux aiguilles. La ponte en forme de manchon contient en moyenne 200 œufs, recouverts d'écailles provenant de l'extrémité de l'abdomen de la femelle.

Les œufs éclosent entre 30 et 45 jours après l'accouplement. La vie larvaire comporte 5 stades, de L1 à L5, au cours desquels les chenilles d'une même ponte resteront groupées. Du fait d'un développement hivernal, ce grégarisme est essentiel à leur survie. Au stade L1, les chenilles tissent un réseau de soies très léger autour de la ponte (appelé pré-nid). Dès l'arrivée des premiers froids, la colonie entreprend le tissage d'un nid d'hiver qui lui permet de résister aux températures basses (Démolin 1965). En effet, ce nid joue le rôle d'un radiateur en captant les rayons du soleil pour augmenter la température à l'intérieur du nid. La nuit, lorsque la température dépasse 0°C, les chenilles quittent le nid pour s'alimenter (Hoch et al. 2009).

La procession de nymphose, qui donne son nom vernaculaire à l'espèce, a lieu à la fin de l'hiver entre décembre et mars. Les chenilles parvenues à maturité descendent le long du tronc de l'arbre hôte pour trouver une zone de sol éclairée et meuble en bordure de parcelle et s'y enfouir (Démolin 1971). Après l'enfouissement, la chenille tisse un cocon de nymphose autour d'elle et se transforme en chrysalide. Elle entre en diapause pour une durée d'environ 4 mois, mais qui peut se prolonger dans le cas de conditions défavorables (Démolin 1974).

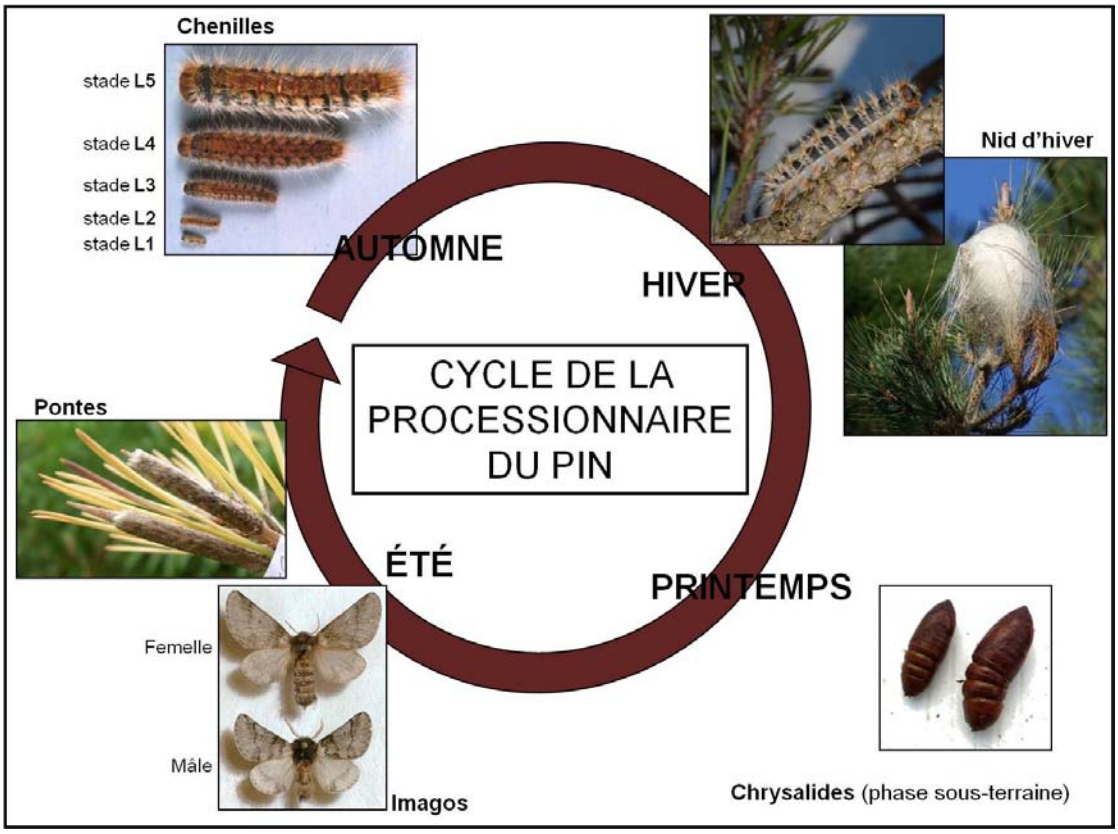


Figure 2 : Cycle de la processionnaire du pin

4.1.2. Ennemis naturels

Une liste des ennemis naturels de la processionnaire à tous les stades de son cycle a été proposée par Martin (2005). Les principales espèces, et plus particulièrement celles présentes dans le Sud Ouest de la France, sont présentées ici.

Prédateurs. Les oiseaux et les chiroptères sont les principaux prédateurs du stade adulte de la processionnaire du pin, notamment l'engoulevent ***Caprimulgus europaeus***. Les œufs peuvent être prédatés par plusieurs espèces d'Orthoptères, notamment l'éphippigère ***Ephippiger ephippiger*** (Démolin et Delmas 1967). Les chenilles de processionnaire peuvent être prédatées à n'importe quel stade dans leur nid d'hiver par plusieurs espèces d'oiseaux, notamment les mésanges (Pimentel 2004). Enfin, les chrysalides peuvent être prédatées par un oiseau, la huppe fasciée ***Upupa epops***, dont le long bec est adapté à la recherche de nymphes enfouies dans le sol. Pour avoir un impact sur les niveaux de population de la processionnaire, cet oiseau a besoin de nicher dans des cavités de vieux feuillus situés à proximité des parcelles de pin (Barbaro et al. 2008).

Parasitoïdes. Deux espèces principales de parasitoïdes attaquent les œufs de processionnaire dans le Sud-Ouest. Leur biologie a été largement étudiée et décrite par Masutti (1964). ***Baryscapus servadeii*** (Domenichini) (Hymenoptera, Eulophidae) est une espèce spécialiste dont les dates d'émergence correspondent avec la période de présence des œufs de processionnaire (Figure 3). Les individus émergés en premier sont capables de parasiter à nouveau les pontes de processionnaire immédiatement après leur émergence, leur permettant de réaliser deux générations par an. ***Ooencyrtus pityocampae*** (Mercet) (Hymenoptera, Encyrtidae) est une espèce généraliste qui a déjà été élevée sur des hôtes variés défoliateurs de résineux et de feuillus (Battisti et al. 1988, Figure 4). Les individus de cette espèce émergent deux mois avant la période de présence des œufs de processionnaire, et sont également capables d'accomplir deux générations par an. ***Phryxe caudata*** (Rondani) (Diptera, Tachinidae) est le principal parasitoïde spécialiste des chenilles. Deux générations de cette espèce peuvent se développer sur une même génération de l'hôte. Les œufs de la première génération sont pondus sur les jeunes chenilles de processionnaire à partir du stade L2. Les adultes émergent avant la mue L4/L5 et pondent directement sur les chenilles du stade L5. Les jeunes larves de la seconde génération quittent la chrysalide de l'hôte pour former leur pupe au moment des émergences des papillons (Biliotti 1956). Enfin, durant sa phase sous-terraine, la processionnaire est essentiellement parasitée par un Diptère, ***Villa brunnea*** (Becker) (Diptera, Bombyliidae), dont les adultes volent de juillet à septembre. Les femelles déposent leurs œufs durant les heures les plus chaudes de la journée, après les avoir enrobés de terre, en les projetant au sol à l'abri du soleil. Après éclosion, les jeunes larves planidium s'enfoncent dans le sol à la recherche d'un cocon. Elles pénètrent à l'intérieur des chrysalides de processionnaire pour y finir leur développement (DuMerle 1979a, 1979b).

Figure 3 : Femelle de ***Baryscapus servadeii***

Figure 4 : Femelle d'***Ooencyrtus pityocampae***

Pathogènes. Plusieurs champignons peuvent infecter les chenilles, notamment ***Beauveria bassiana***, qui ne développe ensuite son mycélium qu'au stade de la chrysalide (Géri 1980). Les nymphes peuvent par ailleurs être infectées directement dans le sol par différentes espèces de champignon, notamment ***Cordyceps militaris***. Des bactéries notamment ***Bacillus thuringiensis*** et des virus comme ***Smithiavirus pityocampae*** peuvent également infecter la processionnaire au stade larvaire.

4.1.3. Moyens de lutte

Les moyens de lutte contre la processionnaire à grande échelle sont assez limités. La lutte chimique, utilisée jusqu'au début des années 90, était principalement basée sur l'utilisation d'un insecticide à base de Diflubenzuron, qui s'avérait très efficace (Ribrioux et Dolbeau 1975). Cependant, cette méthode est aujourd'hui en très fort recul du fait du fort impact écologique du diflubenzuron qui est un insecticide à large spectre (site internet du Ministère de l'Agriculture et de la Pêche).

La lutte microbiologique à base de ***Bacillus thuringiensis*** (Bt) est actuellement la plus utilisée contre la processionnaire (Martin et Bonneau 2006). A l'échelle mondiale, elle représente 90 % du marché mondial des biopesticides. Après ingestion par les chenilles, cette bactérie produit des endotoxines qui conduisent à la mort de l'insecte par perforation de la paroi membranaire des cellules de son intestin. Cette méthode de lutte est principalement ciblée sur les premiers stades larvaires de l'ensemble des chenilles de Lépidoptères (avant qu'ils ne produisent des défoliations trop importantes sur les arbres), mais l'utilisation de doses fortes peut également atteindre les derniers stades larvaires. Cette méthode reste toutefois coûteuse et son impact sur l'environnement controversé.

D'autres méthodes ont été envisagées, comme l'utilisation de la phéromone sexuelle à des fins de piégeage de masse ou de lutte par confusion, mais elles en sont encore au stade expérimental.

4.2. La forêt des Landes de Gascogne

Le plateau des Landes Gascogne s'étend sur trois départements du Sud Ouest de la France (Gironde, Landes, et Lot-et-Garonne) et couvre plus d'un million d'hectares dont 75,4% sont boisés (987 850 ha, IFN 2005), ce qui en fait la plus grande forêt artificielle d'Europe (Figure 5). Ce massif homogène constitue un vaste triangle dont la base d'environ 200 km s'appuie sur la côte atlantique. Le climat qui règne sur cette région est de type océanique avec quelques variations notables entre les zones littorales et les secteurs plus continentaux à l'Est. Les températures moyennes annuelles oscillent entre 12 et 14°C et les précipitations annuelles entre 700 et 1400 mm selon les zones. Les caractéristiques physiques du milieu sont marquées par l'absence de relief (50 m d'altitude en moyenne). La topographie n'est légèrement perturbée qu'à proximité de nombreux petits cours d'eaux qui se jettent dans de grands étangs avant de rejoindre l'océan. La couverture pédologique des Landes de Gascogne est constituée de sols podzoliques à texture sableuse (> 95 %) faisant souvent transition, à quelque mètres de profondeur, avec des grès siliceux ou des grès à ciment ferrugineux imperméables (horizon d'alios).

Historiquement, le pin maritime ***Pinus pinaster*** (Aïton) est une essence autochtone limitée au cordon dunaire mais au cours du XIXème siècle elle a été utilisée pour boiser l'intérieur du territoire aquitain, alors majoritairement voué au pastoralisme. L'objectif était d'assainir les zones marécageuses et de fournir des revenus complémentaires aux populations rurales. L'utilisation principale de la forêt landaise a longtemps été la production de gemme (résine). Cette production a totalement disparu à la fin des années 1970, concurrencée par l'industrie chimique. Depuis, hormis sur le cordon littoral voué à la protection des dunes, la forêt de pin maritime a comme objectif principal la production de bois. La filière comporte aujourd'hui 34 000 emplois directs et génère un chiffre d'affaire équivalent à celui des vins de Bordeaux (EAB 2005). En 50 ans, la production moyenne est passée de 4 à près de 12 m^3 par hectare et par an grâce à l'amélioration génétique de cette essence, la fertilisation phosphatée et la mécanisation. Avec un accroissement annuel avoisinant les 9 millions de m^3, la forêt des Landes de Gascogne produit a elle seule 90% de la récolte nationale en pin maritime (IFN, EAB 2005) et se situe aussi à la première place en France pour la production de bois d'industrie. Ce massif est désormais tristement célèbre pour les dégâts considérables provoqués par l'ouragan Martin en 1999 puis la tempête Klaus du 24 janvier 2009. Face à la récurrence de ces tempêtes, la filière mène à ce jour d'actives réflexions sur la diversification des modes de gestion et des usages du pin maritime.

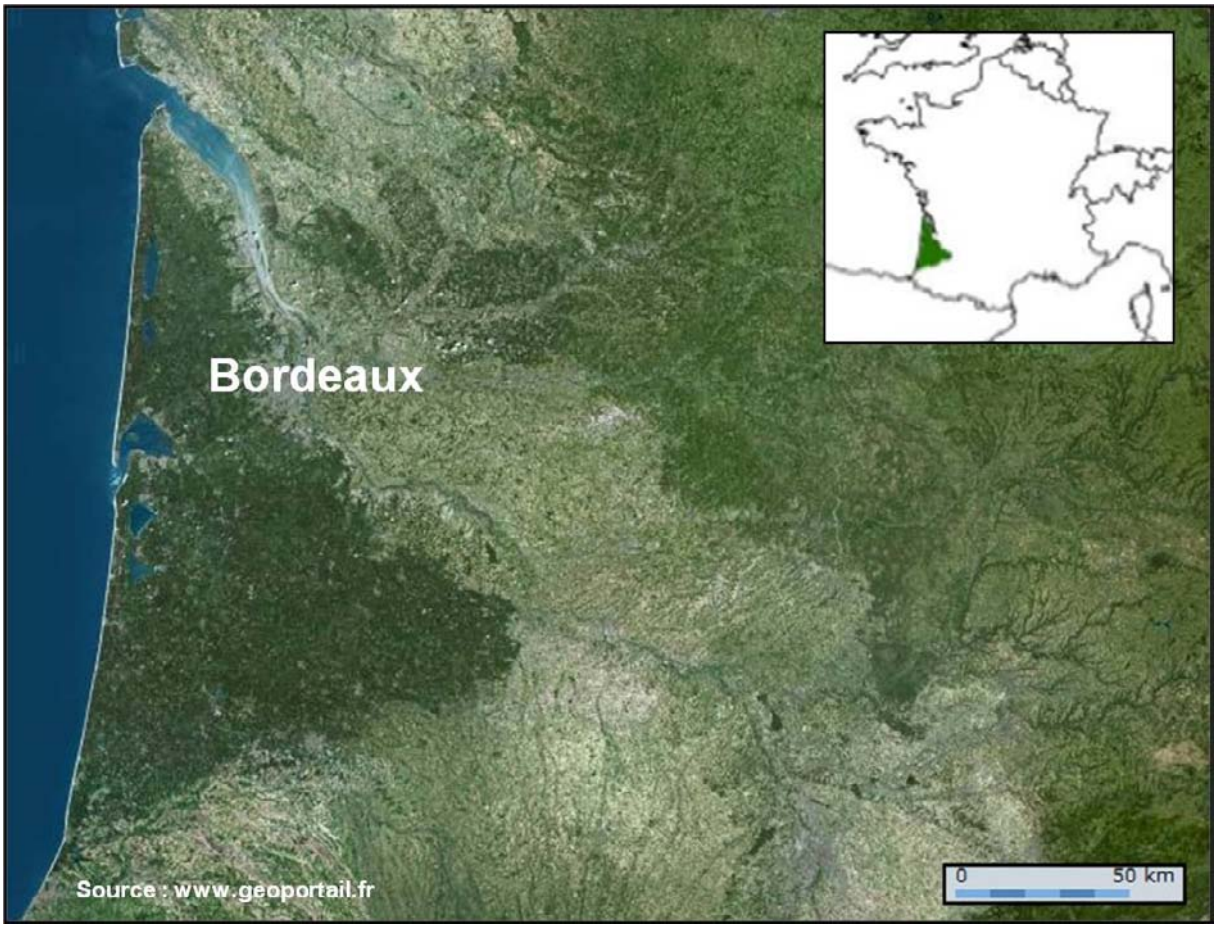


Figure 5 : La forêt des Landes de Gascogne

Le paysage forestier des Landes de Gascogne apparaît comme dense, compact, et entrecoupé de quelques grands domaines agricoles qui se sont développés à partir des grands défrichements des années 1960-70. Ils sont majoritairement dédiés à la culture de maïs. Au niveau des surfaces boisées, le pin maritime est l'essence la plus représentée (82% hors coupes rases, IFN 2005). Espèce de pleine lumière, ce pin est capable de se développer sur des sols pauvres et acides qu'ils soient secs ou humides. Cet arbre au houppier conique et clair peut atteindre 30 mètres de haut. Dans le massif, il est présent en mélange avec des essences feuillues en sous-étage sur environ 3,5% de la surface boisée, et de façon linéaire le long des lisières. Cette diversité d'essences a longtemps été maintenue, les feuillus étant conservés au moment de l'exploitation des pins, mais elle est actuellement menacée du fait de l'exploitation des feuillus pour le bois de chauffage. Ces essences feuillues sont présentes sous forme de peuplements purs sur 12,5% de la surface du massif et la principale essence présente est le chêne pédonculé ***Quercus robur*** (Linné) (8%, IFN 2005). Cette essence se concentre particulièrement au sein de formations le long des cours d'eau (i.e. ripisylve) en association avec des aulnes ou des saules. Plus rarement, elle constitue des peuplements relictuels de quelques centaines de mètres carrés ou implantés par l'homme autour des habitations (airiaux).

La culture du pin maritime conditionne la fragmentation du paysage. Sa structure découle en particulier du statut de la propriété forestière, privée à 90 %, dont une des conséquences est le morcellement au fil des générations. Elle est également le fruit de la gestion par les propriétaires soucieux d'étaler dans le temps les revenus d'exploitation des bois. Le mode de gestion majoritaire est la conduite en plantation équienne (futaie régulière). Par définition, les arbres au sein d'une parcelle présentent donc des caractéristiques similaires en termes d'âge et de diamètre. Associé à ce morcellement, le décalage temporel entre les plantations de chaque parcelle de pin maritime génère une grande diversité de hauteur et de densité d'arbres dans le paysage. Ce phénomène est accentué par les coupes rases qui concernent annuellement 2% de la surface forestière. Ainsi, l'aspect dense et homogène des formations boisées de pins maritimes de ce massif cache en réalité une hétérogénéité structurale à l'échelle du paysage. De plus les grands incendies de la décennie 1940-49, en ravageant près de 40% de la superficie du massif ont conduit de manière indirecte à fractionner la structure du paysage à travers la mise en place de pare-feux et d'un quadrillage dense de pistes forestières. Ces voies d'accès ont été créées pour permettre l'intervention des pompiers en charge de la lutte active, mais sont également utilisées dans le cadre de l'exploitation des parcelles. Elles sont à l'origine de nombreuses lisières ouvertes.

5. De la problématique aux objectifs de la thèse

L'objectif principal de cette thèse est d'étudier la relation entre la diversité des essences forestières et la résistance de l'écosystème forestier à l'herbivorie. Le modèle d'étude choisi est la processionnaire du pin en forêt de plantation. Cette forêt, mono-spécifique, présente en théorie un risque important d'épidémie d'insectes forestiers. En réalité, elle subit des dégâts notables par de nombreux insectes ravageurs tels que la pyrale du tronc, les scolytes ou l'hylobe, ainsi que de champignons tels que l'armillaire ou le fomès (Consultation de la base de données du DSF, Samalens 2009). D'autre part, la présence ponctuelle d'essences feuillues (non hôte pour la processionnaire), et de nombreux milieux ouverts (à la fois habitat et non habitat selon le stade de développement de la processionnaire) fournit un modèle privilégié pour tester les effets de la diversité des essences forestières sur les niveaux de population d'un insecte herbivore à plusieurs échelles spatiales.

Les objectifs de ce travail sont donc de tester quatre hypothèses écologiques majeures reliant diversité des forêts et résistance à la processionnaire du pin en fonction du stade du cycle de développement de l'insecte.

1) Le mode de détection de l'hôte par le papillon femelle est probablement basé sur la reconnaissance visuelle de la silhouette de l'arbre (Démolin 1969). La présence de haies de feuillus en bordure de peuplement de pins étant relativement répandue dans la forêt des Landes, nous avons donc testé l'hypothèse suivante :

H1. Jouant le rôle de barrière physique à l'accessibilité de l'hôte, la présence de haies de feuillus en bordure de peuplement de pin maritime réduit les niveaux de population de la processionnaire du pin dans la parcelle adjacente.

2) La processionnaire possède de nombreux ennemis naturels, notamment deux espèces de parasitoïdes des œufs, l'une spécialiste et l'autre généraliste. Nous avons ainsi testé l'effet d'une alimentation complémentaire provenant de différentes essences forestières sur leur survie, en émettant l'hypothèse suivante :

H2. La consommation de miellat, notamment produit par les espèces de pucerons sur feuillus, accroît la longévité des parasitoïdes des œufs de processionnaire.

3) L'impact des conditions abiotiques a été analysé sur la survie des chrysalides. En effet, les différentes essences végétales présentes dans les Landes peuvent être à l'origine de différences des conditions microclimatiques et édaphiques sous couvert. Nous avons donc étudié les effets de ces conditions sur le stade endogé de la chrysalide pour tester l'hypothèse suivante :

H3. Le taux de survie des chrysalides de processionnaire est plus élevé en milieu ouvert que sous couvert forestier, du fait de différences de conditions microclimatiques et édaphiques.

4) Nous avons intégré l'ensemble de ces mécanismes pour tester à l'échelle du paysage, sur l'ensemble du cycle de développement de la processionnaire, l'effet de l'hétérogénéité des essences forestières. L'hypothèse est la suivante :

H4. Les niveaux d'infestation de la processionnaire sont plus élevés au sein des mosaïques homogènes de pin maritime qu'au sein des mosaïques hétérogènes associant plantations de pin, boisements de feuillus et milieux ouverts.

Ce manuscrit comprend donc quatre chapitres de résultats (Figure 6), rédigés sous forme d'articles scientifiques :

Chapitre 2 : Hide and seek in forests: colonization by the pine processionary moth is impeded by the presence of non-host trees (***Agricultural and Forest Entomology*** 2011, ***sous presse***) ;

Chapitre 3 : Honeydew feeding increased the longevity of two egg parasitoids of the pine processionary moth (***Journal of Applied Entomology*** 2010, ***sous presse***) ;

Chapitre 4 : A case of habitat complementation in forest pests: pine processionary moth pupae better survive in open areas (***Forest Ecology and Management*** 2011, ***sous presse***) ;

Chapitre 5 : Conifer insect herbivory decreases with percent broadleaved area of landscapes (en préparation).

Le manuscrit se termine par une discussion générale (Chapitre 6) qui vise à synthétiser les différents résultats obtenus et dresser des perspectives aussi bien pour la recherche que pour la gestion durable des populations de processionnaire en forêts de plantation.

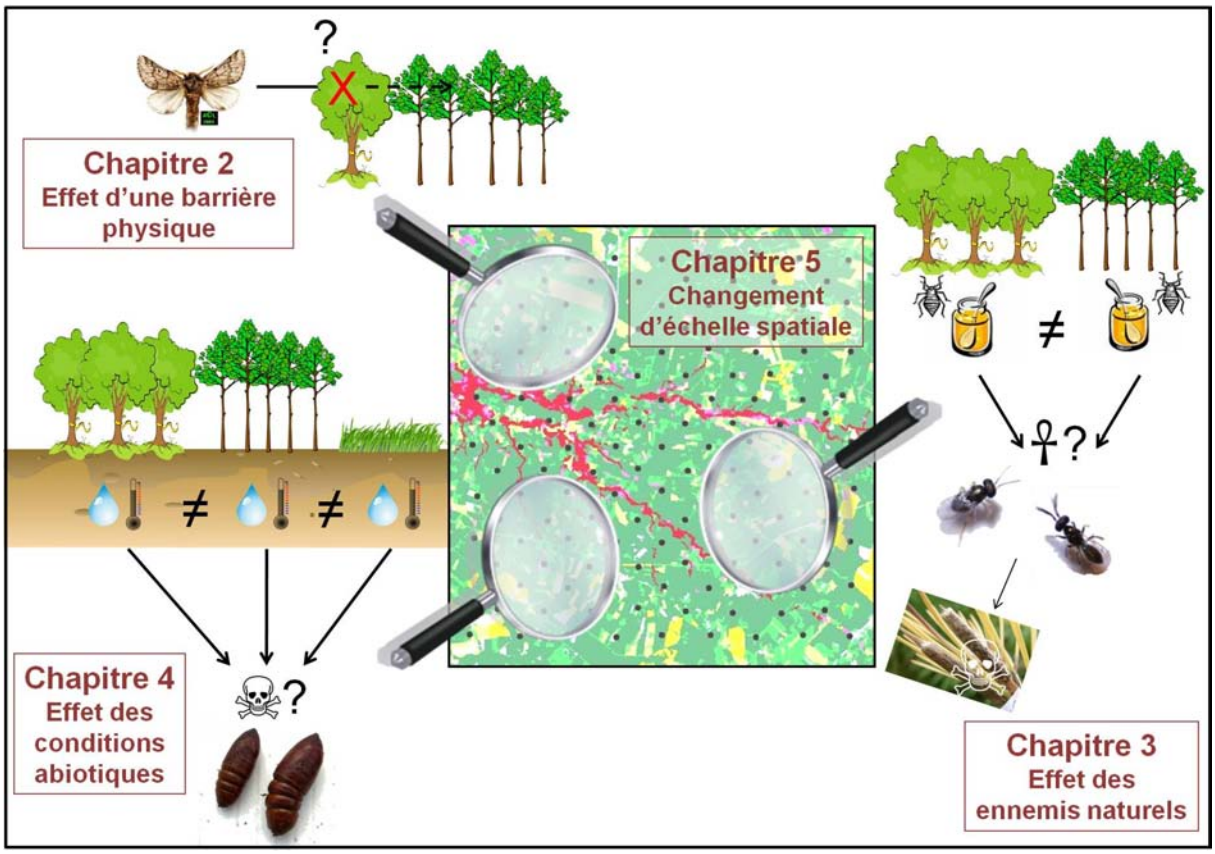


Figure 6 : Organisation du manuscrit de thèse

CHAPITRE 2

Hide and seek in forests: colonization by the pine processionary moth is impeded by the presence of non-host trees

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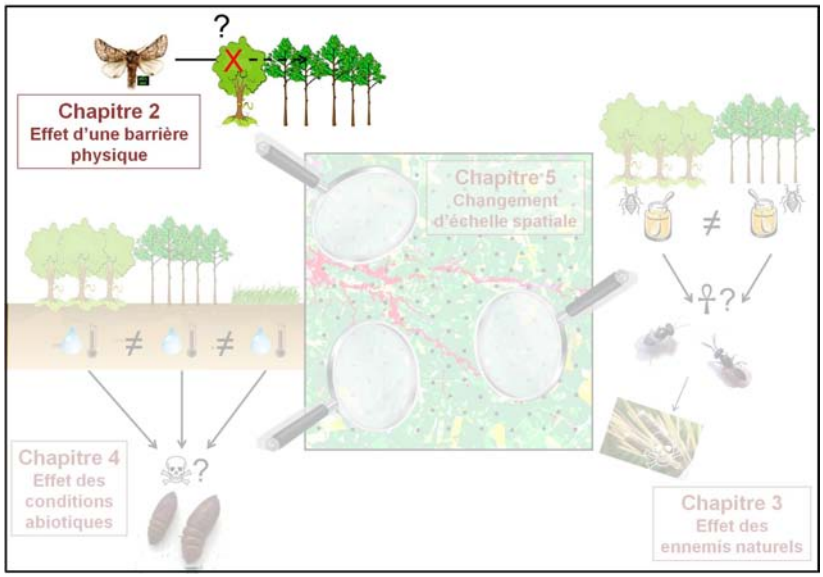

Hide and seek in forests: colonization by the pine processionary moth is impeded by the presence of non-host trees.

Non-host trees impede insect colonization

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Abstract:

1. Reduced tree apparency has been proposed as a key mechanism to interpret lower insect herbivore damage in mixed forests. We tested this hypothesis by investigating the distribution of pine processionary moth (*Thaumetopoea pityocampa*) (Denis & Schiffermüller) (Lepidoptera) (PPM) infestation at stand edge in pure *Pinus pinaster* (Aïton) stands far from any non-host trees (experiment 1) or partly bordered by a broadleaved hedgerow (experiment 2).
2. A “edge effect” was demonstrated, trees at stand edge being largely more infested than in stand interior.
3. The presence of a non-host broadleaved hedgerow in front of a pine stand edge resulted in a decrease of PPM infestation levels. The number of PPM nests was significantly lower behind the hedgerow than on the exposed part of the edge. The presence of the hedgerow did not dilute or repel PPM infestations further into the pine stand but decreased PPM infestations in the whole pine stand. The reduction of PPM infestation behind the hedgerow was more important when the broadleaved hedgerow was higher than the pine trees.
4. The alleviation of PPM infestation level could not be explained by lower larval survival or lower chemical attraction of adults, but more likely attributable to a disruption of visual cues used by PPM flying females when searching for suitable host trees.
5. These results highlight the benefits of using non-host tree species on the edge of monospecific forest stands to reduce insect damage and should be promoted as innovative forest pest management method.

Keywords:

Lepidoptera, associational resistance, broadleaved, conifer, hedgerow, visual cues, edge effect, host detection.

1. Introduction

Since the seminal work of Root and colleagues (Tahvanainen & Root, 1972; Root, 1973), plant-plant associations are increasingly acknowledged as main drivers of host plant detection, colonization and consumption by insect herbivores, and thereby as a potential source of associational resistance (Barbosa *et al.*, 2009). These observations provide a basis for the diversity – resistance hypothesis which states that more diverse plant communities are less prone to insect damage. Two meta-analyses, in agricultural crops (Tonhasca *et al.*, 1994) and forest ecosystems (Jactel & Brockerhoff, 2007), showed that overall, plant species growing in mixtures experience lower pest damage than in monocultures. Two main mechanisms have been proposed to explain lower herbivory damage in richer plant communities (Jactel *et al.*, 2005; Barbosa *et al.*, 2009): 1) mixtures would be better in providing natural enemies with suitable resources and habitats, thus increasing their ability to control herbivore populations and 2) mixtures would reduce the probability of herbivores finding a host, the latter being hidden or diluted among non host plants.

A consequence of this “resource concentration” hypothesis (Root, 1973) is that the more apparent plants are, the more prone to attacks by insect herbivores they would be. In particular, this can be expected for plants that are highly visible, such as those growing

at habitat edges. Several studies have shown higher pest insect infestations at stand edges than in stand interiors (Weaver *et al.*, 2005; DeSomviele *et al.*, 2007). The amount of forest edge per km² was found a good predictor of *Malacosoma disstria* (Lepidoptera) outbreak risks (Roland, 1993). Floater & Zalucki (2000) interpreted the higher infestation level of *Ochrogaster lunifer* (Lepidoptera) on Acacia exposed trees as a result of a lower risk of mortality for females that lay eggs on the first available trees. However the "edge effect" may also be reinforced by higher feeding quality of sun-exposed leaves (Fortin & Mauffette, 2001) or by microclimatic conditions more favorable to insects (Moore *et al.*, 1988).

Host tree location by insect herbivores may be achieved by long distance cues such as volatile signals (Visser, 1986) but also by visually perceived features (Prokopy & Owens, 1983). Both signals can be associated since insects may first be attracted to a host tree from a distance by olfactory cues and then initiate precise approach using visual signals (Wyatt *et al.*, 1997; Goyer *et al.*, 2004). Vision has been shown to be important in plant location for many insect species, such as for *Leptinotarsa decemlineata* (Coleoptera) on potato crops (Szentesi *et al.*, 2002), for woodboring beetles which detect the colour of host trees (Goyer *et al.*, 2004; Campbell & Borden, 2009), for *Euhrychiopsis lecontei* (Coleoptera) on aquatic macrophytes (Reeves *et al.*, 2009) and for *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Lepidoptera) on pine species, which detect the shape of host trees (Démolin, 1969). Insect herbivory can also increase with leaf apparency (the amount of leaf area per unit space) as shown by Moore *et al.* (1991) in oak trees. The presence of non host vegetation may then hide host trees from the vision of insect herbivores (Watt, 1992) as already observed for the pine tip moth *Rhyacionia*

82 *frusfrana* (Lepidoptera) (Sun *et al.*, 2000), the spruce budworm *Choristoneura fumiferana*
83 (Lepidoptera) (Bergeron *et al.*, 1995), the processionary caterpillar *O. lunifer* (Floater &
84 Zalucki, 2000) or leaftying caterpillars of *Quercus alba* (Marquis *et al.*, 2002).
85 The pine processionary moth (PPM) *Thaumetopoea pityocampa* (Denis & Schiffermüller)
86 (Lepidoptera, Notodontidae) is a severe insect defoliator specialized on pines and cedar
87 in southern Europe and north Africa (FAO, 2010). In autumn and winter, PPM caterpillars
88 that feed on needles remain congregated in permanent silky nests they have spun to
89 resist low temperatures. Pine trees can host several larval nests, each corresponding
90 approximately to the egg mass of one female. These nests are easy to sight in the tree
91 crown due to their size (ca. 0.10 to 0.25 m in diameter) and white colour. After pupation
92 into the soil during spring, adult moths emerge in early summer (from the end of June to
93 mid-August) and mate almost immediately in the understorey. Then, fecundated females
94 search for an appropriate host to lay eggs. After about a month, caterpillars hatch and
95 start feeding on needles. Démolin (1969) observed that PPM females use the shape of a
96 tree silhouette against a clear background to select the host tree. There is a common
97 wisdom among foresters that PPM exhibit higher infestation at stand edge but to our
98 knowledge this has never been properly demonstrated. PPM thus represents an
99 interesting species model to investigate the role of physical cues in tree detection and
100 colonization.
101 PPM is the most abundant pest insect in the Landes de Gascogne forest in south-west
102 France (Abgrall & Bouhot, 1990), the largest plantation forest in Europe with nearly one
103 million hectares of pure maritime pine *Pinus pinaster* (Aiton) stands. In this plantation
104 forest, hedgerows of broadleaved species like pedunculate oak (*Quercus robur* (Linné))

105 have persisted along some pine stands. These hedgerows may play a role as physical
106 barrier to pine colonization by conifer insects (Jactel *et al.*, 2005) and they can serve as
107 an experimental treatment to investigate the cues that might disrupt host location by
108 PPM females.
109
110 Two experiments have therefore been carried out to test the role of tree recognition in
111 insect infestation. The objectives of our study were to test the following specific
112 hypotheses:
113 1. PPM infestations are concentrated at pine stand edges;
114 2. Infestation levels of PPM are reduced by the presence of a broadleaved hedgerow in
115 front of pine stand edges;
116 3. Infestation patterns at stand edge are more likely due to the effect of physical cues.
117

118 # 2. Methods

119 ## 2.1. Experiment 1: within stand distribution of PPM infestations

120 In 2006, 25 maritime pine stands of the Landes de Gascogne forest were selected in two
121 sites (12 stands in Site 1, Marcheprime, 44°41’ N, 0° 51’ O, and 13 stands in Site 2,
122 Nezer Forest, 44°35’ N, 01° 02’ O). All stands were even-aged, with pine trees planted
123 on 4 m distant rows. Stand height varied from 8 to 21 m and 6 to 20 m, in site 1 and 2,
124 respectively, thus avoiding census biases as PPM is not common in very young stands
125 (< 3 m high), and as nest counting becomes less accurate in tall trees (> 15 m). Stand
126 age varied from 10 to 23 and 6 to 23 years in site 1 and 2, respectively. Mean tree DBH

(Diameter at Breast Height, m) varied from 0.09 to 0.32 and from 0.10 to 0.32 m in sites 1 and 2, respectively. Tree density varied from 390 to 1630 and from 350 to 2810 pines ha^{-1} in sites 1 and 2, respectively. In each stand, five groups of trees were sampled along a transect, perpendicularly to the south-exposed edge; each group was separated from the next by about 25 m. The furthest group was at least 25 m distant from the opposite north-exposed stand edge to avoid any edge-effect. The south-exposed edge was at least 20 m distant from the opposite stand. The first group ("edge group") comprised 62 trees, 31 trees on the edge row and 31 on the second tree row. The following groups ("interior groups") were located within the stand and comprised each 7 rows of 9 trees for a total of 63 trees per group. The surface of the rectangular area covered by each group of trees was estimated and used to calculate tree density. Egg masses are impossible to detect on high standing trees whereas permanent (winter) nests built by late instar larvae are easy to sight. PPM population levels were therefore estimated as the mean number of permanent nests per tree at each distance from the south-exposed stand edge.

2.2. Experiment 2: Effect of the presence of a broadleaved hedgerow on PPM infestation level

Pure, even-aged maritime pine stands were selected in the Landes de Gascogne forest with a part of their edge hidden by a broadleaved hedgerow (hedgerow treatment) while the rest of the edge remained totally apparent (control treatment, Fig.1). Eleven and ten stands were selected in 2004 and 2009 respectively. Mean stand height varied from 5 to 20 m (Table 1). Two stands ("Canauley" and "CAEPE 5") were sampled twice, in 2004

149 and 2009. The broadleaved hedgerows were distant from the pine stand by a maximum
150 of 3 m, their depths ranged from 2 to 35 m, while their height varied from 5 to 16 m
151 (Table 1). The broadleaved hedgerows had a minimum length of 30 m and 40 m in 2004
152 and 2009, respectively. Sixteen hedgerows were dominated by Pedunculate Oak (*Q.*
153 *robur*), three by Red Oak (*Q. rubra*) and two by Black Alder (*Alnus glutinosa*) (Table 1).
154 Other less dominant deciduous tree species were Silver Birch (*Betula pendula*),
155 Common Aspen (*Populus tremula*), Cork Oak (*Q. suber*), Pyrenean Oak (*Q. pyrenaica*),
156 Black Locust (*Robinia pseudoacacia*), *Liquidambar* spp., *Crataegus* spp., *Salix* spp. and
157 *Prunus* spp. In 2004, PPM permanent nests were counted on trees located on the first
158 two tree rows of pine stand edge, both behind the hedgerow and on the exposed part of
159 the edge, over the same edge length for the two treatments (Fig.1). In 2009, PPM
160 permanent nests were counted in the same way but on the first four tree rows of stand
161 edge. The control section was further divided into two parts, to evaluate the difference in
162 the infestation level near and far from the hedgerow: C1, located at 0 to 20 m from the
163 side of the hedgerow, and C2 located at 20 to 40 m far from the side of the hedgerow
164 (Fig.1). The response variable was the mean number of nests per tree in each treatment.
165

166 ## 2.3. Statistical analyses

167 In experiment 1, differences in mean DBH and mean PPM nest density between the five
168 groups of trees were analysed with a Friedman non parametric analysis of variance.
169 Wilcoxon sign-ranked tests were used for pairwise comparison between mean PPM nest
170 density in the edge group and each interior group of trees and between the first and
171 second tree row of the edge group. A Bonferroni correction was applied to account for

multiple comparisons. A Spearman correlation test was used to evaluate the effect of tree density on the relative difference in PPM infestation between the edge group and the first interior group.

In experiment 2, Wilcoxon tests were used for pairwise comparison of the mean PPM nests per tree between the two treatments (control vs. hedgerow) in each year separately. In 2009, Wilcoxon tests were also used to compare mean PPM nests per tree between the two parts of the control section of the edge (C1 vs C2) and between control and hedgerow sections for each of the four sampled tree rows separately. To better quantify the effect of the presence of a hedgerow on PPM infestation (nests $tree^{-1}$), we calculated a relative infestation ratio (IR):

$$IR=\frac{\text{PPM Infestation behind hedgerow}-\text{PPM Infestation in control}}{\text{PPM Infestation in control}} \quad \text{eqn (1)}$$

We also calculated a relative height ratio (HR):

$$HR=\frac{\text{Height of hedgerow}-\text{Height of pines}}{\text{Height of pines}} \quad \text{eqn (2)}$$

Relationships between the relative infestation (IR) and height (HR) ratios were analysed using an ANCOVA with sampling year as the main effect and HR as the covariate, to test for the parallelism of regression lines. All statistical analyses were performed using Statistica Software 7.1 (StatSoft, France).

3. Results

3.1. Within stand distribution of PPM infestations

The mean PPM infestation level per stand varied from 0.04 to 0.64 and from 0.01 to 0.38 nests per tree in sites 1 and 2, respectively. The density of larval nests significantly differed between groups of trees ($Q_{11,4} = 27.66$, $P < 0.001$ and $Q_{12,4} = 32.99$, $P < 0.001$ for sites 1 and 2, respectively). About 70% of the observed larval nests were counted on trees at the stand edge, which represented about 20% of the total number of observed trees per stand (Fig.2). PPM nest density was significantly lower in interior groups than in the edge group at both sites ($Z_{11,1} = 3.06$, $P = 0.002$ in the four Wilcoxon tests for site 1 and $Z_{12,1} = 3.18$, $P = 0.001$ in the four Wilcoxon tests for site 2, Fig.2). There was no significant difference in nest density between interior groups. At both sites, the nest density was significantly higher on the first tree row (ca. 50% of the total number of nests) than on the second row (ca. 20% of the total number of nests) of the edge group (0.84 vs. 0.46 nests per tree, $Z_{11,1} = 2.94$, $P = 0.003$ in site 1 and 0.56 vs. 0.33 nests per tree, $Z_{12,1} = 2.20$, $P = 0.028$ in site 2, data not shown).

DBH did not differ significantly between the groups of trees ($Q_{11,4} = 7.67$, $P = 0.10$ and $Q_{12,4} = 5.20$, $P = 0.27$ for sites 1 and 2, respectively). The relative difference between PPM infestation in the first and the second line of the edge group was not significantly correlated with tree density ($N = 12$, $\rho = 0.20$, $P = 0.54$ and $N = 13$, $\rho = 0.45$, $P = 0.13$ for sites 1 and 2, respectively).

3.2. Effect of the presence of a broadleaved hedgerow on PPM infestation level

The mean PPM infestation level varied from 0.3 to 2.0 nests tree^{-1} in 2004 and from 0.04 to 2.1 nests tree^{-1} in 2009 at the stand edge (control treatment) indicating that the infestation levels in the two years were similar. Wilcoxon paired tests showed that the number of PPM nests per tree at the stand edge was significantly lower behind the broadleaved hedgerow than on the exposed part of the edge ($Z_{10,1}$ = 2.85, P = 0.004 and, $Z_{9,1}$ = 2.31, P = 0.021 in 2004 and 2009, respectively, Fig.3).

In 2009, we compared the infestation levels between treatments for each sampled tree row. Differences were only significant for the first tree row, right on the edge (0.35 nests tree^{-1} behind the broadleaved hedgerow vs. 1.00 nests tree^{-1} on the exposed section, $Z_{9,1}$ = 2.24, P = 0.025, Fig.4). There was no significant difference in mean PPM infestation between the two sub-sections C1 and C2 of the first tree row of the exposed edge (0.78 and 0.96 nests tree^{-1} in C1 and C2, respectively; $Z_{9,1}$ = 0.42, P = 0.67).

The Infestation Ratio varied from – 86% to + 2% in 2004, and from – 100% to + 44% in 2009, a negative IR meaning that the PPM infestation level was lower behind the broadleaved hedgerow compared to the control. All IR values were negative when HR was positive, i.e. when the broadleaved hedgerow was higher than the pine trees (Fig.5). There was a negative relationship between the infestation and height ratios, indicating that the reduction of PPM infestation behind the hedgerow compared to the control section was more important when the broadleaved hedgerow was higher than the pine trees. The ANCOVA showed a significant effect of the height ratio (P = 0.018) but no

236 significant effect of the year nor the interaction year × HR (Table 2). It was therefore
237 possible to fit a single significant regression model between the Infestation Ratio and the
238 Height Ratio, pooling data from both years (P = 0.014, Fig.5). We did not observe any
239 significant effect of the hedgerow depth, volume nor tree species composition on the
240 Infestation Ratio.

241

242 4. Discussion

243 The first experiment based on the observation of 25 pure pine stands of different ages
244 demonstrated a significant edge effect on PPM infestation. The density of larval nests
245 was much higher at the stand edge than in the interior, and it dropped markedly after the
246 first row of trees. These results are consistent with previous descriptions of an “edge
247 effect” on the distribution of insect attacks (Fortin & Maufette, 2001; Weaver *et al.*, 2005).
248 Higher densities at stand edge were observed for many species, like other Lepidoptera
249 species (*Lymantria dispar* (Lepidoptera) Bellinger *et al.*, 1989) but also several bark
250 beetles (*Ips typographus* (Coleoptera) Peltonen *et al.*, 1997; *Pityogenes chalcographus*
251 (Coleoptera) Peltonen & Helivaara, 1999; *Tomicus piniperda* (Coleoptera) Göthlin *et al.*,
252 2000) and a pine weevil (*Pissodes strobi* (Coleoptera) Lavallée *et al.*, 1996). In contrast,
253 DeSomviele *et al.* 2007 found lower infestation by *Diprion pini* (Hymenoptera) at the
254 edge of conifer forests but this pattern was interpreted as the result of higher predation of
255 sawfly pupae by small mammals.
256 The second experiment clearly indicated that the presence of non-host trees in front of
257 the host pines resulted in the disappearance of the edge effect on PPM infestation. The

difference in nest density between the hidden and exposed part of the pine stand was only significant for the first row of trees (Fig.4). This suggests that the presence of a broadleaved hedgerow did not dilute or repel away the PPM infestations further into the pine stand but decreased PPM infestations in the whole pine stand as a result of reduced nest density at its border. Several studies have shown that the presence of dense vegetation around tree seedlings resulted in lower attack rates by the pine tip moth (*R. frustrana* Ross *et al.*, 1990; Sun *et al.*, 2000) or the pine weevil (*P. strobi* Hodge *et al.*, 1989; Bellocq & Smith, 1995). However, to our knowledge, our study is the first to demonstrate that neighbouring non-host trees can reduce the risk of defoliation at the crown level in mature host trees.

Several hypotheses may account for the pattern of higher PPM larval nest density at stand edges: (i) environmental conditions favouring larval survival (ii) chemical attraction of females (iii) impact of natural enemies on larval survival (iv) physical trapping of females through passive interception of flying individuals or active attraction mediated by visual cues.

(i) As poikilothermic organisms, PPM caterpillars are known to prefer spinning their nests on the south exposed part of pine crowns to absorb a maximum of warmth and to better resist low winter temperatures (Démolin, 1965; Hoch *et al.*, 2009). Other studies have highlighted a preference for adults to lay their eggs on sun-exposed trees such as in the Pine tip moth (Berisford & Kulman, 1967) or the Western tent caterpillars *(*Moore *et al.*, 1988). It has also been shown that leaf quality can change with sun exposure, shady leaves being less palatable for some insect herbivores due to a lower C/N ratio (Fortin &

281 Maufette, 2001; Levesque *et al.*, 2002). These processes can result in lower mortality
282 rates of larvae at the edge compared to the interior. Sun exposure and then quality of
283 pine needles at stand edge can be influenced by the shade of broadleaved hedgerow,
284 and part of PPM first instars hatch before broadleaved trees have lost their leaves
285 (August to September), However, the first experiment, in the absence of broadleaved
286 hedgerow, showed a sharp decrease in the number of nests per tree between the first
287 and the second row of pines, while microclimatic conditions are unlikely to differ greatly
288 within such a short distance (there were only 4 meters between rows).
289 (ii) Another explanation for both the edge effect and its absence behind hedgerows of
290 non-host trees would be related to the host selection of the PPM female using olfactory
291 cues. Plant volatiles are mediators of host plant finding by insect herbivores (Visser,
292 1986) and a recent study has shown that adult female PPM antennae responded to
293 volatiles emitted by pine trees (Zhang *et al.*, 2003). Furthermore, an increasing body of
294 evidence supports the hypothesis that volatiles released by non-host plants may be used
295 by insects to avoid unsuitable habitats within a range of several meters (Zhang &
296 Schlyter, 2004; Mauchline *et al.*, 2005). However, if this had been the case for our
297 experimental conditions, volatiles emitted by non-host broadleaved trees would have
298 reduced host pine tree infestation not only behind the hedgerow but also at its nearest
299 side. And yet we observed no significant differences in PPM nest density between the
300 two parts of the exposed edge, i.e. the closest and furthest from the hedgerow. This
301 suggests that chemical cues may not be the decisive factor for the observed pattern of
302 PPM infestation at pine stand edge with or without the presence of broadleaved
303 hedgerow.

(iii) Natural enemies of the PPM may find complementary habitat or shelter in broadleaved hedgerows. For example, the main bird predator of PPM pupae in the area, the hoopoe *Upupa epos*, is known to nest in the cavities of old broadleaved trees (Barbaro *et al.*, 2008). Several PPM egg parasitoids can also improve their fitness by feeding on honeydew produced by oak aphids (Dulaurent *et al.*, 2010). However, all of these natural enemies are able of long distance dispersal. They should then have the same impact just behind the hedgerow and on the lateral side of the hedgerow which does not reflect the observed pattern of reduced infestation only behind the hedgerow.

(iv) The higher proportion of PPM larval nests at the stand edge may also be linked to a role of physical trap, mechanistic or visual, played by edge trees. These trees may passively intercept flying moths that would stop on the first available host tree found during their post-mating flight. Alternatively, edge trees may also be the first detected hosts during an active search by females. The passive effect of physical barrier resulting in lower impact of herbivores has largely been emphasized for mammals feeding on tree seedlings (Pietrzykowski *et al.*, 2003; Miller *et al.*, 2006), and for forest insects (Bergeron *et al.*, 1995; Floater & Zalucki, 2000).

Favourable conditions for PPM larval burying and pupae survival are often found in front of pine plantation edges, along forest tracks where the grass vegetation is short (Barbaro *et al.*, 2008). After moth emergence, the first tree row of the stand would be then easier to reach by flying females and consequently be more infested than trees less accessible inside the stand. This process should be less relevant in stands with lower tree density because of an easier access to trees inside the stand. However, even if stands with very low planting density were not included in our study, the rate of decrease in nest density

between the first and second tree row was not influenced by tree density. It is then likely that adult females are not simply stopped by the first pine tree met but that they actively search for suitable host trees. Adult females of PPM fly in the late afternoon and dusk, and Démolin (1969) hypothesized that PPM females used the dark shape of the tree silhouette as a visual cue to detect host pine trees. As adult females do not feed and only live for a few days (Démolin, 1969), this active host-finding behaviour would reduce the time required to find a suitable host for their offspring. Visual attraction to hosts has been demonstrated for several phytophagous insects as reviewed by Prokopy & Owens (1983). In particular, the use of host shape contrast by insects has been recorded for *Anobium punctatum* (Coleoptera) (Wyatt *et al.*, 1997), *O. lunifer* (Floater & Zalucki, 2000) and *E. lecontei* (Reeves *et al.*, 2009). Rausher (1981) also observed a reduced detection by the pipevine swallowtail butterfly (*Battus philenor)* (Lepidoptera) of the host plant *Aristolochia reticulata* growing amid higher vegetation and suggested a disruption of visual cues as responsible mechanism. This explanation for the edge effect in PPM infestation is highly consistent with our observations of lower infestation levels behind a broadleaved hedgerow: indeed, pine tree silhouettes are masked in summer when PPM females fly, since the crowns of broadleaved trees are then covered with leaves. This hypothesis is confirmed by the fact that the reduction of PPM infestation behind the hedgerow compared to the exposed part of the edge was more important when the broadleaved hedgerow was higher than the pine trees (Figure 5). The opacity of deciduous tree crowns may then have disrupted host pine finding by PPM females during the flight that precedes egg laying.

Our study clearly indicated that PPM infestations, concentrated on stand edge, are

reduced by the presence of a broadleaved hedgerow in front of the pine stand edge. These findings can be considered as a new piece of evidence to support the associational resistance hypothesis (Barbosa *et al.*, 2009) and particularly to illustrate the mechanism of a physical barrier to host-finding (Jactel *et al.*, 2005). These results also pave the way for the development of environmentally friendly methods of biological control. The use of physical barriers in crop protection has already been developed at the tree scale (Bulinski *et al.*, 2006; Kain *et al.*, 2010), but remains unexplored at the stand scale. Since most of the trees damaged by the PPM are located at the edge of pine stands and because the presence of taller non-host trees in front of the stand edge can result in a significant decrease of nest density, forest managers could be advised to plant hedgerows of fast growing deciduous tree species in the same time as they plant pine trees in order to prevent PPM damage. This method would be more cost effective than curative control methods such as Bt applications and also much better for biodiversity conservation.

5. Acknowledgments

We are grateful to Jean-François Beylard (from the National Forest Office) for the access to some stands, and Amélie Derouault and Bastien Castagneyrol for their technical support during the PPM larval nest counting periods. We thank Mark Bakker, Aurélie Labat and Michel Delroisse for their helpful comments on the manuscript.

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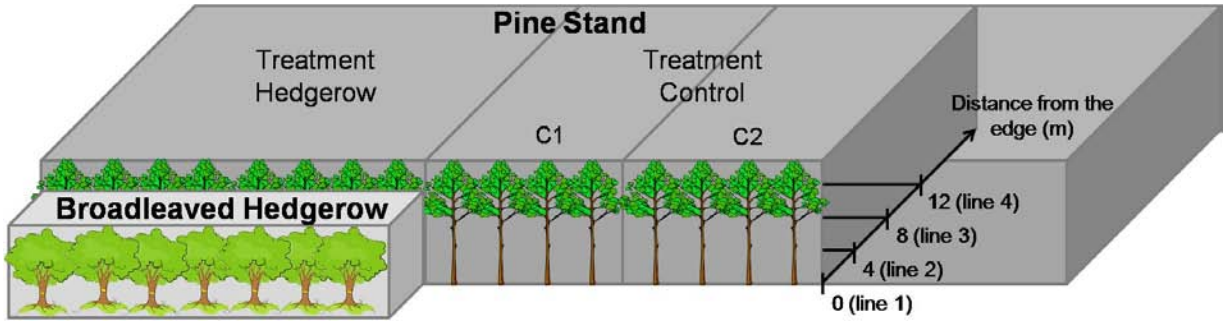

517

518 **Figure 1.** Design of Experiment 2 showing the position of the broadleaved hedgerow
519 relatively to the edge of maritime pine stand.

520 PPM infestation level was estimated by counting larval nests on the same number of
521 trees behind the hedgerow and on the exposed part of pine stand edge, on the first two
522 and four tree rows in 2004 and 2009 respectively. Infestation level in the two sub-
523 sections of the control treatment (C1 and C2) were only compared in 2009. Tree
524 drawings are from Microsoft Office Online (2010).

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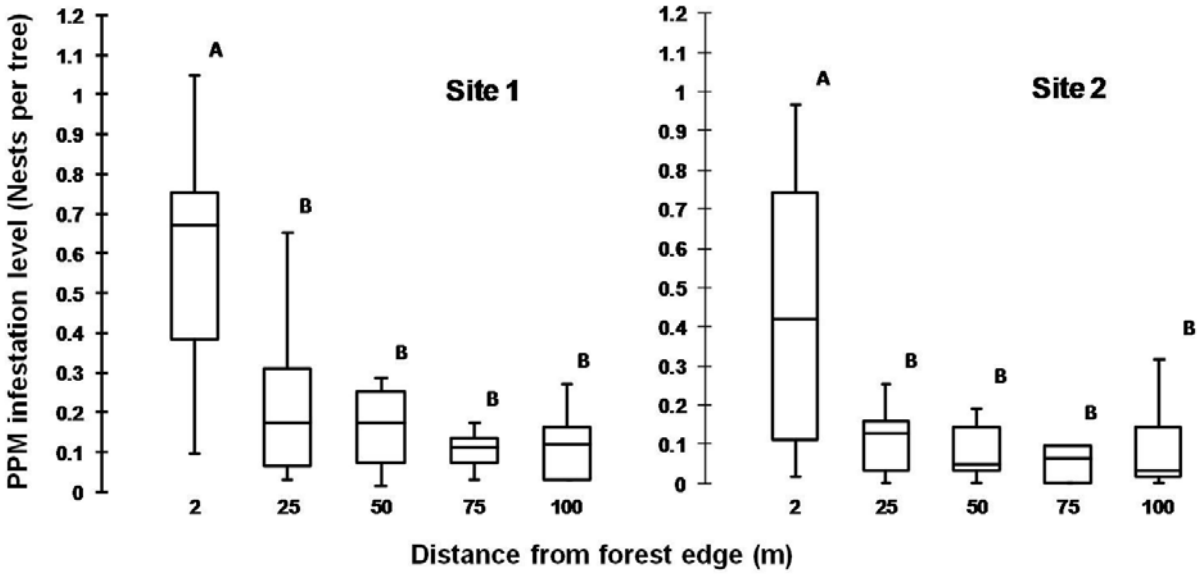

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529 **Figure 2.** Box plot of number of PPM nests per tree in five groups of trees at different
530 distances from the south-exposed edge of maritime pine stands, in both sites. Different
531 letters indicate significant differences (Wilcoxon paired test) in number of nests per tree.

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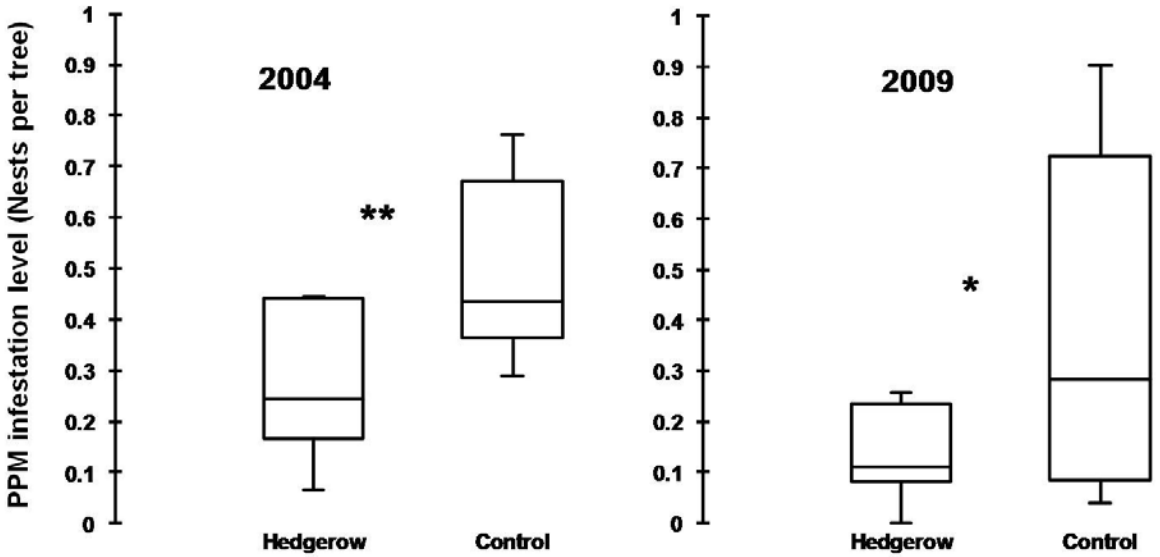

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536 **Figure 3.** Box plot of number of PPM nests per tree on maritime pine trees located
537 behind a broadleaved hedgerow and on the exposed part of the stand edge (two tree
538 lines sampled in 2004 and four in 2009). Wilcoxon tests were used to compare
539 infestation levels between treatments.

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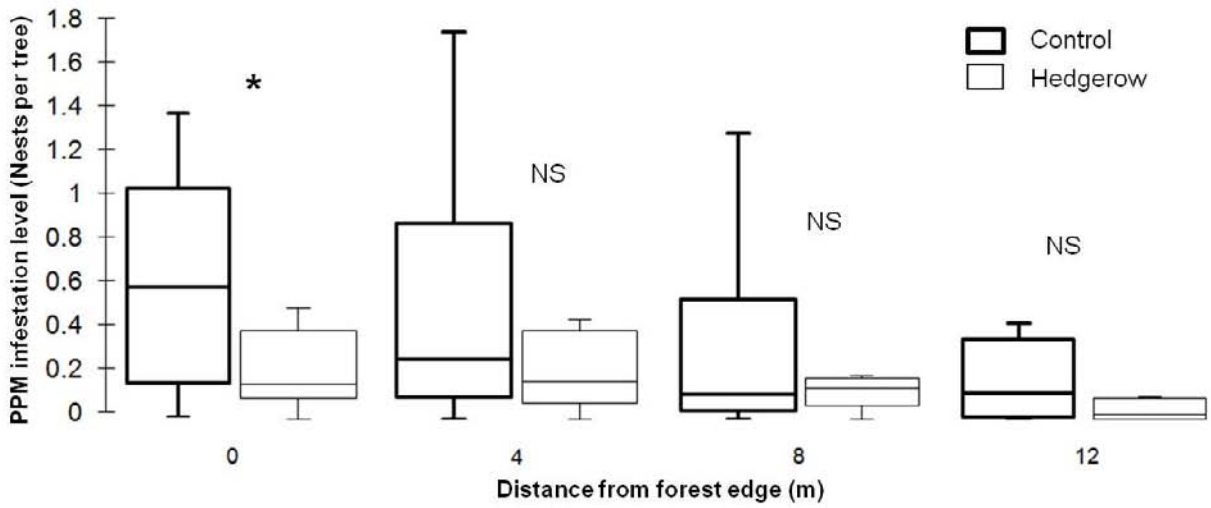

543

544 **Figure 4.** Box plot of number of PPM nests per tree on maritime pine trees located
545 behind broadleaved hedgerows and on the exposed part of stand edges for each tree
546 row separately, in 2009. Wilcoxon tests were used to compare infestation levels between
547 treatments on each tree row ($Z_{9,1}$ = 2.24, P = 0.025 ; $Z_{9,1}$ = 0.84, P = 0.40 ; $Z_{9,1}$ = 0.68, P
548 = 0.50 and $Z_{9,1}$ = 0.68, P = 0.50 for 0, 4, 8 and 12m from the forets edge, respectively).

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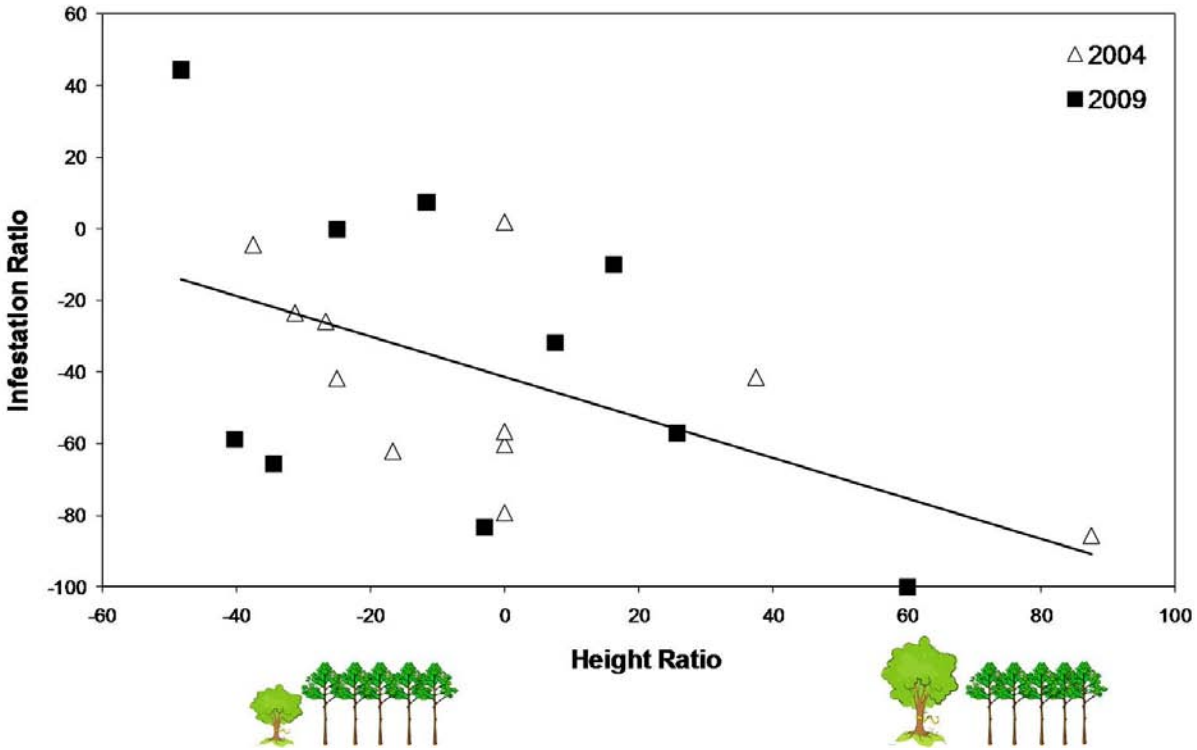

552

553 **Figure 5.** Relationship between relative Infestation Ratio (IR) and Height Ratio (HR).
554 Stands sampled in 2004 are indicated by grey triangles, stands sampled in 2009 by
555 black squares. The regression line corresponds to the pooled dataset, considering the
556 absence of any significant "year" or "year × HR" effects. IR = -0.57 × HR - 41.4 ($F_{20,1}$ =
557 7.26, P = 0.014, r^2 = 0.28). Tree drawings are from Microsoft Office Online (2010).

558

559 **Table 1.** Main characteristics of the stands sampled in the Hedgerow Experiment.

560 Main broadleaved tree species in the hedgerow: PO, Pedunculate Oak; RO, Red Oak; BA, Black Alder.

561 (H) – on the section of stand edge behind the hedgerow; (C) – on the exposed section of stand edge

562 (control treatment).

563 The relative Infestation and Height Ratios were calculated using eqn (1) and eqn (2).

564

Stand	Sampling Year	Main species in hedgerow	Tree height (H) (m)	Tree height (C) (m)	Height Ratio (%)	Infestation level (H) (nests tree $^{-1}$)	Infestation level (C) (nests tree $^{-1}$)	Infestation Ratio (%)
Canauley	2004	PO	5.5	8.0	-31	0.24	0.32	-23
CAEPE 5	2004	RO	11.0	8.0	+38	0.45	0.76	-41
Hostens	2004	PO	12.5	15.0	-17	0.20	0.53	-62
La Barrail	2004	PO	9.0	9.0	0	0.07	0.32	-79
Lagnereau 1	2004	PO	7.5	12.0	-38	0.44	0.46	-4
Lagnereau 2	2004	PO	15.0	20.0	-25	0.17	0.29	-42
LeBray N	2004	PO	15.0	8.0	+88	0.06	0.40	-86
Nezer 1	2004	BA	11.0	15.0	-27	0.90	1.21	-26
Nezer 2	2004	BA	10.0	10.0	0	0.43	0.42	+2
Nezer 3	2004	PO	7.0	7.0	0	0.16	0.41	-60
Nezer 4	2004	PO	15.0	15.0	0	0.88	2.04	-57
CAEPE 1	2009	PO	6.4	8.6	-25	0.07	0.07	0
CAEPE 3	2009	PO	5.1	8.6	-40	0.16	0.39	-59
CAEPE 4	2009	RO	15.1	14.0	+8	1.43	2.10	-32
CAEPE 5	2009	RO	12.3	12.7	-3	0.11	0.64	-83
Canauley	2009	PO	12.5	14.1	-12	0.10	0.09	+7
Caudos	2009	PO	6.1	11.9	-48	0.12	0.08	+44
France	2009	PO	8.4	12.8	-35	0.26	0.75	-66
Hermitage	2009	PO	15.7	13.5	+16	0.81	0.90	-10
Mios	2009	PO	14.9	11.8	+26	0.08	0.18	-57
Smurfit	2009	PO	8.4	5.2	+60	0.00	0.04	-100

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566

567 **Table 2.** Results of the analysis of covariance on the relationship between relative
568 Infestation (IR) and Height (HR) ratios.

569 IR and HR were calculated using eqn (1) and eqn (2).

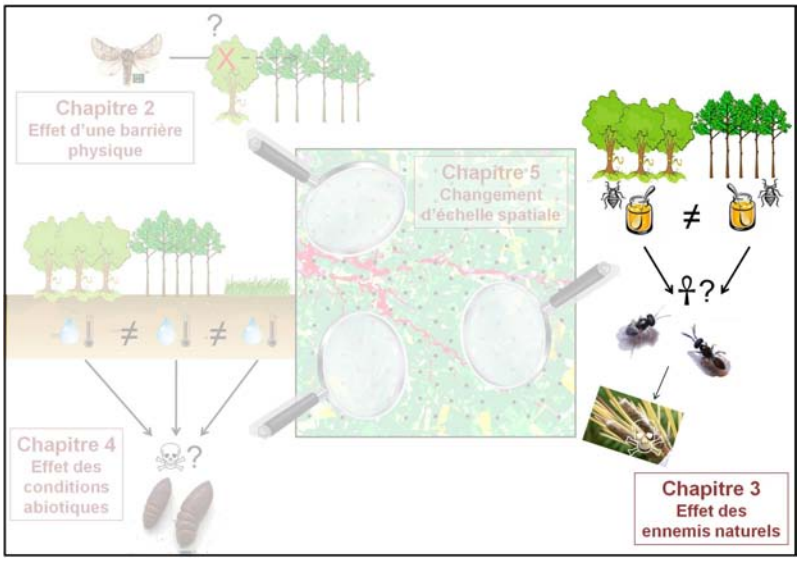
570
571

Source	d.f.	*F*-value	Pr > *F*
Intercept	1	31.8	< 0.001
Year [a]	1	0.10	0.75
HR [b]	1	6.76	0.019
Year × HR	1	0.30	0.59
Error	17		
Intercept	1	32.8	< 0.001
Year [a]	1	0.15	0.70
HR [b]	1	6.77	0.018
Error	18		

572
573 [a] Factor: Year (2004 or 2009) [b] Covariate: Height Ratio

CHAPITRE 3

Honeydew feeding increased the longevity of two egg parasitoids of the pine processionary moth



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J. Appl. Entomol.

Honeydew feeding increased the longevity of two egg parasitoids of the pine processionary moth

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Keywords
Baryscapus servadeii, Ooencyrtus pityocampae, Thaumetopoea pityocampa, diet, generalist parasitoid, insect, specialist parasitoid

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Received: January 27, 2010; accepted: April 18, 2010

doi: 10.1111/j.1439-0418.2010.01547.x

Abstract

The longevity of a generalist (*Ooencyrtus pityocampae*) and a specialist (*Baryscapus servadeii*) egg parasitoid of the pine processionary moth (*Thaumetopoea pityocampa*) was compared under laboratory feeding conditions including water and honeydew from aphid species growing on maritime pine (*Pinus pinaster*) or pedunculate oak (*Quercus robur*).

The longevity of both parasitoid species increased when specimens were fed with honeydew. This increase was larger for the generalist (3.7, 32.0 and 38.0 days) than for the specialist (3.0, 23.3 and 21.5 days) parasitoid species when fed with water, oak and pine aphid honeydew respectively. The phenology of the specialist species *B. servadeii* is well-adapted with its host availability with or without food supply. The generalist species *O. pityocampae* could overlap its host emergence curve during 14.0–20.0 days when fed with oak and pine aphid honeydew respectively, vs. no overlap when no supplementary food was provided. Analysis of honeydew composition indicated that sugars and amino acids may have distinct effects on parasitoid longevity.

Introduction

Parasitoids play an important role in regulation of insect herbivore populations (Lewis et al. 1997; Stiling and Cornelissen 2005). In particular they can have a notable effect on the density of host species with cyclic dynamics by enhancing the deceleration phase of the cycle (Umbanhowar and Hastings 2002). However, parasitoids may not always have a good reproductive success in natural conditions, particularly because they are lacking carbohydrate resources to sustain their foraging activity (Lewis et al. 1998; Wäckers 2003; Winkler et al. 2006; Jonsson et al. 2008). Many studies (Siekmann et al. 2001; Wäckers 2003), including laboratory rearing trials (Fuchsberg et al. 2007; Hogervorst et al. 2007) have shown that sugar-rich food improves adult parasitoid fitness, via increased reproductive life span, fecundity, flight activity or a combination of these elements (Wäckers 2003). Sugar-rich food would be particularly critical for synovigenic species which are born with immature eggs and need to feed on carbohydrates to sustain egg production during their entire lifetime. However the beneficial effect of sugar-rich food may depend on its composition, e.g. presence of specific sugars and amino acids (Wäckers 2001; Williams and Roane 2007; Faria et al. 2008).

Nectar and honeydew (i.e. carbohydrate-rich faeces of plant sap-feeding Homoptera) are important sources of carbohydrates (Völkl et al. 1999; Wäckers 2003; Vattala et al. 2006). Although nectar is the most common liquid carbohydrate-rich food in natural conditions, it can be scarce in intensively managed ecosystems such as plantation forests, where the diversity and abundance of flowering plants are low (Russell 1989; Jactel et al. 2005). In that context, honeydew may be an interesting alternative to nectar (Winkler et al. 2006; Faria et al. 2008;

Wäckers et al. 2008). For example, *Cinara* spp. can produce 400–700 kg of honeydew/ha/year in coniferous forest [Zoebelein (1954) and Zwölfer (1952) *quoted in* Stadler and Michalzik (1999)]. Mixtures of plant species are more likely to provide a consistent supply of honeydew because different species host different aphids which produce at different times and so complement each other (Zoebelein 1957). Furthermore, honeydew differs in sugar and amino acid composition between aphid species and according to their host species (Hendrix et al. 1992; Völkl et al. 1999), thus providing insect parasitoids with various food supplies.

Complementary food requirements may differ between specialist and generalist parasitoid species. Generalist species can reproduce on different host species; they are often less sensitive to the life cycle of a particular host species and may not have evolved a strict adjustment to the phenology of any of their hosts. On top of improving individual fitness, sugar-rich foods may help generalist species to increase adult longevity and allow a better overlap with their host presence in the field, particularly when they need to alternate on several host species with different periods of occurrence. In specialist species, natural selection is likely to have resulted in an optimal overlap with their specific host phenology. In this case, sugar-rich food supply may not be as important for adult longevity but can still be important for improving fecundity or mobility. Surprisingly, to our knowledge, there is no study that addressed this issue, i.e. which compared the response to sugar-rich diets of a generalist and a specialist parasitoid species of a given insect species.

The pine processionary moth (PPM) *Thaumetopoea pityocampa* (Denis & Schiffer-Müller) (Lepidoptera, Notodontidae) is the most damaging insect defoliator of pine species in southern Europe. Larvae are gregarious, they feed on needles in winter and pupate into the soil in spring where they can realize a diapause spanning from few months to several years (prolonged diapause). Adult moths' emergence occurs in early summer and moths immediately mate and lay eggs during the days following their emergence (Démolin 1969). PPM is the most abundant pest insect in the Landes de Gascogne forest (Abgrall and Bouhot 1990; Samalens 2009), the largest plantation forest in Europe with nearly one million hectares of maritime pine *Pinus pinaster* (Aiton). In this plantation forest landscape, some patches of broadleaved species like pedunculate oak *Quercus robur* (Linnaeus) persist. Parasitism by Hymenoptera is the main mortality factor in the egg stage in PPM (Santos et al. 2008). One of the most abundant egg parasitoids in the Landes de Gascogne is *Ooencyrtus pityocampae* (Mercet) (Hymenoptera, Encyrtidae), a generalist species which emerges 2 months earlier than PPM (Masutti 1964) and is known to parasitize other host insects feeding on broadleaved and conifer tree and shrub species (Masutti 1964; Battisti et al. 1988). These insect herbivores can lay eggs during the time lag between *O. pityocampae* emergence and that of *T. pityocampae*, although Battisti et al. (1988) never found any parasitized eggs before the emergence of PPM. The other main PPM parasitoid species is *Baryscapus servadeii* (Domenichini) (Hymenoptera, Eulophidae), a specialist species with an emergence season well matched with the one of its host (Géri 1980). Both species are synovigenic (Battisti et al. 1990 and pers. comm.).

We carried out an experiment to compare the response of *O. pityocampae* and *B. servadeii* to different trophic resources, i.e. two types of honeydew produced by two aphid species feeding on oak or pine trees. The objectives of our study were to test the following hypotheses: (i) honeydew feeding improves the longevity of PPM egg parasitoids; (ii) both types of honeydew have different effects on parasitoid longevity, because they have different compositions in sugar and amino-acids; (iii) the positive effect of honeydew on longevity is more important for the generalist than for the specialist parasitoid species because the latter is already well-adapted to its host phenology.

Materials and Methods

Insect material

Both *O. pityocampae* and *B. servadeii* are bivoltine. The first generation emerges from the PPM eggs parasitized in the previous year and the second from the newly laid PPM eggs (Masutti 1964). Emergent parasitoids of the first generation parasitize PPM eggs when they are available and then give birth to the second parasitoid generation. Individuals of the second generation are able to parasite PPM eggs directly after emergence, in summer and give birth to individuals which realize a diapause by overwintering inside the PPM eggs that have not produced caterpillars. These parasitoids become the first generation of the following year. Both parasitoid species are usually solitary and display unisexual reproduction. The males are only rarely recorded (Battisti 1989; Battisti et al. 1990).

Females of *O. pityocampae* and *B. servadeii* were obtained from 1242 PPM egg masses collected in summer 2007 in eight different *Pinus nigra* stands of Mont Ventoux (South-East of France). Egg masses containing overwintering parasitoids of the second generation were sent to Pierroton (South-West of France) in autumn 2007 and were stored in outdoor conditions until spring 2008. From May 2008, egg masses were monitored daily for parasitoid emergence. Emerging parasitoids from both species were counted and individually placed into 12 ml plastic vials plugged with cotton. The day of the emergence, individual parasitoids were allocated to each experimental feeding treatment.

Honeydew production

The effect of two types of honeydew on the longevity of the parasitoid individuals was tested. Pedunculate oak *Q. robur* and maritime pine *P. pinaster* aphids, i.e. *Tuberculatus querceus* (Kaltenbach) and *Eulachnus* spp. were respectively chosen for the two 'honeydew' treatments, because these two tree species are the most abundant in the Landes de Gascogne forest (Inventaire Forestier National 1999) and these aphid species can produce honeydew in spring, when PPM parasitoids occur.

Approximately 15 individuals of each aphid species were transferred onto ten 5-year-old host trees in a greenhouse, in order to obtain regular honeydew production under standardized climatic conditions (≈25°C, 85% humidity). Honeydew was collected by gravity on plastic A3 sheets suspended underneath the branches of each tree. After 2 days allowing honeydew droplets to cover the plastic sheets, they were collected and preserved at a temperature of −20°C.

Experimental design

A set of ≈40 females of each parasitoid species was assigned to each of the three different trophic resources namely: water (control), oak and pine aphid honeydew. The final number of monitored individuals in each treatment was not always the same because some insects were lost or damaged in the course of experiments.

We used tap water in the 'water' experimental treatment, soaked up on 1 cm × 1 cm pieces of cotton. Plastic sheets (1 cm × 1 cm) covered with honeydew were used in the two 'honeydew' experimental treatments. Diet material was renewed twice a week in all treatments before complete evaporation of water or drying of honeydew. On the pieces of plastic there was not always the same amount of honeydew but it was anyway more than enough food for one individual parasitoid.

Experimental vials were monitored on a daily basis and the status (alive, dead) of each insect recorded.

Monitoring pine processionary moth phenology

Previously collected data were used to obtain the emergence season of the PPM adults. PPM females lay eggs the day following emergence (Démolin 1969), so that adult emergence can be used as a proxy of egg presence. PPM emergence was monitored with light traps. Traps were automatically activated every night from day 166 to day 258, every year from 1978 to 1984 and in 1990. A 100 l container was placed under a 500 W mercury lamp positioned at ≈1 m height in a firebreak next to maritime pine stand border. An automatic clock switched on the lamp from 9 pm to 6 am the following day. Ethyl-acetate was used as insecticide inside the container. Captured pine processionary moths were removed from the container and counted every week.

Characterization of the oak and pine aphid honeydew composition by ^{1}H-NMR metabolic profiling

Honeydew was collected by scratching with a cutter from the plastic A3 sheets, stored at −20°C in Eppendorf® vials and lyophilized before NMR analysis. Two samples of oak aphid honeydew were obtained on days 155 and 160 and four samples of pine aphid honeydew on days 164, 171, 197 and 198. The honeydew dry matter inside the Eppendorf® vials varied from 4.5 to 16.4 mg for pine aphid honeydew and from 26.4 to 57.4 mg for the one from oak. Each lyophilized honeydew sample was dissolved in 0.6 ml deuterated water (99.9%), vortexed for 1 min, submitted to ultrasonic bath for 5 min and then centrifuged 2 min at 17 746 ***g*** (A14 Jouan, Saint–Herblain, France). The honeydew composition was determined using proton Nuclear Magnetic Resonance spectroscopy (^{1}H-NMR) of diluted sample (appendix S1). In order to get the same concentrations in NMR vials for the whole set of samples, a dilution was carried out to reach 4 mg of lyophilized honeydew in 0.5 ml deuterated water.

The compounds identified in the one-dimensional (1-D) ^{1}H-NMR spectra of honeydew were quantified using the integration mode of TOPSPIN software 1.3 (Bruker BioSpin, Karlsruhe, Germany) and the

number of protons of the corresponding resonance, to calculate the concentration in the NMR vial. The relative concentration of NMR unknown compounds (named according to the form of the resonance, S for singlet, M for multiplet and its frequency in ppm) was calculated on the assumption that the measured resonance corresponded to one proton (appendix S1).

Statistical analysis

For each species and each feeding treatment, raw data were used to derive the Kaplan–Meier estimates of the survival functions. We used G^{ρ} family of tests proposed by Harrington and Fleming (1982) to test for significant differences between survival curves stemming from the experimental treatments. G^{ρ} tests were performed using the software R (R Development Core Team 2008).

The available data on PPM emergence were averaged per week to obtain a mean emergence curve of the PPM. The mean gain of longevity brought by each trophic resource was added to the natural emergence season of *O. pityocampae* and *B. servadeii* to estimate the effect of the trophic resources on the overlap between the emergence seasons of the PPM and its egg parasitoids. The surface under each section of the emergence curve of the PPM was calculated. Interpolation was used to obtain a daily proportion of emergent PPM from the raw data. For each trophic resource proposed to the parasitoids, the number of overlapping days between the presence of the parasitoid and its host was calculated. Furthermore, the relative proportion of PPM egg masses potentially parasitized was calculated as the surface of the emergence curve with overlapping divided by the total surface of the emergence curve.

For the study of honeydew composition, principal component analysis (PCA) of ^{1}H-NMR data was used to visualize the global composition of the whole set of samples and search for spectra regions discriminating the two honeydew types. For this multivariate analysis ^{1}H-NMR spectra were reduced into 179 variables (buckets) corresponding to spectral domains and containing integrated regions of equal width of 0.04 ppm scaled to the total intensity of the spectra using AMIX software (Analysis of MIXtures software 3.9, Bruker BioSpin, Karlsruhe, Germany) between 0.7 and 8 ppm. The region of residual unsuppressed water (δ 4.80–4.62) was excluded. PCA was carried out using mean centred data scaled to unit variance for the 179 buckets of the full NMR dataset.

Results

Effect of trophic resources on the PPM egg parasitoids longevity

The descriptive statistics of the longevity of *B. servadeii* and *O. pityocampae* are given in table 1. Figure 1 shows the Kaplan–Meier estimates of the survival functions of both parasitoid species in the different experimental treatments.

Survival curves changed according to the three experimental treatments for each species ($P < 0.001$ in both G^{ρ} tests). The lower average longevity was always observed with the control treatment, i.e. water, with 3.0 and 3.7 days for *B. servadeii* and *O. pityocampae* respectively (table 1). The highest values occurred with honeydew produced by aphids reared either on pine or oak.

Aphid honeydew increased longevity 8–10 folds compared to water control for *B. servadeii* or *O. pityocampae* respectively (table 1, fig. 1). Both honeydew

Table 1 Longevity data (days) of two pine processionary moth (*T. pityocampa*) egg parasitoids (a specialist species: *B. servadeii* and a generalist species: *O. pityocampae*), overlap between their emergence seasons and proportion of the PPM eggs concerned by parasitism, according to different trophic resources supplied to the parasitoid females

Species	Trophic resources	n	Mean	SE	Min	Max	Overlapping period (day)	PPM eggs concerned (%)
Baryscapus servadeii	W.	39	3.0	0.3	1	7	63	100
–	P.H.	40	21.5	1.0	7	38	63	100
–	O.H.	39	23.3	1.5	3	38	63	100
Ooencyrtus pityocampae	W.	39	3.7	0.3	1	7	0	0
–	P.H.	38	38.0	1.8	4	50	20	25.3
–	O.H.	38	32.0	2.6	1	58	14	12.9

W. Water (control); O.H.: Oak aphid honeydew; P.H.: Pine aphid honeydew.

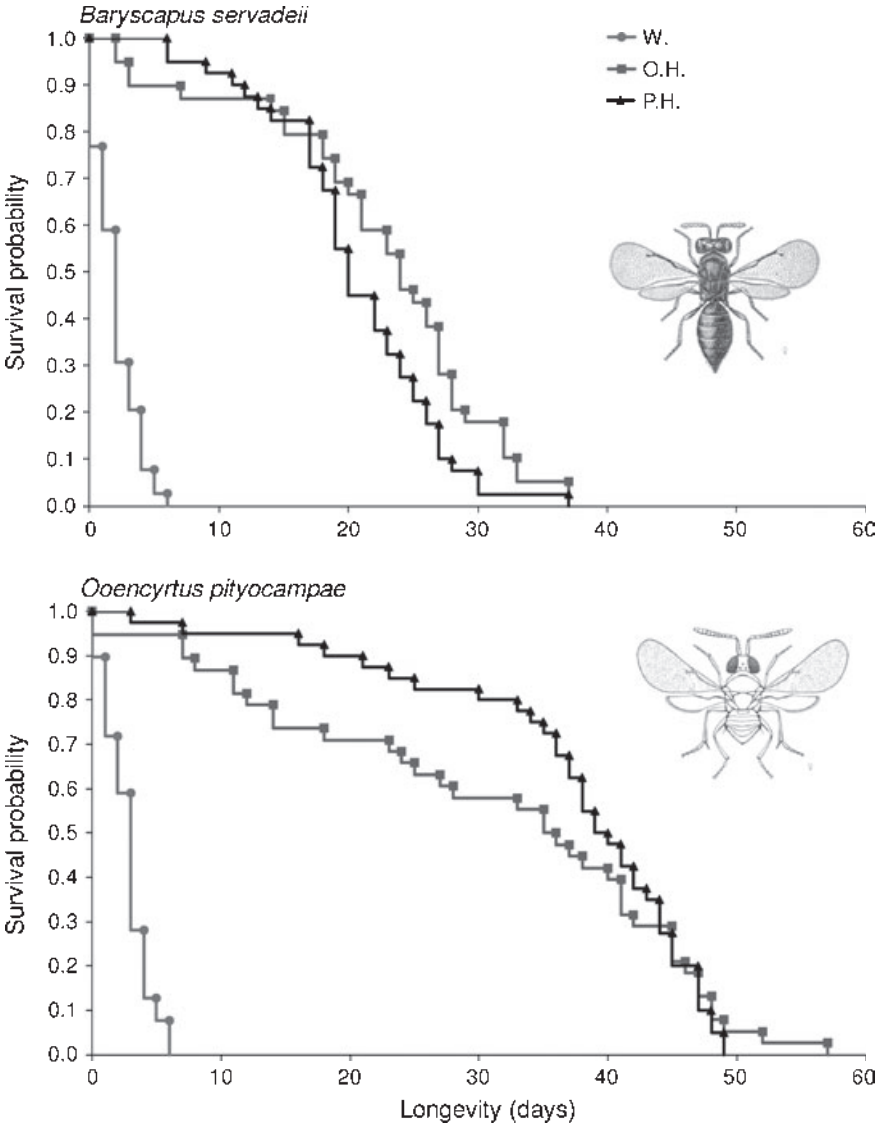

Fig. 1 Kaplan–Meier estimates of the survival functions of the specialist species *B. servadeii* and the generalist species *O. pityocampae* according to trophic resources supplied to the parasitoid females. W.: Water (control); O.H.: Oak aphid honeydew; P.H.: Pine aphid honeydew. Drawings are from PROMOTH (2002).

types increased the longevity of *B. servadeii*, with oak aphid honeydew leading to a slightly longer mean longevity (table 1). Survival curves differed significantly according to the type of honeydew (fig. 1, $P = 0.039$ in G^{ρ} test). However, it had no significant impact on the survival curves of *O. pityocampae* ($P = 0.699$ in G^{ρ} test), even pine aphid honeydew allowed a longer longevity (table 1).

The Kaplan–Meier survival curves, for both types of honeydew, were significantly different between the two parasitoid species ($P < 0.001$ in both G^{ρ} tests). The specialist species *B. servadeii* consistently exhibited shorter longevity than the generalist species *O. pityocampae* (1.4–1.8 times for oak and pine aphid honeydew respectively).

Effect of trophic resources on the overlap between emergence seasons of the PPM and its egg parasitoids

On average, in South-West of France, PPM eggs were laid and thus exposed to parasitism from the beginning of July (day 182) to the beginning of September (day 245), with a peak at the end of July (≈day 210). PPM emergence data were consistent across years, with peak dates varying by ±10 days. It was then possible to compare emergence data of

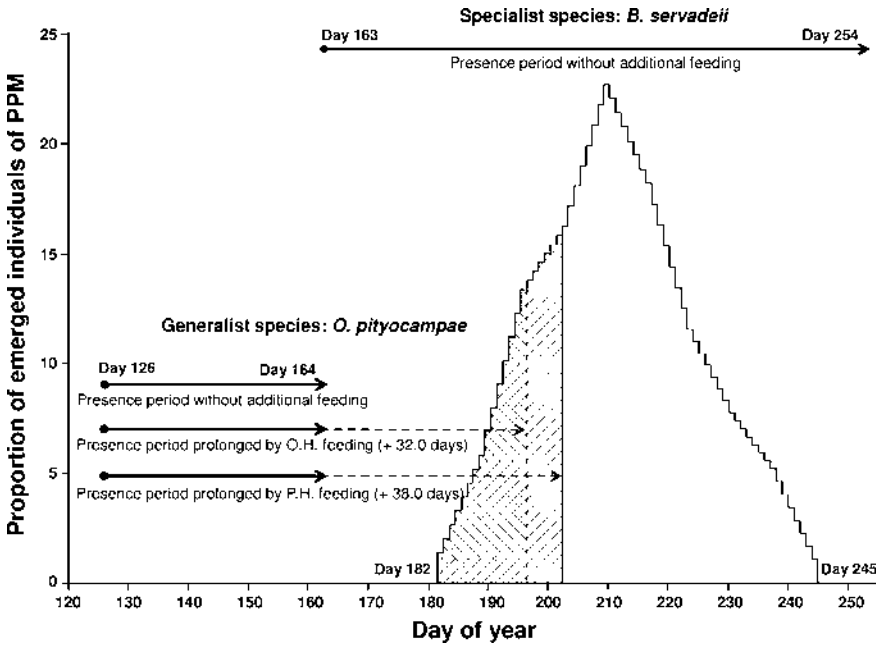

Fig. 2 Mean emergence curve of the pine processionary moth (*Thaumetopoea pityocampa*) and emergence season of its two main egg parasitoids *O. pityocampae* and *B. servadeii* without additional feeding or with honeydew feeding. O.H.: Oak aphid honeydew; P.H.: Pine aphid honeydew. Dotted lines represent the gain of longevity (in days) obtained by honeydew feeding. Hatched areas represent the proportion of PPM eggs concerned by *O. pityocampae* parasitism depending on trophic resources supplied to the parasitoid females.

PPM and its parasitoids from different years. Adults of the specialist egg parasitoid species *B. servadeii* had a flight season well-synchronized with their host (fig. 2), occurring from mid-June (day 163) to mid-July (day 254). On the contrary, the generalist species *O. pityocampae* emerged earlier than the beginning of the egg-laying by PPM for about 2 months. Its emergence season lasted from the beginning of May (day 126) to mid-June (day 164) and is extended to days 196 and 202 when *O. pityocampae* individuals were fed with oak and pine aphid honeydew respectively (fig. 2). Depending on the trophic resource, the emergence season of adult parasitoids would then overlap the one of the PPM for 0–20 days (table 1). These overlaps correspond to proportions of PPM eggs concerned by parasitism ranging from ≈13% (oak aphid honeydew) to ≈25% (pine aphid honeydew) (table 1).

Honeydew composition

The qualitative and quantitative composition of the two types of honeydew was determined using ^{1}H-NMR profiles. Chemical shifts of compounds that were identified from the two types of aphid honeydew spectra are listed in table S1 of appendix S1. Melezitose was only observed in the pine aphid honeydew and two unknowns (unkM1.76 and unkT5.14) were only observed in the oak aphid honeydew (fig. S1 in appendix S1).

The first principal component of the PCA, explaining 48% of the total variability, clearly separated the pine aphid honeydew from the oak aphid honeydew samples (fig. 3). Examination of PC1 loadings suggested that the difference involved sucrose, unkM1.76 on the negative side and glucose, fructose, shikimate, quinate, melezitose, lactate, malate, isoleucine, valine on the positive side.

The compounds identified in the 1-D ^{1}H-NMR spectra of honeydew and highlighted by PCA analysis were quantified. The main identified compounds of oak and pine aphid honeydew are sucrose, fructose and glucose (fig. S2 in appendix S1). Aphid honeydew of oak had higher content of sucrose than the one of pine, but the latter contained more glucose and fructose (fig. S2 in appendix S1).

Discussion

The present study showed that sugar-rich food sources like honeydew do increase the longevity of pine processionary moth egg parasitoids. The longevity was increased by 8–10 times when the specialist *B. servadeii* and the generalist *O. pityocampae* species were

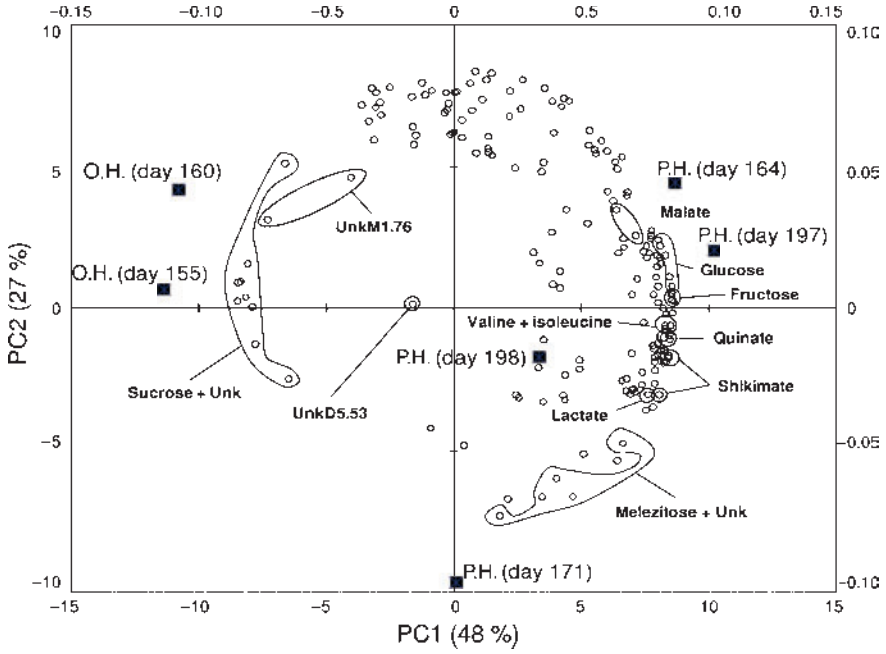

Fig. 3 Principal component analysis (PCA) of ^{1}H-NMR profiling data of the four samples of pine aphid honeydew (P.H.) and the two samples of oak aphid honeydew (O.H.). Plots are based on the two first components, the first and the second axis explaining 75% of total variance. Honeydew samples are identified by a black square and ^{1}H-NMR spectral domains identified by a white circle are annotated with the corresponding metabolite when identified (table S2 in appendix S1). Score plots are varying between −15 and 15 and −10 and 10 on x- and y-axis respectively and loading plots are varying between −0.15 and 0.15 and −0.10 and 0.10 on x- and y-axis, respectively.

respectively fed with honeydew instead of water. Numerous studies have already demonstrated the positive effect of honeydew diet on parasitoids' longevity, fecundity or mobility (Teraoka and Numata 2000; Fadamiro and Chen 2005; Fuchsberg et al. 2007; Faria et al. 2008) and honeydew is known to be directly used by wasps as carbohydrates supply in the field (Casas et al. 2003; Jonsson et al. 2008). Although not tested in this study due to technical difficulties, fecundity is also likely to be improved by honeydew feeding in *B. servadeii* and *O. pityocampae*. Both egg parasitoid species are synovigenic (Battisti et al. 1990) and may then benefit from carbohydrates supply to produce more eggs for a longer time (Wäckers 2003). Honeydew would therefore enhance the biological control of PPM by improving both the longevity and the fecundity of egg parasitoids, thus increasing the chances to find and parasitize a suitable host.

Both parasitoid species exhibited different responses to the type of diet. Survival curves did not differ according to the type of honeydew in the case of the generalist parasitoid *O. pityocampae*, but pine aphid honeydew allowed a longer longevity than oak aphid honeydew for 6 days. This species is known to parasitize eggs of broadleaved herbivorous insects, such as Heteroptera Pentatomidae [*Rhaphigaster nebulosa* (Poda), *Piezodorus lituratus* (Fabricius), *Eurydema oleraceum* (Linnaeus)] or Lepidoptera Notodontidae [*Pheosia tremula* (Clerck)] (Masutti 1964) and also conifer insect herbivores such as Lepidoptera Sphingidae [*Hyloicus pinastri* (Linnaeus)] or Lasiocampidae [*Dendrolimus pini* (Linnaeus)] (Battisti et al. 1988). It can be then assumed that *O. pityocampae* has evolved the ability to feed indiscriminately on diverse types of honeydew found in various forest habitats. On the contrary, the specialist parasitoid *B. servadeii* showed a particular response to the oak aphid honeydew, which slightly improved its mean longevity compared to the pine aphid honeydew. This result is intriguing because specialist parasitoids are more likely to stay in the main habitat of their host, i.e. in pine forest. However in natural conditions, pine forests are most often in admixture with deciduous trees and then even specialist parasitoids of pine herbivores may have evolved the ability to forage on non-pine trees. Further trials, including choice tests, are therefore needed to better investigate the respective effect of honeydew originating from different insect and tree species on a larger sample of PPM egg parasitoids.

The differences in honeydew composition may also explain their different effects on *B. servadeii*.

Pine aphid honeydew contained higher concentrations of glucose and fructose, while oak aphid honeydew contained more sucrose. In most of insect parasitoid feeding experiments, pure solutions of these sugars (Wäckers 2001; Hogervorst et al. 2007, 2009; Williams and Roane 2007; Faria et al. 2008; Lee and Heimpel 2008) provided a longer longevity than honeydew or nectar, without any primacy of one of them. Thus, the lower capacity of pine aphid honeydew to raise the lifespan of *B. servadeii* may not originate in the concentration of these sugars but in the presence of some unfavourable compounds. Some insect-synthesized sugars present in honeydew, such as melezitose, were shown to have a negative effect on parasitoid longevity (Wäckers 2001; Wäckers et al. 2008). This trisaccharide is particularly abundant in conifer aphid honeydew [Maurizio (1985) *quoted in* Wäckers (2000)]. We observed that it was in high proportion in the pine aphid honeydew and under the limit of NMR detection in the oak aphid honeydew which may explain the higher positive effect of the latter (Wäckers 2000). The effect of amino acids on insect parasitoid fitness has been poorly considered although several studies on honeydew composition have been previously published (van Helden 1995; Blüthgen et al. 2004; Faria et al. 2008; Hogervorst et al. 2009). Generally, honeydew contains low levels of amino acids (Wäckers 2003), notably because sap feeding insects tend to excrete carbohydrates and retain nitrogen rich nutrients such as amino acids from ingested phloem sap (Wäckers 2000). Amino acids did not increase the longevity of *Trichogramm* spp. parasitoids (McDougall and Mills 1997), probably because these parasitoids have enough reserves of nitrogen remaining from the larval stage (Wäckers 2003). In our study, we observed that pine aphid honeydew contained more valine and isoleucine than oak aphid honeydew where they were below detection limit. It is then possible that these amino acids were unsuitable for *B. servadeii*, but further studies are required to confirm this assumption. However, some amino acids and other metabolites such as plant secondary compounds might be difficult to detect because of their very low concentration in honeydew, in comparison with sugars with the NMR method. On the other hand some metabolites observed by NMR in honeydew extracts remained unknowns and may correspond to secondary compounds.

As a specialist egg parasitoid, *B. servadeii* exhibited an emergence season that completely matched with the egg laying season of its host. One can thus assume that any supplementary food, such as honeydew, may not be used by adult females to increase their lifespan but to increase their fitness for example through egg maturation in synovigenic species (Hougardy and Grégoire 2000). Prolonged lifespan is particularly important for generalist parasitoids as it increases the likelihood of matching with the time of occurrence of several potential hosts. As confirmed by our study, *O. pityocampae* generally emerges two months before PPM in Southern Europe (Masutti 1964; Battisti et al. 1988; Santos et al. 2008). Even if egg masses have been collected in the South-East of France, they were stocked in South-West of France during winter. Thus, as diapause termination in *Ooencyrtus* spp. is conditioned by environmental parameters (Anderson and Kaya 1975), emergence dates are expected to be the same for the egg masses we used than the ones of the local population in South-West of France, provided that there is no genetic difference between populations. *O. pityocampae* is known to be able to parasitize alternative hosts (Masutti 1964; Battisti et al. 1988). However, Battisti et al. (1988) only recorded parasite eggs of other host species during the flight season of the PPM. These authors had no explanation for that observation. If alternative hosts are missing when *O. pityocampae* emerge in spring, but further research is needed to clarify this point, then the presence of suitable carbohydrate food resources may be of critical value to prolong their lifespan until the occurrence of PPM eggs. We found that the provision of honeydew, which starts to be produced by pine or oak aphids in spring time, would allow parasitizing from 13% to 25% of PPM egg masses. However this is probably overestimated since other mortality factors may constraint the longevity of parasitoids in the field, resulting in shorter overlap. One would therefore expect increased selection pressure on late emerging adults unless the resource of honeydew or other carbohydrates is not limiting.

Our results showed that PPM parasitoid species benefited from honeydew produced by either oak or pine aphids. This trophic resource allowed a marked increase in parasitoid lifespan as compared to water. In particular the increase in longevity of *O. pityocampae*, a generalist species, improves the match between its emergence season and the one of its host. *B. servadeii*, a specialist parasitoid species of PPM, a conifer specialist defoliator, also benefit from oak aphid honeydew to increase its longevity. This finding supports the hypothesis that species-rich tree communities can provide specialist natural enemies with complementary food resources, which may

explain why more diverse forests are less prone to pest insect damage (Jactel and Brockerhoff 2007). Our study lacks replication but replicating specialist species was impossible because the parasitoid community under study only featured one species of this type. Furthermore, our results stem from laboratory experiment and further investigations should be carried out in the field to confirm our findings (Casas et al. 2003; Jonsson et al. 2008). On the other hand, our data focused on the honeydew composition but its availability under natural conditions is another important point which deserves more attention.

Acknowledgements

We thank the Mediterranean Forest Experimental Unit of Avignon for providing us the PPM egg masses containing the egg parasitoids used for the feeding experiments. The authors thank Armelle Cœur d'Acier for aphid species identification. We are grateful to Julien Mercadal and Audrey Jacques-Gustave for their help on the use of LaTeX, Emeline Devaux and Fabrice Vétillard for their technical support during the feeding experiments and Mark Bakker, Bastien Castagneyrol, Jean-Sébastien Jacquet and François Hubert for their helpful comments on the manuscript. We like to thank the reviewers for their valuable comments that helped to improve the manuscript. We are grateful to Mickaël Maucourt for assistance in maintaining the NMR spectrometer used in this study. NMR data were collected by the Metabolome facility of Bordeaux Functional Genomics Centre.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Representative 1–D ^{1}H–NMR spectra of pine and oak aphid honeydew.

Fig. S2. Relative quantification of compounds identified in the 1–D ^{1}H–NMR spectra of pine and oak honeydew.

Table S1. Compounds identified in the 1–D ^{1}H-NMR spectra of pine and oak honeydew.

Table S2. NMR spectral domains (or buckets) annotated on fig. 3.

Appendix S1. Characterisation of oak and pine aphid honeydew composition by 1H–NMR metabolomic profiling.

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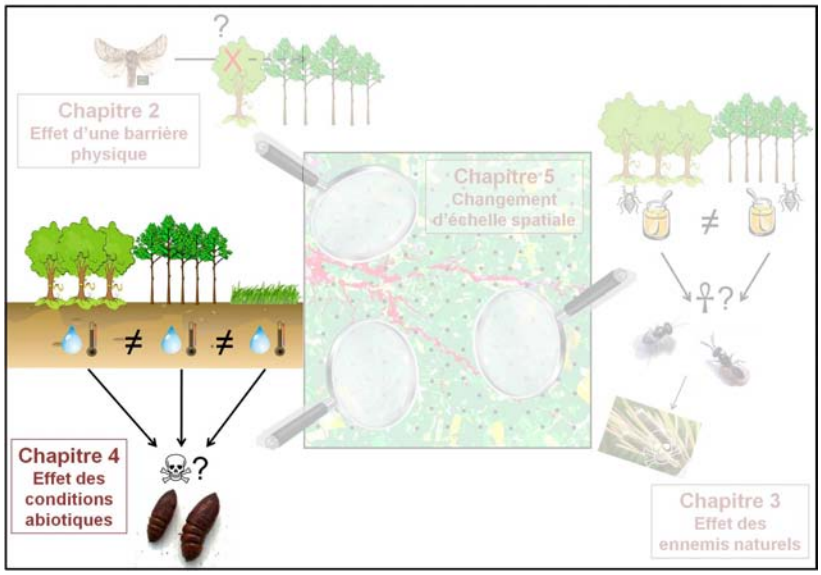
CHAPITRE 4

A case of habitat complementation in forest pests: pine processionary moth pupae better survive in open areas



A case of habitat complementation in forest pests: pine processionary moth pupae survive better in open areas

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Abstract: Little attention has been given to the relevance of habitat complementation concept to the population dynamics of insect herbivores. Late instar larvae of the pine processionary moth (PPM) ***Thaumetopoea pityocampa*** move in late winter from pine stands, their feeding habitat, to neighbouring habitats where they pupate until next summer. They search for sunny exposed soil which they can find in open areas. We investigated the effect of both forest cover and soil origin, with three matching types (pine stand, broadleaved stand and open area) on the survival of PPM pupae. The microclimatic soil variables which significantly differentiated cover types and soil origins were the maximum temperature and the mean relative humidity in spring, soon after pupation has occurred. A significant effect of the cover type, but not of the soil origin, was detected on the proportion of dead, emerged or diapausing pupae. Open areas were more suitable for pupae survival than forest covers (pine or broadleaved stands), due to warmer and more humid soil conditions. In this study, we provide one of the first examples of habitat complementation for an insect herbivore, as PPM population can benefit from the combination of pine habitats for the feeding of larvae with open habitats for pupation. The presence of broadleaved stands next to pine stands might also represent an ecological trap for PPM pupae, as broadleaved habitats may turn to be less suitable for pupae survival in spring when the apparition of leaves creates cooler conditions.

Keywords:Soil, insect, conifer, broadleaved tree.

Research highlights:

- Pine Processionary Moth pupae survive better in open areas that in pine or broadleaved forests
- Pupae survival increases with temperature and humidity in the weeks following pupation in sandy soils.
- Combinations of pine forests and open areas provide the pest with habitat complementation

1 Introduction

For many animal species, not all resources required to complete the life cycle are present in a single habitat. These species depend on the combined presence of different habitat patches providing different, complementary resources; this is known as “landscape complementation” (Dunning et al., 1992). For example, bees (Tscharntke et al., 1998), birds (Barbaro et al., 2008; Mueller et al., 2009), and butterflies (Ouin et al., 2004) may need both suitable habitats for mating or nesting and resource-rich habitats for feeding. Different elements of the landscape can be used at each stage of the life cycle (Delettre et al., 1998). Proximity of different habitat types can have positive effects on animal populations because of complementation of resources but also because they provide suitable microclimates for different vital functions or different stages of the life cycle (McCollin, 1998). For example, many insects overwinter in the soil as larvae or pupae to escape adverse climatic conditions (Tauber et al., 1986) and some of them find more suitable overwintering conditions in habitats that differ from their feeding habitat at the adult stage (McLeod et al., 2004; Magura et al., 2002).

However moving from one habitat type to another to satisfy different, complementary requirements may involve risk of higher mortality. Individuals rely on environmental cues to settle in a new habitat that can later prove to provide unsuitable conditions for survival or reproduction (Robertson and Hutto, 2006). This process, called ecological trap, has been mostly studied in species of conservation interest, but not in pest insects (Battin, 2004; Robertson and Hutto, 2006). And yet insects which overwinter in the soil of habitat different than the feeding habitat (Dennis et al., 1994) may experience dramatic changes in microclimatic conditions between the initiation and the completion of the overwintering stage that result in strong adverse effects since they are trapped in unsuitable habitat.

While the habitat complementation concept have provided a suitable framework for biodiversity conservation in heterogeneous landscapes (Ouin et al., 2004), only little attention has been given to their relevance to the population dynamics of herbivores. Bianchi et al. (2006) indicated that landscape heterogeneity may favour generalist pest insects that can use different habitats to sustain high population levels. They also stressed the role of habitat complementation for the maintenance of natural

enemies that can control insect herbivore populations. However to our knowledge, no study has so far addressed the effect of landscape complementation on pest dynamics via microclimatic drivers.

Thaumetopoea pityocampa [Denis & Schiffermüller] (Lepidoptera, Notodontidae), the pine processionary moth (PPM) provides a good example of such mechanisms. PPM is the most damaging insect defoliator of pine tree in southern Europe. Larvae are gregarious and feed on needles, primarily in winter. In spring, they make a procession to descend from the crown before they bury into the soil and pupate. Prior to entering the soil they can crawl several tens of meters, searching for sunny exposed soil, in gaps or forest edges, probably to find optimal survival conditions for pupae. Adult moths emerge in early summer (Démolin, 1969). PPM is the most abundant pest insect in the Landes forest, South-West France (Abgrall and Bouhot, 1990; Samalens, 2009), the largest plantation forest in Europe with nearly one million ha of pure maritime pine stands (***Pinus pinaster*** Aït.). The forest landscape forms a mosaic of pine plantations with some patches of broadleaved species like pedunculate oak (***Quercus robur***) and many patches of open area, resulting from clearcuts. This forest landscape has also a very dense network of forest roads for fire protection. As a result, ca. 16% of pine trees are less than 10 m from a stand edge (Samalens, 2009), and PPM has therefore many opportunities to find preferred pupation sites in open areas. However, on some occasions, late instar PPM larvae may venture into neighbouring broadleaved stands that resemble open areas when they are without leaves. Because the pupation phase lasts until the next summer, these deciduous trees have time to produce new leaves and microclimatic conditions can change from those of open areas to those of broadleaved forest cover. If these conditions of temperature and humidity are not favourable to pupae survival, neighbouring broadleaved habitats may act as ecological traps.

We carried out an experiment where we forced the burying of PPM caterpillars into different soil origins under different types of land cover. The objectives of our study were to test the following hypotheses:

1. The survival of the PPM pupae is higher in open areas than under pine and broadleaved forest covers;
2. Survival rates of PPM pupae are related to micro-climatic soil conditions that depend on both forest cover type and soil origin.

3. Open areas provide complementary habitats to PPM individuals, whereas broadleaved stands may act as ecological traps.

2 Materials and methods

2.1 Study area

The study was conducted in the Landes de Gascogne forest, South-West of France (44°44' N, 00° 46' W). The climate is oceanic with total annual rainfall around 1000 mm; the mean annual temperature is ca. 13 °C with maxima in July - August and a minimum in December - January. Soils are podzols with fine quartz sand (Jolivet, 2000).

2.2 Experimental design

To test the effects of habitat quality on PPM pupation success, three matching types of both land cover and soil origin were chosen according to their relevance for the ecology of PPM populations: maritime pine forest, which is the natural habitat of PPM moths and caterpillars, clear cuts resembling open area that represent the preferred habitat for pupation of PPM pupae, and oak forest which are known to reduce PPM infestation in neighbouring pine stands (Dulaurent et al., ***in press***). These were arranged in a split-plot design (Figure 1) consisting of three land cover types, replicated twice (resulting in six land cover patches) with three soil origins replicated three times within each patch of land cover. The patches were located at a maximum of 5 kilometres from each other. In February 2008, under each of the 6 land cover patches, 9 buckets of soil (3 of each soil origin) were installed. Each bucket of soil was obtained by taking a cylinder-shaped piece of soil of 35 cm of diameter and 35 cm of height from each of the three soil origins. Soil samples have been considered as free of wild PPM pupae because the probability of sampling soil in a burying site of wild larvae, furthermore with remaining diapausing pupae, was considered as null. Each sample of soil was carefully placed in a plastic bucket of 30 L with a pierced bottom to drainage of rain water. Soil strata were kept in their original vertical order. Within each patch of land cover, 9 holes were dug along three lines separated by 1 m from each other (Fig.1). Buckets were placed into the holes so that the level of their

surface corresponded to the surrounding ground level. A total of 54 buckets were thus installed.

In March 2008, 3062 PPM caterpillars in pre-pupation procession were collected on several forest tracks near the experimental sites. In each collected procession, 10 % of the caterpillars were sampled to be kept under laboratory conditions to evaluate the parasitism rate of caterpillars before the pupation stage. The remaining 90% were split into 54 groups of 50 caterpillars each, by mixing caterpillars from the different collected processions (and so from different genetic origins). The number of 50 was considered as optimum regarding the capacity of buckets and the average size of PPM processions (10 – 100 caterpillars). In each bucket, a group of 50 caterpillars was placed on the soil surface and the buckets were covered with a thin wire netting (mesh size 1.5 by 1.5 mm) to prevent caterpillars from escaping at the beginning of the experiment and to trap emerging moths at the end of the experiment. The next day, every bucket was checked to verify that all caterpillars had buried into the soil.

2.3 Micro-climatic and edaphic conditions

Three additional buckets containing each of the three origins of soil, but no caterpillars, were installed under each patch of land cover to monitor edaphic microclimatic variables. Soil temperature (T_s, °C) was monitored on an hourly basis in each additional bucket using a HOBO ® data logger (U12 Outdoor data logger with PT 100 probes). Soil relative humidity (RH_s, %) at 5 cm of depth was measured every two weeks with a Theta Probe ® sensor (ML2x, DeltaT Devices, Cambridge, UK), following a minimum period of 24h without rain. All the microclimatic variables were recorded from March 30 to September 14, 2008 to cover the whole period from the burying of the caterpillars to the emergence of the last adult moth.

Soil temperature data were averaged per day and maximum and minimum daily values were also extracted. Mean, maximum and minimum data were then averaged over two weeks (from the 1st to the 15th and from the 15th to the 31st of each month) to coincide with soil water content data.

2.4 Insect development assessment

In mid-September, when all moths had emerged from the soil, buckets were collected and carefully emptied by hand, layer after layer, to retrieve the 50 pupae. Moths were not retrieved because early emerged (mid-July) moths were decomposed and then difficult to count. The depth at which pupae were buried was noted. As all the 50 caterpillars could not be found at the end of the experiment, we calculated the number of vanished cocoons (V) as the difference between 50 and the total number of retrieved cocoons. For the retrieved cocoons, the status of pupae was classified according to 5 categories: emerged (E) when silky cocoons were empty, parasitized (P) when cocoons contained obvious signs of parasitism (such as moist PPM pupae leftovers or parasitoid fly pupae), and infected by fungi (F) when cocoons were covered by mycelium. Cocoons that were still full, but without any sign of parasitism or fungi, were opened by hand. When dry caterpillars were found, they were considered as having failed to pupate (C for dead caterpillar). Remaining pupae were collected to determine their status using an X-ray densitometer (shooting of 15 kV and 3 mA during 4.3 minutes; Isovolt 3003 X-ray generator with an Isovolt V4N tube, GE Inspection Technologies Gmbh, Germany). We could then further distinguish between diapausing pupae (D) and additional PPM parasitized pupae (P), of which parasitoids did not exit cocoons. For each bucket, the sum of the individuals from the six categories equalled 50 (E+D+V+P+F+C=50). Counts per category were transformed into percentages and a total mortality rate was calculated as the sum of the four categories of mortality (% M = (V+P+F+C)/50). Percentages were angular transformed prior to statistical analyses. An averaged burying depth was also calculated for each category in every bucket.

2.5 Statistical analyses

We used the soil microclimate data from the 18 buckets (1 bucket of each origin of soil under each land cover patch) set up for microclimatic measures to verify the relevance of the ***a priori*** classification of soil and land cover types. Because microclimatic variables were many and auto-correlated we used a principal components analysis (PCA) with variance maximizing rotation (varimax) (XLStat software 2008.2.03, Addinsoft, France) to explore within and between types variability and develop an alternative ***a posteriori*** classification of land covers and soil origins. PCA was based on 42 edaphic variables (9 soil relative humidity variables,

and 11 mean, maximum and minimum soil temperature variables for two-week periods). A decision tree analysis was then used to confirm the relevance of the ***a posteriori*** classification using the proportion of buckets which were correctly re-classified. Moreover, this method allowed identifying the variables best explaining this classification, and their threshold values (Olofsson and Blennow, 2005, XLStat software 2008.2.03, Addinsoft, France).

The effect of land cover types and soil origins (***a priori*** classification) on the percentage of pupae in the six categories and the total mortality rate were analyzed using a split-plot analysis of variance (ANOVA) (SAS Software 9.2, SAS Institute, USA), with land cover type as the main plot, land cover patches nested inside the land cover type and soil as the subplot. Tukey's tests were carried out as post-hoc comparison tests of the means. A second split-plot ANOVA was performed with the ***a posteriori*** classification, followed by Bonferroni's comparison tests of the means (unbalanced sample sizes).

A multiple linear regression analysis (Statistica Software 7.1, StatSoft, France) was used to relate the proportion of emerged and diapausing pupae with the microclimatic variables revealed by the decision tree analysis as best predictors of land cover types and soil origins.

3 Results

3.1 Insect development

Using the ***a priori*** classification of habitat conditions, the proportion of emerged pupae and the total mortality rate varied from 37.0 to 62.7 % and from 36.7 to 57.3 %, respectively, according to soil and cover types. The proportion of diapausing pupae varied from 0.7 to 9.0 % (Fig. 2a). The main mortality factors were vanished pupae (mean ± SE: 17.5 ± 1.0 % of the total number of pupae) and fungi (17.4 ± 0.9 %), followed by pupation failure (6.3 ± 0.7 %) and parasitism (6.1 ± 0.6 %). As a comparison, the proportion of parasitized larvae from the control sub-sample was of 8.7 %.

The type of land cover and soil as defined in the ***a priori*** classification (pine trees, broadleaved trees, and open area) had a significant effect on the proportion of emerged or dead pupae (Table 1a). The proportion of diapausing pupae was only

affected by the type of land cover (Table 1a). There was no significant effect of the interaction between the two factors. The proportion of emerged pupae was significantly higher whereas the proportion of diapausing pupae and the total rate of pupae mortality were lower in open areas compared to pine or broadleaved tree covers (Fig. 2a). The effect of the soil origin on the proportion of emerged pupae and on the total rate of pupae mortality was significant (Table1a). Mortality was indeed higher in the soil of pine stand compared to the soil of broadleaved stand (Fig. 2a). There was no significant effect of any single factor on the proportion of dead pupae from different cause of mortality (Table 1), nor on the burying depth of pupae (data not shown).

3.2 Impacts of environmental factors

Using the 42 soil temperature and humidity variables, we were able to better characterise and reclassify the soil and cover types used in our experiment. The first axis of the PCA, which explained 44.1 % of the total variance, clearly separated plots from forest covers (pine or broadleaved trees) vs. open areas (Fig. 3a). The first 10 variables contributing to axis 1 were the maximum soil temperatures between April and August on a fortnightly basis (correlation to axis between 0.85 and 0.96). Soil in open areas appeared to be warmer than under forest covers (18.6 ± 0.25, 16.9 ± 0.26 and 16.1 ± 0.18 ℃ in open areas and under pine and broadleaved covers, respectively). The second axis of the PCA, which explained 15.5 % of the total variance, allowed separating pine soils from other, more humid, non-pine soils (28.8 ± 1.26 %, 34.5 ± 1.84 % and 38.9 ± 1.94 % in pine, broadleaved and open area soils, respectively) (Fig. 3b). The 5 main variables contributing to axis 2 were the soil relative humidity between April and June on a fortnightly basis (correlation to axis between 0.94 and 0.97). A new classification with four groups (2 land cover types × 2 soil origins) was then made on the basis of these results. To test the relevance of the new, ***a posteriori*** classification and identify the best predictors, a decision tree analysis was made with the same 42 explanatory edaphic variables. The proportion of buckets properly allocated to the four new classes were of 80 %, 100 %, 100 % and 100 %, respectively, for an overall error of classification of 5.6% (Fig. 4). Moreover, the decision tree method allowed identifying a single variable to discriminate the different cover types which was the maximum soil temperature

during the first 15 days of May ($T_s$max-May_{1-15}). The separation between covers could be attributed to warmer conditions in open areas (above 18.7 ℃). Then a single additional variable, which was the same for both cover types, sufficed to discriminate soil origins: the soil relative humidity during the first 15 days of April (RH_s-$April_{1-15}$). The separation between soil origins was due to drier conditions in pine soils than in non – pine soils (humidity below 34% in forest covers and below 31% in open areas respectively, cut-off points in the decision tree analysis) (Fig. 4).

3.3 Effect of environmental variables on PPM pupae survival

With the ***a posteriori*** classification of land cover types and soil origins, the significant effect of forest cover on the proportion of emerged, diapausing and dead pupae was confirmed (Table 1b and Fig. 2b). It was more significant than with the ***a priori*** classification. On the contrary, there was no effect of the origin of soil and no effect of the interaction between cover types and soil origins. The two variables revealed by the decision tree analysis, $T_s$max-May_{1-15} and RH_s-$April_{1-15}$, were significantly correlated with the proportion of emerged pupae (***P*** = 0.05 and ***P*** = 0.0007 in the multiple linear regression, respectively) and the proportion of diapausing pupae (***P*** = 0.001 and ***P*** = 0.01 in the multiple linear regression, respectively, Table 2). The proportion of emerged pupae increased with soil maximum temperature and humidity in early spring, while the proportion of diapausing pupae showed the opposite pattern.

4 Discussion

In our study the type of land cover significantly affected the survival of PPM during its pupal stage in the soil. The highest rates of moth emergence were observed in open areas and the lowest under forest covers, which is consistent with many observations of PPM caterpillars making procession towards forest gaps, clear cuts, edges or forest trails where they dig into the soil (Démolin, 1971). By contrast we found no consistent effect of soil origin. When the three soil origins were differentiated (initial classification), the mortality of pupae was slightly higher in pine soil than in broadleaved soil, which is more humid. However, when soil categories were refined according to microclimatic data, no significant differences were observed in the fate

of pupae. The three origins of soil used in this experiment (from pine stands, broadleaved woods and open areas) were very similar in their composition, as they are all sandy podzols (Jolivet, 2000), which may explain the lack of strong difference in mortality of pupae.

The main microclimatic characteristics which allowed discriminating the different land cover types were the edaphic conditions. Interestingly, the same edaphic variables (maximum soil temperature of the first 15 days of May and mean soil relative humidity of the first 15 days of April) were also significantly correlated with the proportion of emerged pupae. Extreme values in soil temperature and moisture, whether high or low, have been found to have negative impact on the survival of PPM pupae (Démolin, 1974; Markalas, 1989) and many other insect hibernating as pupae in the soil such as Lepidoptera (***Panolis flammea***, Leather, 1984; ***Mamestra configurata***, Turnock et al., 1983), Coleoptera (***Diaprepes abbreviates***, Lapointe, 2000) or Diptera (***Ceratitis capitata***, Eskafi and Fernandez, 1990; ***Bactrocera tryoni***, Hulthen and Clarke, 2006). We observed that the proportion of emerged pupae increased with increasing soil temperature and relative humidity in April and May, the months that just followed the burying of caterpillars (in March). These findings are consistent with those of previous studies showing that microclimatic conditions right after pupation of PPM are decisive for their survival (Démolin, 1974; Markalas, 1989). However, our results concerning the effect of soil humidity contradict the trend observed in a previous study which showed increased PPM pupae mortality with annual precipitation (Markalas, 1989). The lack of information about soil type and realized soil humidity in this study does not allow proper comparison with the conditions of our experiment. Moreover, total mortality in our study varied from 40 to 50 %, whereas it ranged from 60 to 95 % in Markalas (1989), which suggests that another factor may have obscured the effect of humidity. In the present study, soil humidity was 20 – 60 %, which falls within the range of variation in this type of sandy soil (Achat et al., 2010).

The proportion of dead pupae (all mortality causes included) was higher under forest cover (broadleaved or pine forest) than in open areas. However, none of the different biotic causes of mortality (infestation by fungi, parasitism and caterpillars having

failed to pupate) could be specifically related to soil or land cover types. This absence of relationship is probably due to the fact that the main biotic causes of PPM pupal mortality are initiated before pupation. The main fungi killing pupae, ***Beauveria bassiana*** and ***Scopulariopsis*** sp., infect PPM during caterpillar stages either within the larval nest or during the procession (Géri, 1980). Moreover, the proportion of parasitized pupae in the control sample kept in laboratory conditions was of the same magnitude as that of the pupae in experimental buckets, suggesting that the latter were parasitized before pupation. The main parasite of the caterpillar stage, ***Phryxe caudata*** (Diptera), pupates inside PPM silky cocoons or directly in the soil (Biliotti, 1956). Some adults of ***Phryxe caudata*** were indeed found at the surface of the buckets at the end of our experiment. PPM pupae can also be parasitized by ***Villa*** sp. larvae (Diptera) (Du Merle, 1979) but since ***Villa*** females deposit eggs on the soil surface (Billioti et al., 1965), it is unlikely that any egg had been thrown through the wire netting of buckets. However because ***Villa brunea*** is known to prefer open areas for egg laying (Billioti et al., 1965), we may have underestimated the natural rate of pupal parasitism in this type of habitat. The other types of mortality are more difficult to attribute because their origin is not clear. Caterpillars having failed to pupate remained in their larval shape and were completely dry. They were probably not infested by any parasite or virus, but probably sensitive to edaphic conditions that can impair caterpillar development in extreme cases (Eskafi and Fernandez, 1990; Lapointe, 2000). The pupae which were not retrieved at the end of the experiment ("vanished") may have been infested by viruses and later consumed by microorganisms. In this case, death would have happened during the larval stage before the cocoon was spun.

The proportion of prolonged diapausing pupae was significantly higher under forest covers (broadleaved or pine trees) than in open areas. The proportion of diapausing pupae decreased with increasing soil temperature and relative humidity. It is already known that low temperatures during the pupal stage (12-14 ℃) can induce prolonged pupal diapause in PPM (Démolin, 1974; Géri, 1980); the lowest soil temperature recorded during our experiment was of 14.1 ℃ which is close to this threshold value. We observed 5.1 ± 0.7 % of prolonged diapausing pupae, which is consistent with the 6.7 ± 1.6 % of prolonged diapausing pupae observed by Abgrall (2001) over three

years in different places of the same region (Aquitaine). In contrast, the effect of soil humidity on prolonged diapause has received little attention, as soil moisture is rarely considered as a cue for diapause induction (Tauber et al., 1998). Prolonged diapause may be viewed as an adaptation of insect species to escape unfavourable conditions in time (Tauber et al., 1986), or a strategy to avoid synchronizing the emergence of all individuals from the same population at the same time (Menu, 1993). However, diapause may also represent an increased risk of mortality for pupae as they stay longer in an immovable and defenceless stage.

Overall PPM overwintering pupae experienced higher survival in open areas than in pine stands, the habitat of larvae. Active habitat selection by arthropods to gain shelter for the winter is well documented for carabid and staphylinid beetles (Dennis et al., 1994; Magura et al., 2002; MacLeod et al., 2004; Purtauf et al., 2005; Geiger et al., 2009). Many species living in crop fields and hibernating as larvae are known to move to field margins or adjacent non-crop areas with a permanent vegetation cover. The main mechanism responsible for higher survival in these overwintering habitats is the occurrence of more suitable microclimatic conditions such as milder temperatures (Sotherton, 1985; Dennis et al., 1994) or lower temperature fluctuations (Desender ,1982; Thomas et al., 1992) in winter. In our study we could also relate the better survival of PPM pupae to higher temperatures in the soil of open areas. Arthropods that are able to disperse during the life cycle can benefit from the spatial distribution of contrasting abiotic conditions among different adjacent microhabitats. Landscape complementation is then important not only for the provision of different life stages with complementary diets but also with complementary abiotic conditions (Dunning et al., 1992). For example Weiss et al. (1988) showed that checkerspot butterfly populations would persist better in mosaics of habitats that are either cooler and benefit larval growth or warmer and benefit pupal survival. However, to our knowledge, our study is one of the first to report on complementation of microclimatic conditions in a forest insect herbivore.

However the outcome of multi-habitat use might be the opposite if PPM caterpillars would bury under broadleaved forest cover. Most maritime pine plantations have a closed canopy and so very few gaps where late PPM instar larvae could find suitable habitat for pupation. They are forced to migrate out of their larval habitat. At the period of procession, which occurs in late winter, neighbouring broadleaved forests or

hedgerows have no longer leaves in canopy trees. Caterpillars would be then mislead, burying in sun exposed areas within these stands. And yet, broadleaved forests proved to be unsuitable for pupae survival compared to open areas, notably because of colder temperatures in spring when the tree canopy closes again. In this case broadleaved habitats adjacent to pine stands may be considered as ecological traps for PPM populations. This ecological process has already been reported for few insect species of conservation value such as saproxylic beetles that colonize transient habitats such as tree logs (Hedin et al., 2008), or mayflies and dragonflies that lay eggs on inappropriate substrates like asphalt or waste oil because they mimic water by polarizing light horizontally (Horváth et al., 1998; Kriska et al., 1998). However further investigations are needed before to conclude about the role of broadleaved forests as ecological traps for PPM. In particular its remains to be demonstrated that different open and forest habitats are equally preferred by PPM caterpillars during the procession for burying (Robertson and Hutto 2006).

5 Conclusion

In a recent review Bianchi et al. (2006) suggested that natural pest control would be enhanced in more complex agricultural landscapes due to higher proportion of non-crop habitats providing suitable refuges for natural enemies. We previously observed that the presence of broadleaved hedgerows can impede PPM infestation in adjacent pine stands (Dulaurent et al. ***in press***). Here we suggest that neighbouring broadleaved habitat may also reduce PPM pupae survival while open areas would increase pupae survival. Depending on the suitability of adjacent habitats, heterogeneous forest landscapes may then either result in lower or higher PPM damage, i.e. associational resistance or susceptibility (Barbosa et al., 2009). These findings therefore indicate that landscape composition can be more important than heterogeneity ***per se*** for the effect on insect pest damage just as species composition is more important than species richness at the stand scale (Jactel and Brockerhoff, 2007).

6 Acknowledgments

We are grateful to Frédéric Lagane for his help to make X-rays measures at the GenoBois Facility of Pierroton (Cestas) and to Michel Sartore for providing a place for pupae observation. The authors thank Amélie Derouault, Marion Devaux, and Frédérique and Loïc Dulaurent for their technical support to empty the buckets. We would like to thank Bastien Castagneyrol, Ecki Brockerhoff and three anonymous reviewers for their helpful comments on earlier versions of the manuscript. Funding was provided by grants from the Agence Nationale de la Recherche (ANR 07 BDIV 013-07-URTICLIM).

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583

584 Figure legends

585

586 **Figure 1** Design of the split-plot experiment to test the effect of land cover types and
587 soil origins on the survival of pine processionary moth (PPM) (***Thaumetopoea***
588 ***pityocampa***) pupae. Forest cover was the main plot with three modalities (B:
589 Broadleaved cover, P: Pine cover, O: Open Area) and two replicates. Soil origin is
590 the sub-plot with three modalities (B: Broadleaved soil, P: Pine soil, O: Open Area
591 soil) and three replicates. In each plot, HOBO sensors were set up to measure soil
592 temperature and relative humidity

593

594 **Figure 2** Mean proportion of PPM pupae (%) (a) for the 3 classes of land cover and
595 soil from the a priori classification and (b) for the 2 classes of land cover and soil from
596 the a posteriori classification. (% E) Emerged pupae, (% D) Diapausing pupae and
597 (% M) total Mortality rates. B = Broadleaved trees, O = Open area, P = Pine trees.
598 Different letters in figure 2a indicate significant differences between classes with the
599 Tukey's test within each variable, different letters in figure 2b indicate significant
600 differences between classes with the Bonferroni's test (= 0.05)

601

602 **Figure 3** PCA of soil microclimatic variables. Projection of the sampling units
603 (buckets) on the factorial plane 1-2. Large symbols are placed at the centre of gravity
604 of position of all buckets from the same land cover type (a) or soil origin (b). B:
605 Broadleaved trees, P: Pine trees, O: Open area.
606 Correlations of the 10 variables of maximum soil temperatures on a fortnight basis
607 from April to August with PC1 were of 0.87, 0.85, 0.96, 0.85, 0.86, 0.88, 0.89, 0.93,
608 0.87 and 0.89, respectively. Correlations of the 5 variables of soil relative humidity on
609 a fortnight basis from April to June with PC2 were of 0.943, 0.951, 0.951, 0.953 and
610 0.966, respectively

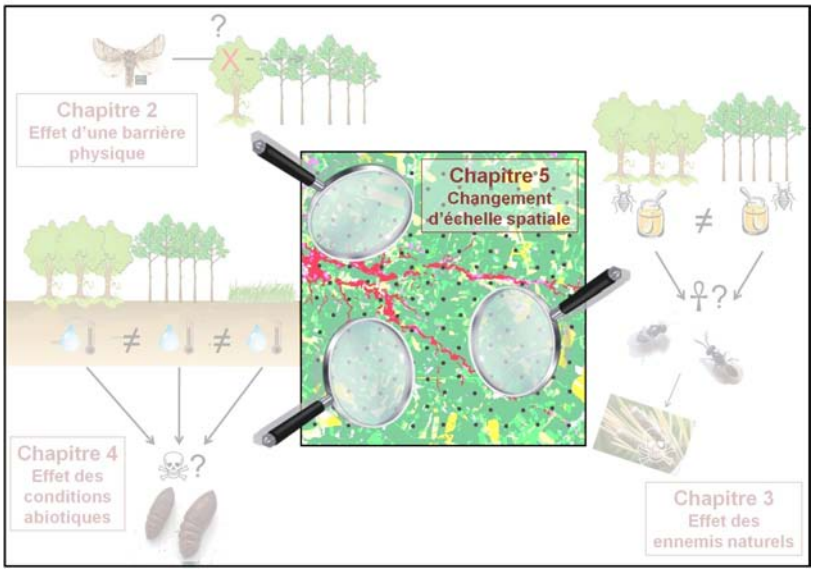
611

612 **Figure 4** Decision tree model for the classification of land cover types and soil origins
613 based on environmental variables. $T_s$max-$May_{1\text{-}15}$: maximum soil temperature during
614 the first 15 days of May (°C); RH_s-$April_{1\text{-}15}$: soil relative humidity during the first 15
615 days of April (%). External rings show the proportion of samples in each category at

616 the previous step. Purity indicates the proportion of buckets correctly classified.
617 $T_s$max-May$_{1\text{-}15}$ and RH_s-April$_{1\text{-}15}$ range over values indicated between brackets
618
619

CHAPITRE 5

Conifer insect herbivory decreases with percent broadleaved area of landscapes



Conifer insect herbivory decreases with percent broadleaved area of landscapes

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1 Introduction

Since the early seventies (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976), a large body of observational and experimental evidence has accumulated to support the view that damage caused by insect herbivores not only depend on intrinsic plant resistance but also on plant – plant interactions. In particular, depending on the number and identity of neighbouring plants, a focal plant may suffer less herbivory, i.e. associational resistance (Karban 2007, Barbosa et al. 2009). Two quantitative reviews of published studies recently provided support to this theory, showing that in agricultural crops (Tonhasca et al. 1994) and forest ecosystems (Jactel and Brockerhoff 2007), plant species growing in mixtures experience lower pest damage than in monocultures. However most of these studies were made at the stand scale, whereas insects have often flight dispersal capacities of several kilometres, and thus are able to migrate beyond stand boundaries. Moreover, plant species diversity is not restricted to a given area (alpha diversity) but may be also distributed among patches of different vegetation (gamma diversity, Whittaker 1972). The interactions between plants and their consequences for insect herbivore populations may then be also relevant at the landscape scale.

Two main hypotheses have been proposed to explain lower insect herbivory with increased plant diversity: the success of herbivores locating host plants is reduced when they are proportionally less frequent and/or hidden among non-host plants (the "resource concentration hypothesis", Root 1973); richer plant assemblages offer a larger array of complementary food or habitat resources that benefit natural enemies, thus increasing their ability to control herbivore populations (the "natural enemies hypothesis", Russell 1989). Similar mechanisms may well apply at the landscape scale. Landscapes, as mosaics of habitat patches, can be characterized by three main features: heterogeneity, which relate to the diversity of paches types; connectivity, which decreases with the mean distance between patches of a same type; and fragmentation, which increases with the number of patches per area (Fahrig 2003). Higher landscape heterogenity may result in lower resource concentration for insect

herbivores. Heterogenous landscapes would offer a lower number of habitat patches, smaller habitat patches due to higher fragmentation and lower connectivity between these patches thus reducing both the likelihood of finding habitat and of surviving within a single patch. Moreover landscape heterogenity would benefit natural enemies through habitat supplementation, i.e. the use of substitutable resources in nearby patches, or habitat complementation, i.e. the use of patches of different types to meet different needs such as reproduction or feeding (Dunning et al. 1992).

Several studies have already shown the positive effect of landscape heterogeneity on the infestation level of insect herbivores. For example, damage by the rape pollen beetle (***Meligethes aeneus***) were lower in stands surrounded by heterogeneous landscapes (Thies and Tscharntke 1999, Thies et al. 2003). Similar patterns were observed with the spruce budworm (***Choristoneura fumiferana***) which showed lower infestation in conifer stands within landscapes with high proportion of mixed broadleaved stands (Cappuccino et al. 1998, Mackinnon and MacLean 2003, Campbell et al. 2008). In a recent review of the literature, Bianchi et al. (2006) found that natural enemies populations were higher and herbivore damage lower in heterogeneous landscapes than in simple landscapes in 74 % and 45 % of the reviewed studies, respectively.

The pine processionary moth (PPM) ***Thaumetopoea pityocampa*** [Denis & Schiffermüller] (Lepidoptera, Notodontidae) is probably the most damaging defoliator of pines in southern Europe and north Africa (FAO 2010). In autumn and winter, PPM caterpillars feed on needles and remain congregated in silky nests they have spun to resist low temperatures. Pine trees can host several larval nests, each corresponding approximately to the egg mass laid by one female. These nests are easy to sight in tree crowns due to their size (ca. 0.10 to 0.25 m in diameter) and white colour. After pupation into the soil during spring, adult moths emerge in early summer and mate almost immediately in the understorey. Then, fecundated females search for an appropriate host pine to lay eggs, using both visual (Dulaurent et al., submitted A) and olfactory cues (Paiva et al. 2010). PPM is the most abundant pest insect in the Landes de Gascogne forest in south-west France (Abgrall and Bouhot 1990), the largest plantation forest in

Europe with nearly one million hectares of pure maritime pine (***Pinus pinaster*** [Aiton]) stands. Within this simplified forest landscape with ca. 90% of pure pine plantation, PPM develops cyclic outbreaks (Robinet 2006) that can affect several thousands of km² with more than 25% of defoliation, as in 1992, 2004 and 2010 (DSF Pauly, 2010). However within this plantation forest, broadleaved species like pedunculate oak (***Quercus robur*** [Linnaeus]), silver birch (***Betula pendula*** [Roth]), black alder (***Alnus glutinosa*** [Linnaeus]) and ***Salix*** spp. have persisted in riparian forests or as isolated patches of natural forest remnants.

This particular context therefore provided the opportunity to compare PPM infestation levels in pure pine stands within simple landscapes of pine monoculture vs. complex landscapes associating pine plantations and patches of broadleaved forest. In particular the objectives of our study were to test the hypothesis that PPM infestation level at stand scale decreases with the proportion of non-habitat in the surrounding landscape, and to estimate the threshold value of percent non-host habitat resulting in significant PPM reduction.

2 Materials and methods

2.1 Study site

In 2005, 145 maritime pine stands of the Landes de Gascogne forest, South-West of France, were selected on a systematic grid size of about 1.4 km (Fig. 1) around Pontenx-Les-Forges (44°14’ N, 00° 07’ O) covering a 16 x 16 km area (ca. 25 000 ha). An initial sampling grid was designed, and some sampling locations had to be slightly displaced when they were located in a patch of non-host (broadleaved) species. All sampled stands were then even-aged maritime pine (***Pinus pinaster*** Aït.) plantations with trees planted on 4 m distant rows. Stand height varied from 2 to 28 m, and stand age from 4 to 61 years. Mean tree Diameter at Breast Height (DBH) varied from 3.86 to 49.2cm. Tree density of each stand was estimated on the basis of relascopic estimates, and varied from 113 to 2500 trees per ha. The volume of the understorey was estimated in tons of dry matter per hectare (t.DM.ha^{-1}) by species type: fern, woody species and herbaceous species (see methods in Porté et al. 2009). Fern volume varied between 0

and 19.3 t.DM.ha^{-1}, woody species volume between 0.03 and 24.4 t.DM.ha^{-1}, and herbaceous species volume between 0 and 5.4 t.DM.ha^{-1}.

In each stand, PPM nests were counted on 80 trees into four plots. Three plots of 20 neighbouring trees were located within the stand and separated by a distance of 25 meters. The fourth plot was located at the closest edge of the stand and at a maximum distance of 200 meters from the others. The exposure of the edge was also noted. PPM population levels were estimated as nest density, i.e. mean number of nests per ha in the four plots.

2.2 Landscape mapping

Landscape description was based on a high-resolution and multispectral satellite image (SPOT 5 XS, 10m) covering the study area (© CNES, distribution Spot Image SA, 13 July 2005). Land cover of the study site was first categorized into eight main types: pine plantation, broadleaved riparian forest, broadleaved coppice, crop, clear cut, bare soil, urban area and water.

The landscape around each sampled stand was described using circular areas of different radius, hereafter referred to as buffers. As the minimum distance between two stands was 1.4 km, seven buffers were tested (100, 200, 300, 400, 500, 600 and 700 m) to avoid overlapping between buffers. The mean percent cover of water and urban cover types were, respectively, 0 and 0.16 % in the 700 m buffers, and therefore, these classes were ignored. Crops, clear cuts and bare soil types were grouped together as “open areas” (Fig. 1). Finally we retained four land cover types: two PPM habitat (pine plantations for PPM caterpillars and open-areas for PPM pupae) and two PPM non-habitats (broadleaved riparian forests and broadleaved coppices). The percentage cover of each type was calculated for each buffer size with GRASS and R.le softwares.

2.3 Statistical analyses

In a first step, the effect of 8 stand-scale variables (categorical variable: stand edge aspect; continuous variables: fern, herbaceous and woody volumes in understorey, tree age, height, DBH and density) on PPM nest density was tested on the 145 stands

sample. Because PPM nest density was not normally distributed, a Generalized Linear Model (GLM) was used with a log link function and a quasi-Poisson variance function (Kindt and Coe, 2005). We used a complete model to identify the significant explanatory variables (< 5%) and run a second model with the subset of significant variables in a backward selection approach.

In a second step, the landscape-scale variables (percentage cover of four land cover types) were entered in the model. Because the percentage covers of the four land cover types were not independent for a given buffer, and because the percentage covers for the same land cover type in different nested buffers were correlated, we made separate GLMs with the stand-scale variables retained in the first step of the analysis and only one landscape variable. We therefore compared the outcomes of 28 GLMs as we entered separately one landscape variable corresponding to one combination of 4 land cover types by 7 buffer sizes. GLM were performed using the software R (R Development Core Team 2008).

In order to quantify the independent effect of broadleaved riparian forests on PPM infestation, each stand with more than 5 % of this land cover type in the 700 m buffer (hereafter referred to as stand within heterogeneous landscape) was matched with a comparable control stand with less than 5 % of broadleaved riparian forest cover in the 700 m buffer (hereafter referred to as stand within pine monoculture). Additional variables were taken into account to match the paired stands: spatial proximity, edge aspect and fern volume. Paired stands were located at a distance of less than 3 km from each other, to take into account the aggregation pattern of PPM infestation that has been observed at a scale of several kilometres (Samalens 2009). To avoid edge aspect effects (Géri 1980) stands with a cold, northerly aspect were matched together, whereas stands with other, warmer aspects were considered all together. To test the effect of broadleaved trees independently from the fern volume in the understorey, a maximum difference in fern volume of 0.005 tons of dry matter per hectare was allowed between both stands of each pair. In total, we obtained 18 of such pairs of stands and Wilcoxon tests were used for pairwise comparison of PPM nest density between pine stands within

heterogeneous landscape vs. stands within pine monoculture. Three distinct tests were realized with pairs including a stand within heterogeneous landscape with more than 5% (n = 18), 10% (n = 10), or more than 15% (n = 6) of broadleaved riparian forest cover. Unilateral Wilcoxon tests were performed using Statistica Software 7.1 (StatSoft, France). A Bonferroni correction was applied to account for multiple comparisons (alpha = 0.05/3 = 0.017).

3 Results

The GLM models with stand-scale variables revealed a significant effect of edge aspect (explained deviance = 913.4, ***Pr*** (>F) = 0.025) and fern volume in the understorey (explained deviance = 554.4, ***Pr*** (>F) = 0.017) on PPM nest density (total deviance = 14439). PPM nest density was lower in north-exposed stands (79 ± 12 nests/ha) than in south, east or west exposed stands (126 ± 22 nests/ha). PPM nests density was negatively correlated with the fern volume in the understorey. It appeared that high volume of fern resulted in lower and less variable PPM nests density (Fig.2) thus suggesting that the presence of fern was a limiting factor for PPM infestation.

Edge aspect and fern volume were then entered in new GLM models with one landscape composition variable. The percent area of pine plantations (***Pr*** (>F) varied from 0.99 in 100m buffers to 0.48 in 700m buffers), broadleaved coppices (***Pr*** (>F) from 0.37 to 0.17) and open areas (***Pr*** (>F) from 0.71 to 0.32) had no significant effects on PPM nests density, whatever the buffer size considered. On the contrary, the effect of the percent area of broadleaved riparian forest on PPM nest density was consistently significant for buffers with radius larger than 300 m (Fig.3). The percentage of explained deviance by the percent area of broadleaved riparian forest increased (from 10 to 15%) with the size of the buffer (Fig.3), whereas the deviance explained by the two stand-scale variables was of similar magnitude (10.1% in total, 6.3% for edge aspect and 3.8% for fern volume). High proportion of broadleaved riparian forest in the surrounding landscape resulted in lower and less variable PPM nests density (Fig. 4) indicating that the presence of non-host habitat was a limiting factor for PPM infestation.

We used the percent area of broadleaved riparian forest in 700 m buffers to search for a threshold value beyond which PPM nest density was significantly lower in stands within heterogeneous landscape than within pine monocultures. PPM nest density was significantly lower (***P*** = 0. 015) in stands within heterogeneous landscape including more than 15 % of broadleaved riparian forest than within pine monoculture landscapes. The difference in nest density was marginally significant in landscapes with more than 10% (***P*** = 0.08) and non significant in landscapes with more than 5% (***P*** = 0.48) of riparian forest. The presence of more than 15% of broadleaved riparian forests in surrounding landscapes resulted in a reduction of ca. 90 nests/ha in pine stands (Fig.5) which represented on average 60% less than in similar stands located within pine monocultures.

4 Discussion

In our study, we observed a significant decrease in PPM infestation at the stand scale with the proportion of non-host habitat, i.e. broadleaved riparian forest, in the surrounding landscape. This result is in accordance with the conclusions of a recent study on the effect of landscape composition on PPM distribution at a large scale (16 × 16 km area), which detected a significant negative effect of riparian forests on PPM nests distribution (Samalens and Rossi 2010). These outcomes are also consistent with the negative effect of hardwood content of surrounding forest landscapes on the infestations of another conifer defoliator, ***C. fumiferana***, in balsam fir stands (Cappuccino et al. 1998, Mackinnon and MacLean 2003, Campbell et al. 2008).

Two main ecological hypotheses have been proposed to explain the effect of plant diversity on insect herbivory: the reduction in host resource concentration (Kareiva1983) and the enhancement of natural enemies (Root 1973). The presence of patches of non-host plants in a given area results in a proportional decrease in the proportion of host plant which may in reduce herbivore abundance (Kareiva 1983). However in our study, the proportion of pine in surrounding landscapes had no effect on the PPM infestation in sampled pine stands, which suggested that host tree concentration was not a significant driver of local PPM abundance. We did not find either any effect of the proportion of

222 open areas in surrounding landscapes. When caterpillars search for a place to pupate,
223 open areas appear to be the optimum habitat for burying into the soil (Démolin 1971). It
224 is then assumed that PPM populations may benefit from the complementation of habitats
225 which results from the close proximity of pine stands for feeding the larvae and open
226 areas for sheltering the pupae (Dulaurent et al., submitted B). However we were not able
227 to test this hypothesis in our study because PPM caterpillars crawling distance (few
228 meters) is shorter than the minimum radius (100m) of buffers used to characterize
229 landscape composition.
230 The presence of non-host trees can decrease forest insect herbivory by creating barriers
231 to host colonisation. At the stand scale, mixed forests can disrupt the visual or/and
232 olfactory signals sent by host tree species (Jactel et al. 2005). For example, it has been
233 shown for two processionary moths, ***Ochrogaster lunifer*** (Floater and Zalucki 2000) and
234 ***T. pityocampa*** (Dulaurent et al., submitted A) that host trees hidden behind non-host
235 trees are less infested, probably because their silhouette is less apparent. In the same
236 manner, Jactel et al. (2010) observed that non-host volatiles released by broadleaved
237 trees could reduce PPM infestation in pine stands. However, these physical and
238 semiochemical cues are known to affect host location behaviour at short scale. It is
239 therefore unlikely that their effect could be perceived at distance as far 700m.
240 Thus, the predominant ecological hypothesis explaining the negative impact of riparian
241 broadleaved patches on PPM infestation levels is most probably the effect of natural
242 enemies. It has been already shown that the rates of parasitism in insect herbivores such
243 as the maize armyworm ***Pseudaletia unipuncta*** (Marino and Landis 1996), or the rape
244 pollen beetle ***Meligethes aeneus*** (Thies and Tscharntke 1999), were higher in complex
245 landscapes than in simple landscapes such as crop monocultures. In the heterogeneous
246 forest landscapes of our study, predators and parasitoids would benefit from the
247 presence of broadleaved forests because the latter can supply shelter or complementary
248 food resources such as alternative prey or sugar-rich diet like pollen, nectar or aphid
249 honeydew (Root 1973). Barbaro et al. (2008) demonstrated that the predation rates by a
250 major PPM pupae predator, the hoopoe ***Upupa Epops*** (Battisti et al. 2000), were higher
251 in stands close to broadleaved woodlands, where hoopoes can nest. Dulaurent et al.
252 (2010) also revealed that the specialist parasitoid of PPM eggs, ***Baryscapus servadeii***,

had a longer lifespan when fed with honeydew produced by aphids living on oak trees. The effect of broadleaved riparian forest was significant in buffer of 700m radius, a flight distance which is easily covered by insectivorous birds or insect parasitoids. Moreover the increasing part of deviance in GLM models explained by the proportion of broadleaved forest with increasing buffer radius may be interpreted as the higher likelihood of encompassing new broadleaved patches, i.e. additional refuges for natural enemies. No effect of broadleaved coppices was detected in our study, probably because patches of this habitat were too young or too small to harbour a large amount or variety of natural enemies (4-5 meters height, data not shown). In the contrary, riparian forests are more permanent and less fragmented structures, composed of higher and older trees which are more likely to present resources or microhabitats favourable to predators.

Two stand-scale variables were shown as significant drivers of PPM density. First, stands with northerly aspect were less infested. As poikilothermic organisms living in winter, PPM caterpillars are already known to prefer spinning their nests on the sunny exposed part of pine crowns in order to absorb a maximum of warmth and to better resist low temperatures (Géri 1980, Hoch et al. 2009). Second, the absence of fern in the understorey resulted in higher PPM nests density. This result may originate in the mortality factors of PPM pupae, which are particularly sensitive to the soil microclimatic conditions (Markalas 1989). Recently Dulaurent et al. (submitted B) showed that pupae survival was higher in warm and moderately humid soils. High fern cover may reduce ground insulation and then soil temperature. Moreover, in the Landes de Gascogne forest, ferns are more abundant in mesic moorlands (Porté et al. 2009) where soil conditions are dryer and then less favourable to PPM pupae.

In this study, we demonstrated that PPM infestations would be 60% lower in pure pine stands within highly heterogeneous landscapes than within pine monoculture landscapes. This reduction was observed above a threshold of 15 % of broadleaved forest in a buffer of 700m radius which is equivalent to ca 20 ha of broadleaves per 150 ha of forest landscape. This estimate provides the first quantitative response to the “how

much is enough" question when it comes to design landscapes that minimize pest problems. However this is just the first step of cost-benefit analysis. Further multidisciplinary studies are needed to balance the wood production loss due to replacement of pine plantations by broadleaved woodlands with the benefit of these natural forests for ecosystem services such as pest regulation and biodiversity conservation.

6 Acknowledgments

We are grateful to Michel Goulard for his help with the GLM method and to Fabrice Vétillard, Pierre Menassieu and Thomas Compagnon for their technical assistance. This work was conducted in the framework of the European programme "Forest Focus" and the project titled "NetForPest: New ways to improve the efficiency of monitoring networks to assess the sanitary condition of Europoean forests" coordinated by Dominique Piou. Supplementary fundings were provided by grants from the Agence Nationale de la Recherche (ANR 07 BDIV 013-07-URTICLIM coordinated by Alain Roques). We also want to thank the CNES and the ISIS program for allowing access to high resolution data.

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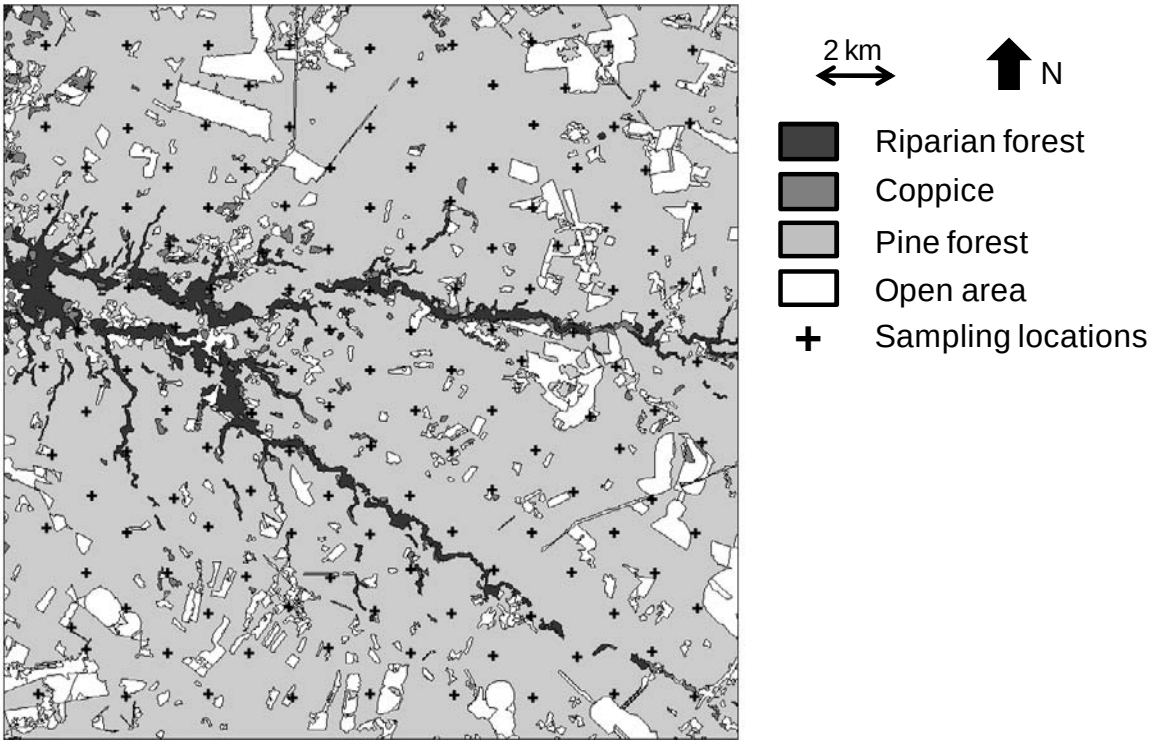

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410 **Figure 1.** Satellite-based map of the study site.

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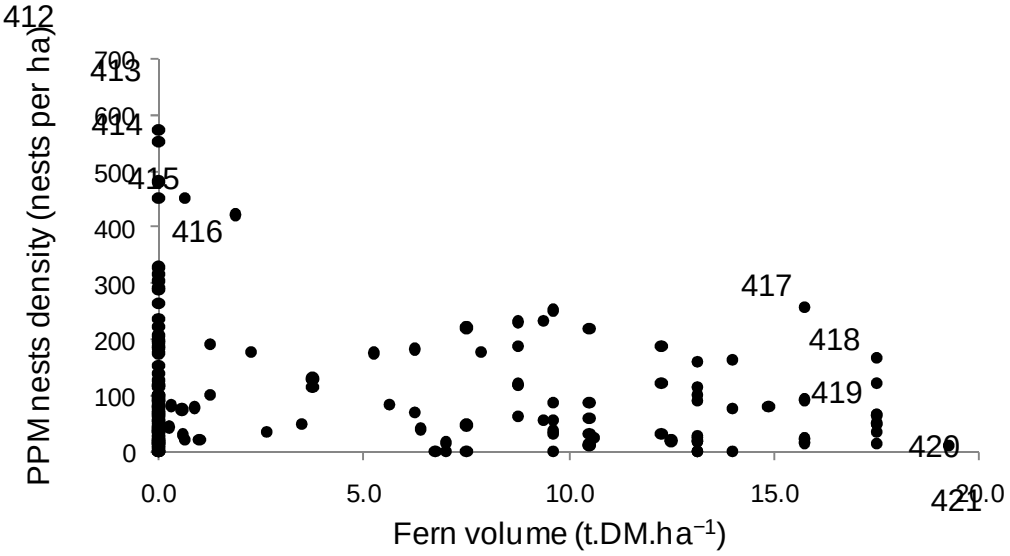

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424 **Figure 2.** Effect of fern volume (t.DM.ha^{-1}) in pine stand understorey on PPM nest
425 density (nests per ha).

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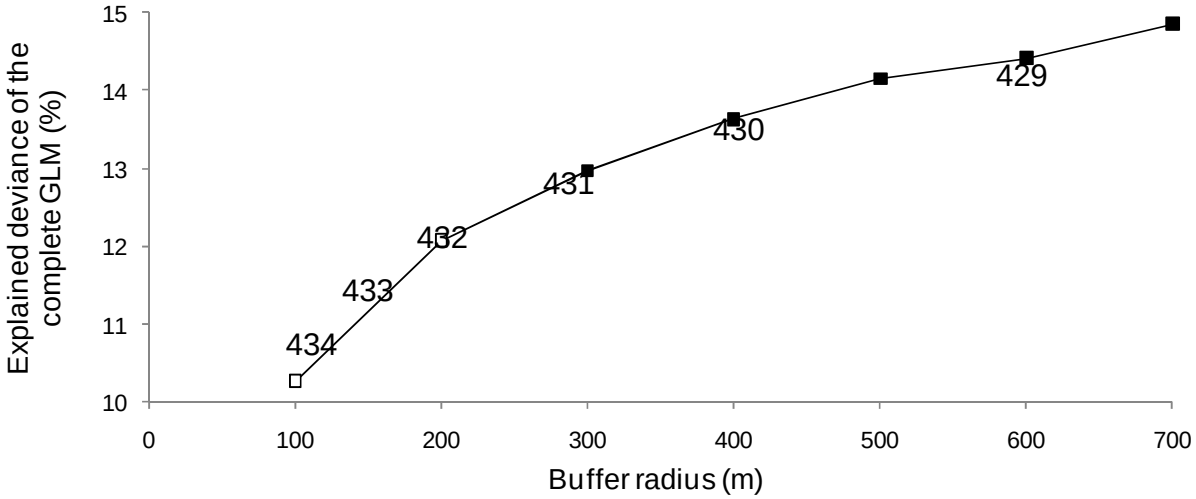

Figure 3. Proportion of explained deviance in complete GLM models constructed with stand edge aspect, fern volume in the understorey and proportion of broadleaved riparian forest in the surrounding landscape as explanatory variables, at seven spatial scales.

Black symbols represent a significant effect of the proportion of broadleaved forest, and open symbols a non significant effect.

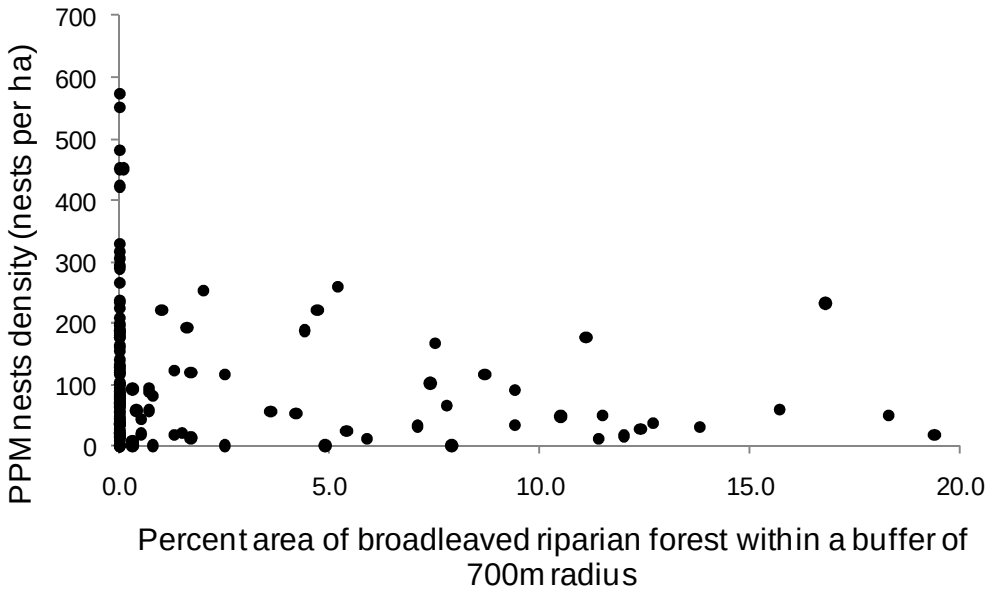

Figure 4. Effect of percent area (in 700m buffers) of broadleaved riparian forest in surrounding landscape on PPM nest density (nests per ha) in central pine stands

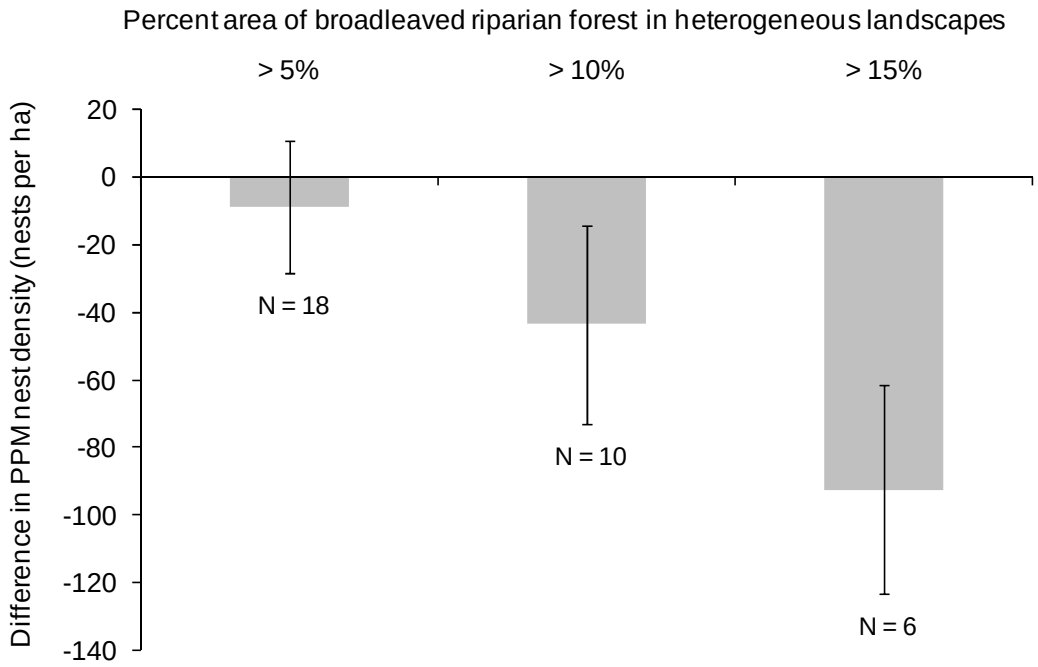

Figure 5. Mean difference in PPM nest density between pine stands within heterogeneous landscape and paired stands within pine monocultures, for different samples of stands corresponding to increasing percent of broadleaved forests in heterogeneous landscapes.

CHAPITRE 6

Discussion générale

A partir des résultats des études précédentes et des discussions qu'elles ont suscitées, cette discussion générale vise à répondre aux objectifs initiaux de ce travail, à savoir (i) estimer l'effet de la diversité des essences forestières sur les niveaux de population de la processionnaire du pin, ensuite (ii) proposer des mécanismes écologiques pouvant expliquer, aussi bien à l'échelle locale que paysagère, cet effet de la biodiversité. Ce chapitre présente donc dans un premier temps un bilan des résultats de ce travail doctoral, puis développe une réflexion sur les possibilités de transfert vers la gestion forestière de la forêt des Landes de Gascogne, et se conclut par l'énoncé de perspectives en termes de recherche scientifique.

1. Bilan des effets de la diversité des essences forestières sur les niveaux d'infestation de la processionnaire du pin, dans le massif des Landes de Gascogne

Nos études ont clairement mis en évidence que la diversité des essences forestières pouvait permettre de diminuer les niveaux d'infestation de la processionnaire du pin dans certaines conditions. En effet, la présence d'une haie de feuillus en bordure d'un peuplement de pin maritime permet de réduire significativement le nombre de nids de processionnaire (chapitre 2, Figure 1). De même, à l'échelle du paysage, nous avons montré que la présence d'une ripisylve de feuillus dans un rayon de 700 mètres autour d'une parcelle de pin maritime s'accompagne d'une diminution des niveaux de population de la processionnaire (chapitre 5, Figure 1). Ces résultats confirment ceux de Géri (1980) qui a observé, dans la vallée du Niolo en Corse, moins d'attaques de processionnaire dans les peuplements de pin noir mélangés avec une essence non-hôte (hêtre, bouleau ou sapin) que les peuplements purs (chapitre 6, Figure 1). A ces trois échelles on note une relation positive entre la proportion d'essences non hôtes et l'ampleur de la réduction des infestations de processionnaire du pin (chapitre 6, Figure 1).

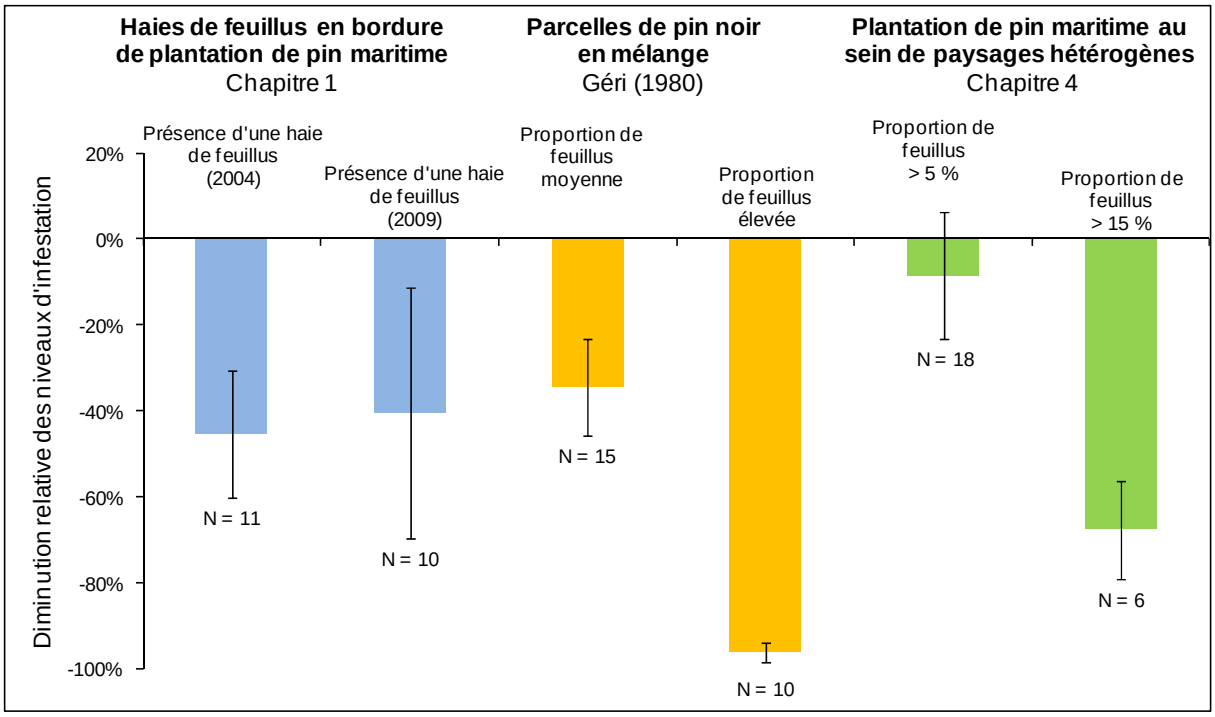

Figure 7 : Bilan des effets de la présence d'essences feuillues sur les niveaux d'infestation de la processionnaire du pin, à différentes échelles spatiales. L'axe des X correspond aux différentes études disponibles. L'axe des Y correspond à la réduction relative des niveaux d'infestation par rapport à un témoin pur, calculée sous forme d'écart standardisé (voir la méthode de calcul du log-ratio dans Borenstein et al. 2009)

D'autre part, nous avons mis en évidence que les essences feuillues sont à l'origine d'une modification des conditions microclimatiques du sol (plus froides et plus sèches), qui sont moins favorable à la survie des chrysalides de processionnaire que les milieux ouverts (chapitre 4) Elles permettent aussi de favoriser les parasitoïdes des œufs de processionnaire en leur fournissant une alimentation complémentaire qui améliore leur longévité (chapitre 3). Il est probable que ces mécanismes induiraient une diminution des niveaux de population de la processionnaire, soit en augmentant la mortalité des chrysalides, soit en augmentant le taux de parasitisme des œufs mais nous n'avons pas pu vérifier cette hypothèse.

2. Mécanismes expliquant la relation entre diversité des essences forestières et résistance des forêts à la processionnaire du pin

2.1. Limitation de l'accès à la ressource pour l'insecte

L'accès à la ressource est dépendant de la détection de l'arbre hôte par la femelle de la processionnaire du pin, lors de sa recherche d'un site d'oviposition. Cette détection peut être limitée par une réduction de la disponibilité en arbres hôtes et/ou entravée par différents types de barrières physico-chimiques, à l'échelle locale comme à l'échelle du paysage.

Concernant l'effet de la disponibilité (quantité et concentration) de la ressource, les résultats du chapitre 5 montrent que les niveaux d'infestation par la processionnaire sont significativement plus élevés dans les plantations de pin entourées de monocultures de pin que dans celles qui se trouvent au centre d'une mosaïque plus hétérogène, c'est-à-dire comprenant également des boisements de feuillus (ex. ripisylve). Cependant, le fait que l'abondance locale de processionnaire ne soit pas corrélée au pourcentage de pins dans le paysage environnant, suggère que l'effet de ***barrière quantitative*** ne serait pas prépondérant pour limiter les niveaux de population de la processionnaire dans la zone d'étude. Cela pourrait s'expliquer par la faible variabilité des proportions de pins observée dans les paysages étudiés (80 ± 15 %), qui restent fortes même dans les plus hétérogènes d'entre eux. Ainsi, dans un grand massif forestier dominé par l'essence hôte (environ 80 % de pin maritime hors coupes rases, IFN 2005) tel que celui de,la forêt des Landes, la ressource disponible pour la processionnaire n'est probablement jamais un facteur limitant.

Les résultats du chapitre 2 mettent en évidence que la présence d'une haie de feuillus, de même hauteur ou plus haute que les pins, diminue significativement les niveaux d'infestation de la processionnaire dans les parcelles situées derrière la haie. Il est probable que les femelles de processionnaire soient perturbées par cette ***barrière physique*** lors de leur recherche d'un site d'oviposition. En effet, elles sont connues pour reconnaître leur hôte d'après sa silhouette (processionnaire du pin, Démolin 1969 ; processionnaire de l'acacia ***Ochrogaster lunifer***, Floater and Zalucki 2000). Les feuillus présentant un houppier très différent de celui des pins, leur présence pourrait perturber la reconnaissance par la processionnaire des signaux visuels (forme ou couleurs) émis par l'arbre hôte situé derrière la haie.

A l'échelle du paysage, la présence de ripisylves pourrait également jouer un rôle naturel de barrière physique à la dispersion. En effet, ces formations boisées s'organisent de façon linéaire le long des cours d'eau, et à proximité directe des parcelles de pin. Ainsi, le paysage que nous avons étudié dans le chapitre 5 est coupé par deux ripisylves de plus de 20 km de long. Cette double barrière pourrait perturber le comportement de dispersion des femelles de processionnaire dans la zone intermédiaire de forêt, et ainsi expliquer pourquoi les niveaux de population de la processionnaire y sont significativement plus faibles (Samalens 2009).

L'effet des ***barrières chimiques*** à la reconnaissance olfactive de l'hôte par les adultes de processionnaire n'a pas été explicitement testé dans nos travaux. Dans le chapitre 2 sur l'effet des haies de feuillus, aucune différence de niveau d'infestation n'a été détectée entre les pins situés à proximité ou loin des feuillus (sur la partie non cachée visuellement par la haie), suggérant l'absence de composés répulsifs émis par les feuillus. Cependant, le dispositif expérimental avait pour objectif principal de tester l'existence d'une barrière physique à la détection de l'hôte par les femelles de processionnaire. Aussi, la gamme d'essences forestières composant la haie, ou encore la variation de volume de haie, n'étaient probablement pas suffisamment larges pour vérifier efficacement l'hypothèse d'une barrière chimique à la reconnaissance de l'hôte. En effet, une étude de Jactel et al. (2010) a récemment démontré l'existence et l'efficacité de ce type de mécanisme pour limiter les niveaux d'infestation de la processionnaire. Dans cette expérience, la présence de branches

fraîchement coupées de bouleau au pied de pins a conduit à une réduction du nombre de nids de processionnaire dans leur houppier. De même la présence de fragments de branches ou de feuilles de bouleau a diminué significativement le taux de capture de mâles de la processionnaire dans des pièges à phéromone. Ceci laisse à penser que l'attraction des mâles de processionnaire par la phéromone sexuelle produite par les femelles est perturbée par la présence d'odeurs émises par des essences non hôte.

2.2. Renforcement du contrôle par les ennemis naturels

Les ennemis naturels peuvent avoir un effet à tous les stades du cycle de développement de la processionnaire. Certains de ces ennemis naturels semblent favorisés par la présence d'essences feuillues qui peuvent leur fournir une alimentation complémentaire ou un abri.

Ainsi, nous avons démontré dans le chapitre 3 que le miellat produit par les pucerons de chêne permet aux principaux Hyménoptères parasitoïdes des œufs de processionnaire de prolonger leur durée de vie. Cela peut être d'un intérêt vital, notamment pour l'ooparasitoïde généraliste de la processionnaire, ***Ooencyrtus pityocampae***, dont l'émergence précède de deux mois celle des adultes de processionnaire (Masutti 1964). En l'absence d'hôte à parasiter, la présence d'une alimentation riche en sucre dans le milieu représente donc un atout pour la survie des populations de parasitoïdes jusqu'aux premières pontes de processionnaire. Pour l'ooparasitoïde spécialiste de la processionnaire, ***Baryscapus servadeii***, une meilleure longévité peut permettre d'allonger la durée de prospection du milieu à la recherche d'hôte disponible. D'autre part, les ooparasitoïdes de la processionnaire sont synovigéniques (Battisti et al. 1990, communication personnelle): les femelles disposent dès leur émergence d'un stock d'œufs matures disponibles pour la ponte, mais la maturation des œufs se poursuit ensuite pendant toute la durée de vie, et elle est favorisée par la consommation de sucre (Wäckers 2003). Il est donc également probable que la présence d'une alimentation complémentaire riche en sucre permettrait aux ooparasitoïdes de la processionnaire de produire davantage d'œufs durant de plus longues périodes et donc de parasiter davantage d'hôtes. Ces effets positifs, pour la fitness des parasitoïdes, de la ressource trophique liée aux arbres feuillus permettrait donc, ***in fine***, un contrôle plus efficace des populations de processionnaire. Il serait d'ailleurs intéressant de tester l'efficacité d'une alimentation à base de miellat de pucerons sur le développement de ***Phryxe caudata*** et ***Villa brunnea***, principaux Diptères parasitoïdes des chenilles et des chrysalides de processionnaire.

Lorsque les feuillus sont suffisamment âgés pour présenter des cavités, ils représentent aussi une ressource essentielle pour la nidification des oiseaux cavernicoles. Ainsi, Barbaro et al. (2008) ont mis en évidence l'importance des îlots et des haies de feuillus jouxtant des milieux ouverts herbacés ras pour la huppe fasciée ***Upupa epops***, un des principaux prédateurs des chenilles et chrysalides de processionnaire. L'occupation d'un îlot feuillu par la huppe peut ainsi résulter en un fort taux de prédation sur les chrysalides de processionnaire enfouies dans les lisières adjacentes (Battisti et al. 2000). D'autres espèces d'oiseaux, telles que les coucous ***Cuculus canorus*** et les mésanges ***Parus*** spp., peuvent également se nourrir

de chenilles de processionnaire directement dans les nids d'hiver (Gonzalez-Cano 1981) ou sur le sol (Barbaro and Battisti 2010). La présence d'îlots forestiers permanents tels que les îlots de feuillus présents dans les Landes peut favoriser localement leur présence et donc leur impact potentiel sur les populations de chenilles de processionnaire (Barbaro and Battisti 2010). Les îlots feuillus peuvent également abriter d'autres espèces d'insectes phytophages, notamment des Lépidoptères géométrides ou tordeuses, dont les chenilles représentent une ressource essentielle pour les prédateurs généralistes comme les passereaux forestiers durant la période de reproduction (Giffard et al., submitted). Ainsi, il est important de tenir compte de la « qualité » des feuillus, qui n'est pas toujours la même au sein de la forêt des Landes, comme habitat potentiel pour certains ennemis naturels de la processionnaire du pin (chapitre 5). En effet, nous avons observé que les taillis de jeunes feuillus n'avaient aucun effet sur les niveaux de population de processionnaire dans les parcelles de pin environnantes. Cela pourrait être dû au fait qu'ils n'offrent pas une structure favorable à la nidification. En revanche, les ripisylves et les îlots de feuillus offrent une structure haute composée d'arbres plus âgés, et probablement plus propices à la nidification des oiseaux insectivores.

2.3. Modification des conditions abiotiques

L'expérimentation sur l'enfouissement des chenilles de processionnaire (chapitre 4) a montré que le type de couvert forestier a un effet important sur les conditions microclimatiques du sol. Ainsi, les sols de milieux ouverts sont en moyenne plus chauds et plus humides que les sols sous couvert de pins ou de feuillus. Ces conditions abiotiques semblent plus favorables à la survie des chrysalides de processionnaire. Cet effet de la température est en accord avec l'observation que les chenilles, lors de la procession de nymphose, recherchent les zones les plus ensoleillées pour s'enfouir (Démolin 1971). Ce phénomène de changement d'habitat en cours de cycle représente l'un des premiers cas de complémentation de ressource décrit pour un insecte herbivore ravageur. À l'échelle du paysage, nous n'avons pas pu déceler d'effet de la proportion de milieu ouvert sur le niveau local de processionnaire du pin (chapitre 5). Cela peut s'expliquer par le fait que les chenilles de processionnaire ne processionnent que sur une distance maximum de quelques dizaines de mètres avant de s'enfouir. Or les pistes séparant les parcelles, qui représentent une zone ensoleillée particulièrement favorable à l'enfouissement des chenilles, n'ont pas été prises en compte dans les types d'occupation du sol étudiés à l'échelle du paysage. L'effet de la proportion de milieu ouvert n'est donc probablement détectable qu'à une échelle inférieure à 100 mètres, qui représente la taille de buffer minimum utilisée dans notre étude. Il serait donc intéressant d'envisager une nouvelle expérimentation à l'échelle locale, afin de comparer les niveaux d'infestation dans des parcelles plus ou moins entourées de milieux ouverts favorables à l'enfouissement des processionnaires. Ainsi, un dispositif basé sur des comparaisons appariées (présence / absence de milieu ouvert en bordure de plantation) pourrait être proposé, en considérant également un gradient de largeur de milieu ouvert (ex. pare-feu ou bord de piste) en contact direct avec les parcelles étudiées.

D'autre part, la présence de feuillus à proximité directe des pins semble représenter un piège écologique pour les chenilles de processionnaire. En effet,

lorsqu'elles processionnent pour trouver un site favorable à leur enfouissement, elles sortent de la parcelle de pin pour s'enfouir dans une zone plus chaude et plus ensoleillée. Elles peuvent ainsi être trompées par l'absence de feuilles dans les boisements ou haies de feuillus au moment de l'enfouissement (février-mars) et se chrysalider dans ces habitats feuillus. Les chrysalides sont alors soumises aux conditions rendues plus défavorables par la mise en place des feuilles, induisant une diminution de l'ensoleillement au sol et donc un refroidissement préjudiciable à leur survie. Ce phénomène correspondrait au premier exemple décrit de piège écologique chez un insecte herbivore, d'après le troisième scénario (« equal preference trap » : les individus sont attirés dans un habitat particulier sur la base de stimuli qui ne rendent pas compte de la mauvaise qualité de cet habitat pour la survie) proposé par Robertson et Hutto (2006). Pour valider cette hypothèse il serait par ailleurs intéressant de mieux estimer la probabilité que les chenilles de processionnaire viennent à s'enfouir dans les habitats de feuillus en fonction de leur distribution à l'échelle du paysage.

En associant expérimentations et observations de terrain à différentes échelles spatiales et à plusieurs étapes du cycle de développement de la processionnaire (chapitre 2 à 5), nous avons donc mis en évidence plusieurs effets de la diversité des essences forestières contribuant à diminuer les niveaux de population de la processionnaire dans les peuplements de pin. Ces effets touchent l'ensemble des stades de développement de la processionnaire du pin. Les adultes femelles représentent le stade qui sélectionne l'arbre hôte via le choix du site d'oviposition. Ce comportement semble être perturbé par les stimuli physiques et sémiochimiques délivrés par les essences non hôtes. Les stades œuf et chenille apparaissent comme particulièrement sensibles aux ennemis naturels (parasitoïdes, oiseaux) favorisés par les boisements de feuillus. Enfin, les chrysalides semblent sensibles aux conditions microclimatiques du sol sous couvert feuillu (température, humidité). L'ensemble de ces résultats représente donc une contribution originale à l'analyse des mécanismes expliquant les effets de la biodiversité sur la diminution de l'impact des insectes herbivores. D'autre part, ce travail offre les bases d'une nouvelle approche écologique pour la gestion des populations de la processionnaire du pin, basée sur l'augmentation de la diversité des essences forestières dans les plantations de pin.

3. Implications pour la gestion de la forêt des Landes de Gascogne

Les résultats apportés lors de ce travail doctoral permettent de tirer plusieurs conclusions utiles aux gestionnaires forestiers pour limiter les niveaux d'infestation de la processionnaire du pin.

A l'échelle du paysage, nous avons mis en évidence que les feuillus permettent de réduire d'environ 30 % les niveaux de population de la processionnaire dans une parcelle située au cœur d'une mosaïque composée de 15 % de feuillus dans un cercle de 700 mètres de rayon. Cela représente environ 25 ha de feuillus pour 125 ha de forêt de pin. A l'extrême, nous avons pu observer une

réduction allant jusqu'à 90 % des densités de population de processionnaire lorsque les feuillus étaient majoritaires (environ 60%) dans le paysage environnant une parcelle. Une modification des essences de boisement dans de telles proportions semble difficilement réalisable à l'échelle du massif des Landes, pour des raisons de rentabilité économique. Mais certaines zones moins favorables à la croissance du pin maritime, trop sèches, trop humides ou infectées par les pourridiés racinaires (fomes et armillaire) pourraient être plus facilement converties en mosaïques hétérogènes à forte composante feuillue.

Une solution alternative pour bénéficier de la protection induite par la présence de feuillus est la constitution de haies en bordure de plantations de pin. La présence d'une haie de feuillus plus haute que les pins permet en effet de diminuer de l'ordre de 60 % les infestations de processionnaire dans la parcelle située derrière elle. D'autre part, la présence de feuillus en contact direct avec des pins pourrait représenter un piège pour les chenilles qui, une fois chrysalidées, subissent un taux de mortalité plus élevé que sous milieu ouvert (l'habitat qu'elles recherchent lors de la procession de nymphose). Cependant, cet effet des feuillus a été observé dans des zones plus larges que des haies. Il faudrait donc vérifier que sous une haie de feuillus, les conditions microclimatiques du sol sont les mêmes que sous un îlot de feuillus, et qu'elles ont donc le même impact négatif sur le développement nymphal des processionnaires. Enfin, nous avons démontré que le miellat de puceron de chênes était particulièrement favorable aux parasitoïdes des œufs de processionnaire. Une haie comprenant quelques chênes abriterait probablement assez de pucerons pour produire la quantité de miellat nécessaire à l'alimentation de nombreux parasitoïdes d'œufs. Comme les infestations de processionnaire sont concentrées en lisière de peuplement (70 % des nids en lisière), cela signifie que la plupart des masses d'œufs seraient proches de la haie et donc facilement accessible pour les ennemis naturels qu'elle abrite. Ainsi, il semble prometteur d'utiliser les haies de feuillus comme un nouveau moyen de favoriser la lutte biologique naturelle contre la processionnaire. Au moment de la mise en place d'une parcelle de pin (par semis ou plantation), il conviendrait donc de remplacer les deux ou trois premières lignes de pin sur la lisière la plus exposée aux attaques de processionnaire par une plantation en ligne de feuillus à croissance rapide (ex. bouleau) en mélange avec des feuillus facilitant à plus long terme la présence de cavités pour l'installation des oiseaux et fournissant une alimentation aux parasitoïdes (ex. chêne).

4. Perspectives de recherche

4.1. Changement d'échelle temporelle

De nombreux Lépidoptères présentent des niveaux de populations cycliques comprenant des phases de pullulation alternant avec des périodes durant lesquelles les niveaux de populations sont plus faibles. Différentes hypothèses ont été proposées pour expliquer ce phénomène (Berryman 1996). Ainsi, la qualité du feuillage après une forte défoliation pourrait diminuer en raison de la mise en œuvre de mécanismes de défense induits par la plante hôte (Herms et Mattson 1992). Cette baisse de qualité alimentaire pourrait entraîner une plus forte mortalité des chenilles l'année suivante et ainsi contribuer à une diminution du niveau total de population, jusqu'à un retour à l'état initial de qualité du feuillage et une nouvelle augmentation

des niveaux d'infestation. D'autre part, les ennemis naturels pourraient également expliquer cette cyclicité (Bjørnstad et al. 2002). Plus particulièrement, les parasitoïdes Hyménoptères ou Diptères, dont la dynamique des populations est dépendante de la densité d'hôtes, pourraient induire une mortalité élevée dans les populations d'herbivores en phase de gradation, déclenchant la phase de diminution de leur cycle épidémique. La gradation suivante interviendrait lorsque les parasitoïdes, se trouvant eux-mêmes en manque d'hôte, subiraient une plus forte mortalité.

A l'échelle du paysage, l'effet de la structure des forêts sur la durée des pullulations d'insectes herbivores a déjà été étudié, notamment sur la livrée des forêts ***Malacosoma disstria***. En particulier, Roland (1993) a démontré un effet positif de la fragmentation du paysage sur la durée des pullulations de cet insecte dans les monocultures de peuplier ***Populus*** spp. La présence de zones d'habitat défavorable pourrait rendre la ressource en arbres hôtes moins accessible et ainsi augmenter la compétition intraspécifique pour les insectes herbivores (Dalin et al. 2009). Par ailleurs l'hétérogénéité du paysage pourrait favoriser la dynamique des populations de parasitoïdes par des mécanismes de supplémentation ou de complémentation de ressources (Menalled et al. 2003).

Ainsi, la diversité des paysages pourrait permettre de limiter l'intensité et la durée des phases de pullulations des Lépidoptères ravageurs (Roland et al. 1998). Dalin et al. (2009) ont récemment démontré de façon empirique que le risque de pullulation de ***Phratora vulgatissima*** (Chrysomelidae) était plus fort dans les monocultures de saule ***Salix viminalis*** que dans les peuplements naturels de ***Salix cinerea*** et que les populations de ce ravageur étaient moins stables (soumis à de plus grandes variations démographiques) dans les peuplements purs.

La processionnaire du pin, qui présente des niveaux de population cycliques dans la forêt des Landes, pourrait représenter un modèle d'étude intéressant pour tester cette hypothèse. Les niveaux de population de la processionnaire ont été observés dans de nombreuses régions de France présentant des paysages plus ou moins hétérogènes, et ce depuis de nombreuses années. Il serait intéressant d'étudier les relations entre les variations démographiques de la processionnaire sur toute la durée d'un cycle, et l'hétérogénéité du paysage environnant les parcelles inventoriées.

4.2. Changement d'échelle hiérarchique

Dans ce travail doctoral, nous avons mis en évidence un effet des mélanges de feuillus sur les niveaux d'infestation de la processionnaire du pin. Cependant, il serait intéressant de connaître la composition optimale de ce type de mélange, en termes de proportion et d'identité des essences feuillues, pour améliorer le contrôle de la processionnaire du pin. En effet, au-delà de la diversité spécifique (nombre d'essences), la diversité fonctionnelle (des traits de vie des essences) peut avoir un effet prépondérant sur la diminution de l'herbivorie (Vehvilainen et al. 2008). Cela pourrait expliquer l'absence d'effet des jeunes taillis de feuillus, qui présentent probablement un assemblage de traits fonctionnels différent de celui des ripisylves (chapitre 5). Des observations pourraient être menées dans des contextes paysagers

plus diversifiés que la forêt des Landes, par exemple les forêts mélangées du Sud-Est de la France. L'effet d'un gradient de diversité fonctionnelle pourrait ainsi être testé sur les niveaux d'infestation de la processionnaire. Par ailleurs, un dispositif expérimental de grande ampleur (ORPHEE) a été mis en place par l'équipe d'Entomologie Forestière de l'UMR BIOGECO afin de déterminer l'effet de la composition des mélanges d'essences forestières sur les niveaux d'herbivorie par les insectes (thèse de B. Castagneyrol). Il permettra à terme de mesurer l'effet de la composition des mélanges assemblant pin maritime et bouleau, chêne pédonculé, chêne tauzin ou chêne vert sur le niveau d'infestation par la processionnaire du pin.

Des expérimentations ont récemment fait émerger une nouvelle dimension dans la compréhension des effets de la biodiversité sur le fonctionnement des écosystèmes. Elles concernent les effets de la diversité génétique des populations d'espèces végétales sur le fonctionnement des écosystèmes. Les premiers résultats montrent un effet positif de la diversité des génotypes sur la productivité (Crutsinger et al. 2006, Kotowska et al. 2010), la résistance aux invasions (Crutsinger et al. 2008), la résilience après une perturbation abiotique (Ehlers et al. 2008) et la stabilité (Whitlock et al. 2007) des écosystèmes. Cependant, la plupart de ces études concernent des systèmes simples de communautés de plantes herbacées ou aquatiques. Peu de résultats sont disponibles sur des systèmes plus complexes comme les forêts.

Une seule étude, très récente, concerne l'effet de la diversité génétique sur l'herbivorie par les insectes. Elle montre que la fitness de l'herbivore généraliste ***Trichoplusia ni*** (Lepidoptera, Noctuidae) augmente avec la diversité des génotypes d'***Arabidopsis thaliana*** plantés en mélange (Kotowska et al. 2010). Cet effet pourrait être dû à une plus grande diversité de la qualité des plantes présentes dans le mélange et à l'aptitude des insectes généralistes à se nourrir sur plusieurs hôtes différents. Une étude est actuellement en cours dans l'équipe d'Entomologie Forestière de l'UMR BIOGECO pour tester l'effet de la diversité génétique du chêne pédonculé sur l'herbivorie par les insectes, en prenant en compte tous les herbivores potentiels, spécialistes et généralistes (thèse de B. Castagneyrol). Par ailleurs, il existe un programme d'amélioration génétique du pin maritime à l'INRA de Bordeaux (UMR BIOGECO) qui produit des variétés pures et hybrides. Il pourrait donc être intéressant d'utiliser ce matériel végétal pour tester l'effet du mélange de ces variétés sur la résistance à la processionnaire du pin dans le contexte landais.

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Annexes

Chapitre 3 - Dulaurent et al. (2010)

Appendix 1 - Characterisation of oak and pine aphid honeydews composition by ^{1}H-NMR metabolomic profiling

1 Materials and Methods

^{1}H-NMR metabolomic profiles were recorded on a BrukerTM Avance Spectrometer (Wissembourg, France) at 500.162 MHz and 300 K using a 5 mm Broad Band Inverse probe (BBI). Spectra were acquired using a water suppression pulse sequence (NOESYGPPR1D: RD-90°-t1-90°-tm-90°-acquire) set with a 9.4 µs 90°pulse, 10 ms mixing time (tm), 4 µs t1, and 10 s relaxation delay (RD), and 512 scans of 64 k data points were collected. The spectral width was 10000 Hz and the acquisition time was 3.28 s. An electronic reference ERETIC (Electronic Reference To access In vivo Concentration) was used for the quantification of metabolites (Moing et al. 2004). The ERETIC signal was located at a chemical shift of 9.5 ppm. An automation procedure (automatic gradient shimming and automatic sample loading) requiring about 120 min per sample was used for data acquisition. Preliminary data processing was carried out with TOPSPIN 1.3 software (Bruker Biospin, Karlsruhe, Germany). Free Induction Decays (FIDs) were Fourier transformed (0.3 Hz line broadening), manually phased and baseline corrected. The assignments of metabolites in the NMR spectra were made by comparing the proton chemical shifts with literature or database values (Anteunis et al. 1975; Fan 1996; Moing et al. 2004; MeRy-B 2009), by comparison with spectra of authentic compounds and by spiking the samples. Metabolite concentrations in the NMR vial were calculated using integration mode of TOPSPIN software for calculation of

resonance areas, followed by data export to Excel software. ^{1}H-^{1}H COSY and TOCSY (2D-homonuclear Correlation Spectroscopy and Total Correlation Spectroscopy), ^{13}C and HSQC (Heteronuclear Single Quantum Coherence Spectroscopy) experiments were carried out to verify the identity of known compounds and to check whether unknown signals really correspond to different compounds (data not shown).

2 Results

Figure S1 shows a typical ^{1}H-NMR spectra obtained at 500 MHz and annotated following Table S1, for oak aphid honeydew from day 155 collection, and pine aphid honeydew from day 171 collection. These two samples are representative of the spectra of their honeydew type. Pine aphid honeydews contained more diverse components, compared with oak aphid honeydews.

3 References

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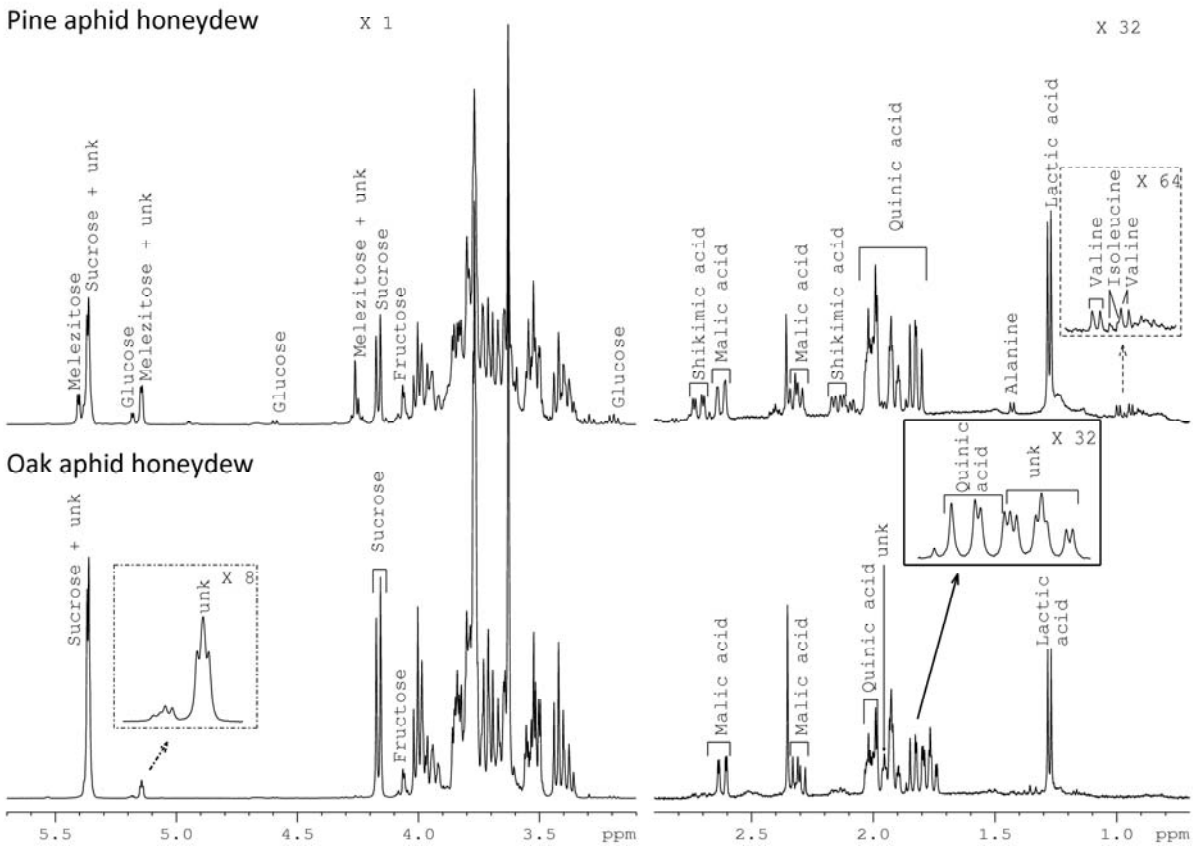
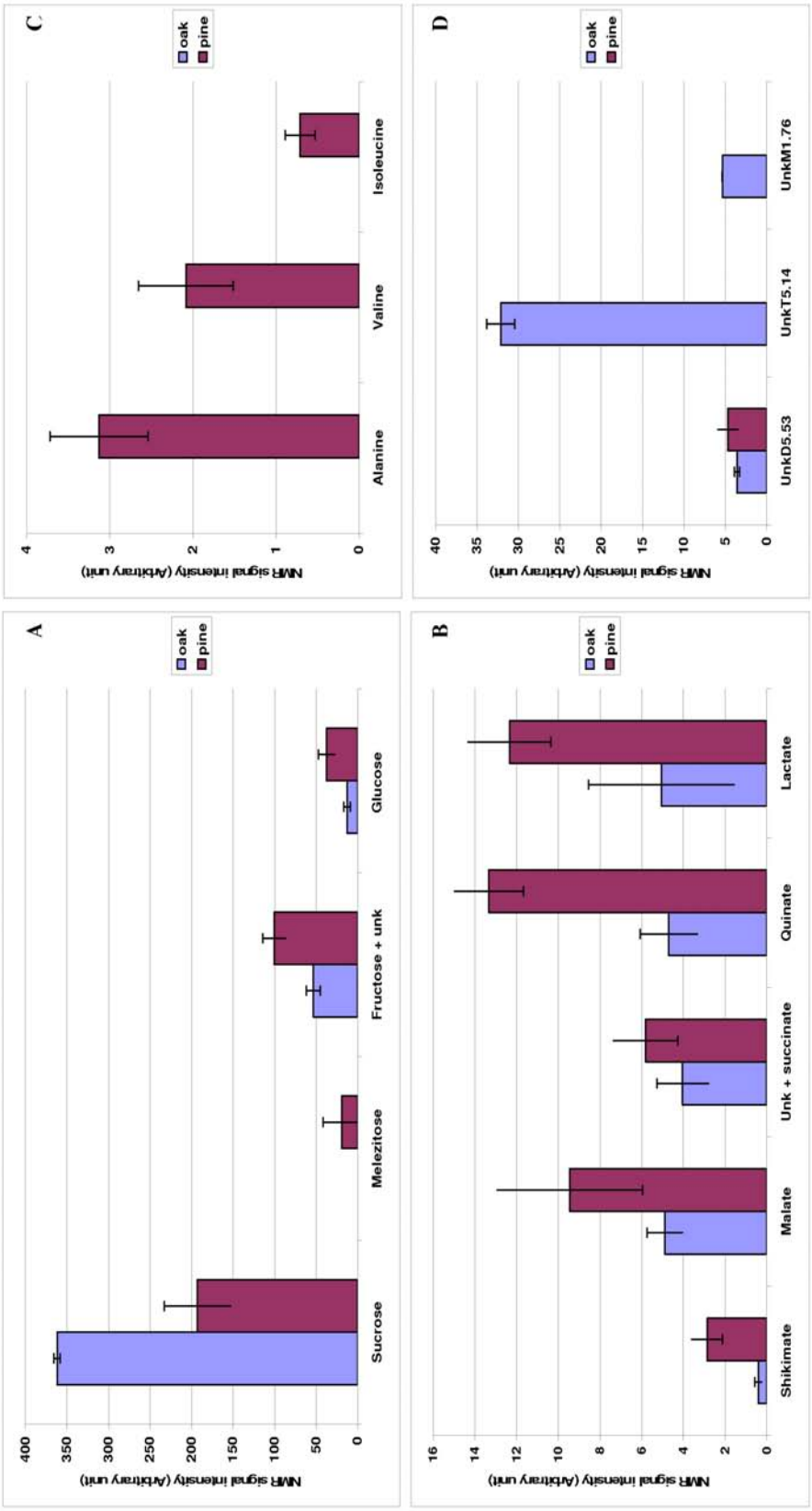


Figure S1. Representative 1-D ^{1}H-NMR spectra of pine and oak aphid honeydews. Dotted frame box (zoom X 64) showed some valine and isoleucine resonances. Dashed frame box (zoom X 8) showed unkT1.14 resonances. Solid frame box (zoom X 32) showed some quinic and unkM1.74 resonances. Resonances are annotated according to Table S1.


A
oak
pine
NMR signal intensity (Arbitrary unit)
400
350
300
250
200
150
100
50
0
Sucrose
Melezitose
Fructose + unk
Glucose
B
oak
pine
NMR signal intensity (Arbitrary unit)
16
14
12
10
8
6
4
2
0
Shikimate
Malate
Unk + succinate
Quinate
Lactate
C
oak
pine
NMR signal intensity (Arbitrary unit)
4
3
2
1
0
Alanine
Valine
Isoleucine
D
oak
pine
NMR signal intensity (Arbitrary unit)
40
35
30
25
20
15
10
5
0
UnkD5.53
UnkT5.14
UnkM1.76

59

60

Figure S2. Relative quantification of compounds identified in the 1-D ^{1}H-NMR spectra of pine and oak honeydews. 2 samples of oak aphid honeydew and 4 samples of pine aphid honeydew were averaged. A: Sugars. B: Organic acids. C: Amino acids. D: Unknown compounds, UnkD5.53: compound with a resonance : doublet at 5.53 ppm. UnkT5.14: compound with a resonance: kind of triplet at 5.14 ppm (see also zoom X8 on Figure S1). UnkM1.76: compound with a resonance: multiplet at 1.76 ppm (see also zoom X32 on Figure S1).

Table S1. Compounds identified in the 1-D ^{1}H-NMR spectra of pine and oak honeydews. d, doublet; dd, doublet of doublets; dq, doublet of quadruplet, m, multiplet; s, singlet; t, triplet.

Compound	Group	Multiplicity	δ^{1}H (ppm)	
Alanine	$C3H_3$	d	1.43	quantified
Fructose	α(C3H+C5H)+ β C5H	m	4.06	quantified
Fumarate	C2H + C3H	s	6.46	detected
Glucose	α C1H	d	5.18	quantified
-	β C1H	d	4.59	quantified
-	β C2H	t	3.19	-
Isoleucine	$C6H_3$	d	0.96	quantified
Lactate	$C3H_3$	d	1.28	
Malate	$C3H_1$	dd	2.31	quantified
-	$C3H_2$	dd	2.62	-
Melezitose	α Glucopyranosyl -C1H	d	5.40	quantified
-	α Glucopyranosyl -C1H	d	5.15	-
-	β Fructofuranosyl-C3H + C4H	m	4.26	-
Quinate	-	dd	1.82	-
-	-	t	1.89	-
-	-	t	1.93	-

-	-	d	1.98	-
-	-	m	2.0	-
Shikimate	$C7H_1$	m	2.14	-
-	$C7H_2$	dd	2.72	-
-	C4H	t	4.35	-
-	C3H	m	6.38	-
Sucrose	Glucopyranosyl –C1H	d	5.42	quantified
-	-	d	4.16	-
UnknownM1.76	-	m	1.76	quantified
UnknownS2.36	-	s	2.36	detected
UnknownT1.95	-	t	1.95	quantified
UnknownT5.14	-	-	5.14	quantified
Valine	$C5H_3$	d	1.05	quantified

73

74

75

Table S2. NMR spectral domains (or buckets) annotated on Figure 3. Most of them have an absolute value of loading higher than 0.10 on PC1 and therefore contribute to the separation between the two honeydew groups along this PC. “unknown”: compound with resonance not attributed. Ex : “UnkD5.X” for an unidentified compound with a doublet at X ppm; “Sucrose + unknown” means that the bucket did not contain only sucrose, but one or several other unidentified compounds contributed to the intensity of this bucket.

Bucket position±0,02 (ppm)	PC1 loading	Compound
3.78	-0.1061	Sucrose + unknown
3.62	-0.1057	Sucrose + unknown
4.18	-0.1045	-
4.02	-0.1021	Sucrose + unknown
4.14	-0.1011	Sucrose
5.38	-0.0989	Sucrose + unknown
3.42	-0.0974	Sucrose
1.78	-0.0911	Quinate + UnkM1.74
5.34	-0.0826	Sucrose + unknown
3.50	-0.0810	Sucrose + unknown
1.74	-0.0501	UnkM1.74
5.54	-0.0204	UnkD5.53
3.86	0.0223	Fructose + Melezitose + unknown
5.42	0.0431	Melezitose
4.26	0.0502	Melezitose
5.14	0.0581	Melezitose + unknown
2.62	0.0797	Malate
3.38	0.0829	Melezitose + unknown
2.58	0.0893	Malate
1.26	0.0950	lactate
1.66	0.1000	-

4.3	0.1001	-
5.22	0.1003	Glucose + unknown
2.1	0.1004	-
4.58	0.1004	Glucose
2.74	0.1007	Shikimate
5.3	0.1011	-
1.18	0.1014	-
3.26	0.1015	-
2.38	0.1016	-
4.22	0.1017	-
4.34	0.1029	-
1.02	0.1029	-
0.9	0.1033	Isoleucine + unknown
0.98	0.1033	Valine + Isoleucine
1.82	0.1034	Quinate
0.94	0.1037	Valine + Isoleucine
4.62	0.1038	Glucose
1.9	0.1039	Quinate
3.58	0.1040	Glucose + unknown
2.7	0.1042	Shikimate
2.18	0.1050	Shikimate
4.94	0.1053	-
2.14	0.1053	Shikimate
2.02	0.1056	Quinate
3.34	0.1058	Glucose + unknown
1.98	0.1059	Quinate
1.86	0.1059	Quinate + unknown
3.14	0.1062	-
3.02	0.1069	-
4.06	0.1070	Fructose

3.22	0.1070	Glucose + unknown
3.18	0.1071	Glucose + unknown
5.18	0.1072	Glucose + unknown
1.7	0.1074	-
4.1	0.1080	Fructose

83

84

Now, it's time to open up, and breath...
(Winston, 2009)