Thèse pour obtenir le grade de docteur
Délivré par l'UNIVERSITE MONTPELLIER 2 Sciences et Techniques du Languedoc

Préparée au sein de l'école doctorale Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosciences, Environnement (SIBAGHE)
Et de l'unité de recherche Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)
Spécialité : Biologie des populations et Ecologie

Effets des changements climatiques sur l'activité des organismes du sol et la décomposition des litières en milieu méditerranéen

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le 12 décembre 2013 devant le jury composé de

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Thèse réalisée au

Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)

Centre National de la Recherche Scientifique

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Résumé

La disponibilité en eau est le principal facteur limitant le fonctionnement des écosystèmes méditerranéens. Des sècheresses plus marquées ou plus fréquentes pourraient avoir d'importantes répercussions sur l'activité et la diversité de la faune du sol qui régule la décomposition des litières et le cycle des nutriments. Dans cette thèse j'ai étudié expérimentalement les interactions entre une modification des apports en eau et l'impact de la macrofaune détritivore sur les processus de décomposition en conditions méditerranéennes.

Dans une première partie, j'ai étudié l'effet d'une espèce de détritivore très abondante localement, *Ommatoiuus sabulosus*, sur la décomposition des litières d'arbustes de garrigue. Une expérience d'un mois en microcosmes a permis d'étudier ses effets directs (via la consommation de litière) et indirects (via l'activité microbienne dans ses fèces) sur la perte de masse des litières et les communautés microbiennes à deux niveaux d'humidité contrastés. Dans une autre expérience d'un an sur le terrain, la mise en place de sachets de litières et de fèces à deux profondeurs dans un sol de garrigue a permis d'étudier les effets d'*Ommatoiulus* à plus long terme. Les principaux résultats montrent que sa consommation de litière est moins affectée par la sècheresse que la décomposition microbienne, mais que, à court terme, *Ommatoiulus* ne stimule pas la minéralisation de la matière organique, quelles que soient les conditions d'humidité. En revanche, à plus long terme, *Ommatoiulus* peut accélérer la décomposition de certaines litières comme le chêne kermès, puisque des fèces issues de cette litière déposées à la surface du sol pendant un an perdent plus de masse que de la litière non-consommée. Cette stimulation semble liée à un lessivage plus important des composés organiques solubles dans les fèces et ne se produit qu'à la surface du sol. En profondeur, où l'humidité du sol est plus favorable à la décomposition, la perte de masse des fèces augmente. Ce résultat suggère qu'en facilitant l'enfouissement de la matière organique dans le sol, les détritivores peuvent accélérer la décomposition.

Dans une seconde partie, j'ai cherché à évaluer l'importance de la diversité fonctionnelle des litières et des détritivores pour le processus de décomposition. Grâce à une approche basée sur les traits, des assemblages d'espèces représentant un fort gradient de dissimilarité fonctionnelle mais ayant une richesse spécifique constante, ont été créés pour étudier la réponse de la relation diversité-fonction à la sécheresse. Les résultats de cette expérience menée à l'Ecotron de Montpellier, montrent que la dissimilarité fonctionnelle des litières et des détritivores explique jusqu'à 20% de la variation observée dans plusieurs processus clefs du fonctionnement du sol, tels que la perte de masse des litières et le lessivage du carbone et de l'azote dans le sol superficiel. Toutefois, les effets de l'identité des espèces présentes aux deux niveaux trophiques restent plus importants que ceux de la dissimilarité fonctionnelle. Bien que la sécheresse influence fortement les processus étudiés, les relations diversité-fonction ne sont pas modifiées par un changement de la disponibilité en eau. Cependant, les assemblages d'espèces les plus performants en conditions d'humidité favorables sont aussi les plus fortement affectés par la sécheresse, ce qui suggère qu'il existe un compromis entre l'efficacité des organismes du sol et leur capacité à résister à une perturbation.

Abstract

Water availability is a major limiting factor for the functioning of Mediterranean ecosystems. More pronounced drought could severely impact soil fauna activity and diversity that could in turn affect litter decomposition and nutrient cycling. In my PhD thesis I investigated experimentally the interactions between changing water availability and detritivorous macrofauna on decomposition and associated processes in a “garrigue”, a typical Mediterranean woody shrub dominated ecosystem.

In the first part of my thesis, I studied the impact of *Ommatoiulus sabulosus*, an abundant diplopod species in garrigue ecosystems, on shrub litter decomposition. During a one month experiment, I studied the direct (litter consumption) and indirect (microbial activity in feces) effects of this detritivore on litter mass loss and microbial communities under two contrasted moisture levels. In a different experiment, I placed litterbags filled with litter or feces in the field at the soil surface or at 5cm soil depth during one year in order to study the long term impact of *Ommatoiulus* on decomposition. A key result was that detritivores maintain litter consumption in dry conditions when microbial driven decomposition drastically dropped. However, this detritivore effect does not lead to an overall increased organic matter mineralization irrespective of moisture conditions, at least in the short term. In contrast, under field conditions and over a longer time period, *Ommatoiulus* increases decomposition of certain species such as *Quercus coccifera*, since feces from this species decompose faster than un-ingested litter after one year at the soil surface. This stimulation is likely due to a higher leaching of soluble compound in feces. Moreover, in depth feces decomposition increases relative to that of intact leaf litter, possibly indicating that more favorable soil humidity is more favorable to decomposition. Collectively, my results suggest that detritivores can strongly increase decomposition by transforming leaf litter into feces of different organic matter quality, and by facilitating the transfer of organic matter into the soil.

In the second part, I evaluated the importance of functional dissimilarity of leaf litter and detritivores on decomposition processes. Using a trait based approach, species assemblages were constructed in order to obtain a gradient of functional dissimilarity of both, leaf litter and detritivore communities, while keeping species numbers constant. The different communities were kept under controlled conditions at the European Ecotron in Montpellier to study the effect of changing functional dissimilarity on process rates at two different moisture conditions. I found that detritivore and litter functional dissimilarity explain up to 20 % of the observed variation for several key soil processes including litter mass loss and the leaching of dissolved organic carbon and nitrogen from top soil. However, effects of species identity at both trophic levels have a larger impact on process rates than functional dissimilarity. In general, drought strongly affects soil processes but does not alter the diversity-function relationship. Species assemblages resulting in highest process rates at favorable moisture level are also the most negatively affected by drought, suggesting a tradeoff between the efficiency of soil organisms and their ability to resist perturbation.

Remerciements

Je tiens à remercier en premier lieu les deux formidables encadrants que j'ai eu pendant ma thèse. Parfois il suffit simplement de croire dans les choses pour qu'elles se réalisent, Stephan je te remercie d'avoir cru en moi et me m'avoir permis de faire cette thèse. Jean-François, je te remercie de m'avoir aidé tout au long de cette thèse. J'ai particulièrement apprécié ta rigueur et ton esprit critique ainsi que ton immense connaissance en biologie. Je remercie également Nathalie qui n'est pas officiellement ma co-encadrante de thèse mais qui le mérite amplement.

Merci aux membres du jury, Virginie Baldy, Thibaud Decaëns, Doyle McKey, et particulièrement à Martin Zimmer de se déplacer jusqu'à Montpellier pour participer à mon jury de thèse. Je remercie également les membres de mon comité de thèse, Mickaël Hedde, Philippe Hisinger et Pascal Mirleau qui ont eu le rôle, moins gratifiant mais tout aussi important, de m'écouter parler d'un travail inachevé et de m'aider à le faire avancer.

Merci à Jordane et à Aurélien qui m'ont accordé leur confiance en choisissant de faire leur stage avec moi.

Je tiens à remercier particulièrement deux collègues du CEFE. Sylvain sans toi je n'aurais peut être pas fait de recherche, merci pour m'avoir donné envi de faire ce métier et aussi pour tes commentaires sur le 2ème chapitre de cette thèse. Merci à François-Xavier avec qui j'ai eu le plaisir de passer mes deux dernières années de thèse. Nous avons pu avoir d'intéressantes discussions et faire des collaborations toutes aussi fructueuses les unes que le autres…tu es maintenant plus qu'un collègue.

Je remercie aussi les collègues du CEFE avec qui j'ai eu des discussions scientifiques enrichissantes : Florence Volaire, Eric Garnier, Karim Barkaouï, Sandra Barantal, Xavier Morin, Simon Chollet, Nicolas Fanin, Johanne Nahmani, Nicolas Martin, Emmanuel Defossez. Merci Ameline de m'avoir fait les cartes de répartition des espèces que je n'ai pas incluses (désolé).

Je remercie Gaëlle Rolland du LEPSE et Claude Plassard de Eco&Sols de m'avoir aidé à lyophiliser mes échantillons de litière.

Ma thèse faisait partie du projet CLIMED, ce qui m'a permis de collaborer avec des étudiants et des chercheurs de Marseille. Je remercie tous les membres du projet avec qui nous avons passé plusieurs jours sous le cagnard du site de l'étoile pour monter et installer les dispositifs d'exclusion de pluie. Je tiens également à remercier Anaïs Racon pour son aide précieuse dans la manip. Ecotron, Mathieu Santoja pour son important travail de mesure des chutes de litières et Natalia Rodríguez pour ses relevés de végétation sur le site qui ont été précieux pour l'ensemble du projet. Merci également à Nicolas Montès pour son implication dans la mise en place de l'ensemble du dispositif expérimental.

J'ai eu la chance de travailler à l'Ecotron au cours de ma thèse. C'est une occasion exceptionnelle et j'en suis reconnaissant. Cette partie de ma thèse fut une réelle aventure humaine et scientifique. Je remercie pour cela Jacques Roy, toute l'équipe de l'écotron et particulièrement Gilbert Jacquier.

Enfin les plus beaux et les plus fort ! Merci à tous ceux du terrain d'expérience du CEFE qui m'ont aidé: David Degueldre, Thierry Mathieu, Jérémy Devaux et Frédéric Tanguy.

Et tout à la fin, la plus belle et la plus forte : merci à toi Elodie de m'avoir supporté polysémiquement.

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Introduction

« La science se forme plutôt sur une rêverie que sur une expérience et il faut bien des expériences pour effacer les brumes du songe »

Gaston Bachelard
La psychanalyse du feu

– « Lorsqu'on cherche, on ne trouve que ce que l'on cherche. Et c'est souvent pas grand-chose…
– Pourquoi n'est-ce pas grand-chose que de trouver ce que l'on cherche ?
– On n'atteint alors à aucune connaissance.
– Heu… Précisez ce que vous voulez dire…
– Préciser c'est toujours fatiguer ce que l'on a voulu dire.

Le vénérable soupire, quitte l'antenne de la voiture et va se poser sur une plante minuscule, couverte de poussière, qui végète au pied d'un panneau du rond point. Le jeune l'y rejoint en veillant à ne pas s'empoussiérer les ailes et fixe son tourmenteur avec des yeux de luciole morte.

– Quand tu cherches, tu sais ce que tu cherches, sinon tu ne le chercherais pas ? lui demande l'ancien qui finit par céder.
– Oui.
– Donc, ce que tu cherches tu le connais déjà, tu l'as déjà imaginé, et tu es déjà en train de l'espérer ?
– Oui, possible.
– Dès lors, tu tournes en rond en trouvant ce que tu espères. Il y a là peut-être une re-connaissance, mais en tout cas aucune vraie connaissance.
– Comment cela ?
– La connaissance survient d'abord dans ce que l'on est incapable d'imaginer, et qu'il nous a été impossible jusqu'alors d'espérer. »

Patrick Chamoiseau
Le papillon et la lumière

Le rayonnement solaire est la principale source d'énergie pour les écosystèmes de la planète. Grâce au processus de photosynthèse, les végétaux ont la capacité d'utiliser cette énergie pour convertir des composés minéraux (CO_2, NO_3, HPO_4,…) en composés organiques. Dans les écosystèmes terrestres dominés par les plantes ligneuses (forêts, landes, garrigues,…), la part de la biomasse végétale consommée par les herbivores est faible (environ 10%), et la majorité de cette biomasse demeure intacte jusqu'à la sénescence pour rejoindre la matière organique morte au niveau du sol – la litière (Cebrian & Lartigue 2004). C'est l'utilisation de cette matière organique morte par les organismes décomposeurs qui constitue le processus de décomposition. A l'issue de la décomposition, une partie des éléments chimiques (C, N, P, K,…) contenus dans la matière organique est libérée sous forme minérale (minéralisation) alors qu'une autre partie est stabilisée et demeure sous forme organique stable dans le sol (humification) pendant de longues périodes (plusieurs centaines d'années selon Schmidt *et al.* 2011). La décomposition est donc une étape majeure des flux d'énergie et de matière, pendant laquelle est dissipée une grande partie de l'énergie fixée par la photosynthèse et sont recyclés les éléments chimiques contenus dans la matière organique morte.

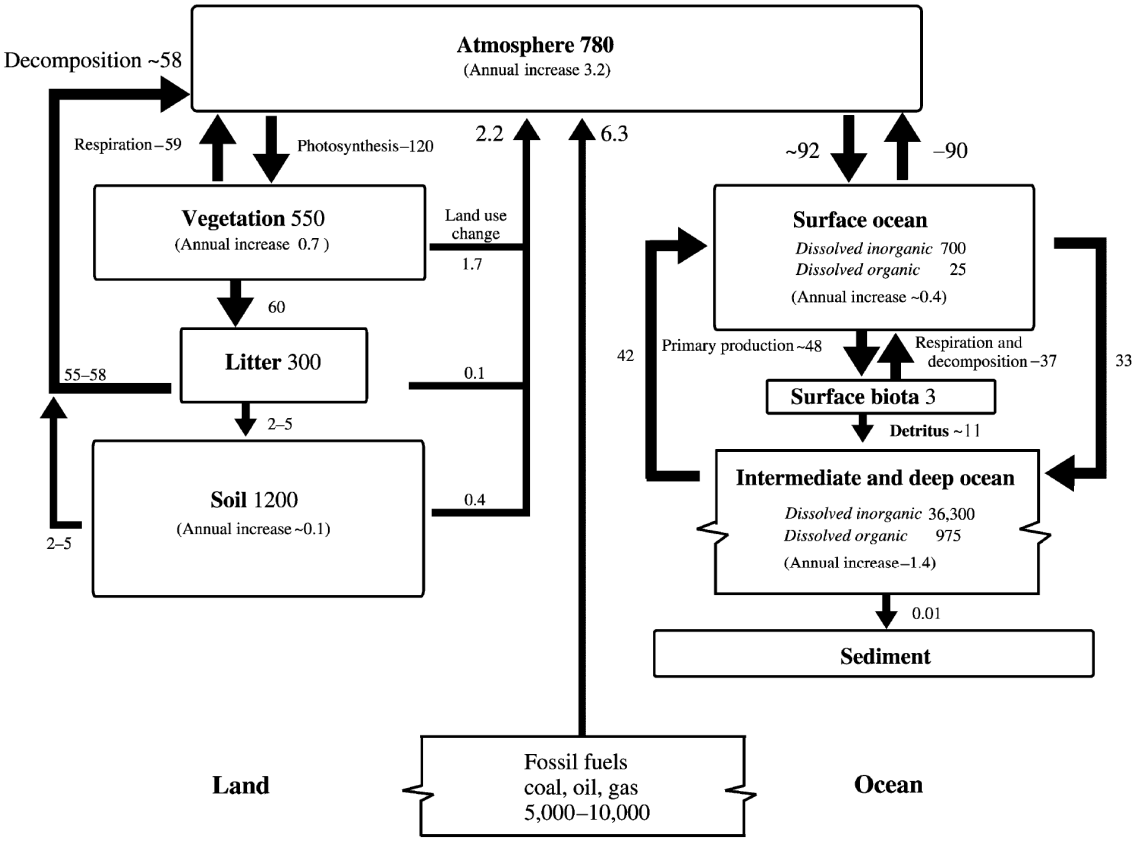

Figure 1. Cycle du carbone à l'échelle planétaire. les unitées sont en Pg de carbone ou en Pg de carbone par an. Tiré de Schlesinger (2005).

LES ENJEUX LIES A L'ETUDE DU PROCESSUS DE DECOMPOSITION

La compréhension du processus de décomposition présente de multiples enjeux. Au niveau global, des quantités significatives de gaz à effet de serre tels que le CO_2, le méthane ou des oxydes nitreux sont relâchés lors de la décomposition (Figure 1). La quantité de carbone organique contenu dans le sol et les litières est d'environ 1500 Pg, ce qui représente environ 2 fois le C atmosphérique ou 3 fois le C contenu dans la biomasse végétale vivante (Schlesinger 2005). Les émissions de CO_2 liées à la décomposition de la matière organique du sol sont de 58 Pg par an, soit 9 fois plus que les émissions de CO_2 d'origine anthropique ce qui représente un flux de matière considérable à l'échelle de la planète. Une modification même minime du processus de décomposition pourrait donc avoir d'importantes répercussions. C'est pourquoi il est important de comprendre finement les mécanismes et les facteurs contrôlant le processus de décomposition et comment ce processus pourrait être affecté par les changements globaux.

LES FACTEURS CONTROLANT LE PROCESSUS DE DECOMPOSITION

La décomposition est un processus complexe résultant principalement de 4 mécanismes : (i) l'oxydation chimique d'origine abiotique (radiations UV, cycles de ré-humectation et dessèchement, gel et dégel…), (ii) le lessivage, (iii) la décomposition microbienne principalement via des exo-enzymes ainsi que (iv) la décomposition due à la faune, par la fragmentation et la digestion (Chapin III & Matson 2002).

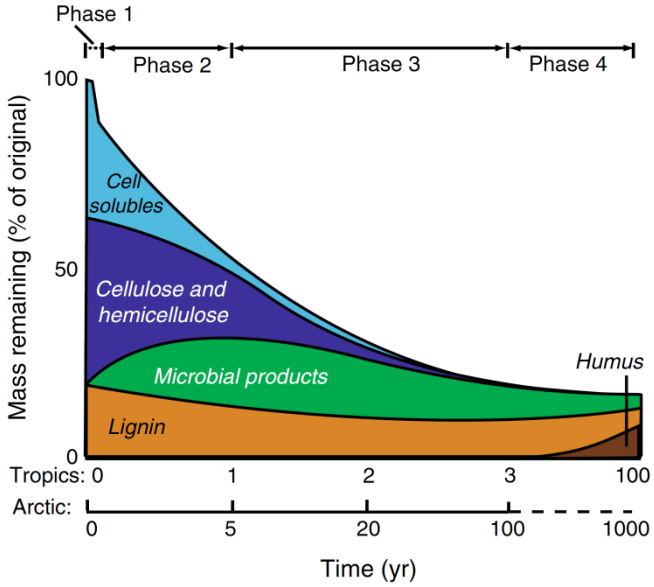

Figure 2. Les différentes phases de la dynamique de décomposition. Tiré de Chapin III & Matson (2002)

Au cours de la décomposition, la masse des détritus décroit approximativement de manière exponentielle (voir Wider & Lang (1982) pour plus de détail sur les modèles de dynamique de décomposition). Cette dynamique de décomposition peut être divisée en trois grandes phases (Figure 2). Durant la première il y a un fort lessivage des éléments solubles et la masse décroit rapidement sur une courte période. Les phases suivantes sont sous l'influence de l'activité biologique des microorganismes, modulée par de nombreuses interactions avec la faune du sol. Enfin durant la quatrième phase, la décomposition est très lente, l'origine de la matière organique n'est généralement plus discernable de plus, les contrôles du processus sont différents des précédentes phases (Swift *et al.* 1979; Berg & McClaugherty 2008). Au cours de ma thèse je me suis focalisé sur l'étude des premières phases du processus pendant lesquelles la décomposition peut être fortement influencée par (1) les facteurs abiotiques que sont le climat et les propriétés du sol, (2) la qualité de la matière organique et (3) l'activité des décomposeurs.

A l'échelle globale, le climat explique une part importante de la constante de décomposition [r^2=0.51 (Meentemeyer 1978) ; r^2=0.46 (Aerts 1997) ; r^2=0.3 (Zhang *et al.* 2008)] car le taux métabolique des organismes décomposeurs est directement lié à la température et aux précipitations qui influencent la disponibilité en eau. Par conséquent, de la même manière que la productivité primaire, la décomposition tend à augmenter des pôles vers l'équateur. Les propriétés du sol influencent aussi la décomposition, en modulant par exemple la disponibilité en eau pour les organismes décomposeurs. Enfin, les facteurs pédoclimatiques ont un effet indirect important via leur influence sur la composition des communautés végétales qui détermine la qualité de la matière organique (Zhang *et al.* 2008).

Suivant le modèle hiérarchique de Lavelle et al. (1993), le climat a une influence sur la décomposition à de larges échelles géographiques alors qu'au sein d'une même zone climatique, la qualité des litières a une influence prépondérante. La notion de qualité fait directement référence aux caractéristiques physiques ou chimiques (traits) des litières qui sont les mieux corrélées à la vitesse de décomposition. A l'instar des plantes, les organismes décomposeurs peuvent être limités par les nutriments. Les litières de bonne qualité ont donc généralement une teneur en **nutriments** élevée, leur ratio avec le carbone (C/N, C/P) étant plus faible que pour les litières de mauvaise qualité. La nature des **composés carbonés** a un effet sur la qualité des litières. Une forte proportion de composés stables et difficiles à dégrader tels que la lignine ou la cutine sera généralement associée à une décomposition plus lente et donc à une mauvaise qualité. Les alcaloïdes, les tannins ou d'autres **composés secondaires** produits par les plantes peuvent également ralentir la décomposition en ayant un effet inhibiteur ou toxique sur les organismes décomposeurs (Coq *et al.* 2010). Enfin des **traits physiques**, tels que la capacité de rétention en eau ou la dureté, sont des propriétés des litières qui peuvent influencer de manière importante la décomposition (Makkonen *et al.* 2012).

L'activité des organismes décomposeurs est un des trois principaux facteurs influençant le processus de décomposition. Les décomposeurs microbiens ainsi que la faune du sol sont au cœur du processus de décomposition puisqu'ils se nourrissent de la matière organique morte du sol. Les décomposeurs microbiens (bactéries et champignons) ont un rôle très important car ils digèrent la matière organique morte en excrétant des enzymes dans leur environnement proche puis en assimilant les produits issus de la dégradation. Les microorganismes sont ainsi responsables de 80 à 95 % de la respiration hétérotrophe du sol (Petersen & Luxton 1982; Lavelle & Spain 2001). Néanmoins, bien que les décomposeurs microbiens soient les principaux organismes décomposeurs, leur activité est fortement régulée par l'activité de la faune du sol.

LES EFFETS MULTIPLES DE LA FAUNE SUR LE PROCESSUS DE DECOMPOSITION

Le rôle de la faune du sol dans le processus de décomposition est pour le moment moins bien compris que le rôle du climat ou de la qualité chimique des litières. On peut y voir deux raisons principales, la première est l'immense diversité de la faune du sol (Decaëns 2010) qui rend difficile la connaissance du rôle exact des espèces impliquées dans le processus. L'autre raison tient à la complexité des effets de la faune sur le processus de décomposition. En effet la faune n'a pas seulement un effet direct en se nourrissant de litière, mais elle influence également la décomposition via une multitude d'interactions avec les microorganismes. Ces interactions ont la particularité de se produire à des échelles spatiales et temporelles multiples (Figure 3) et, comme la plupart des interactions entre organismes, d'être fortement dépendantes des conditions environnementales.

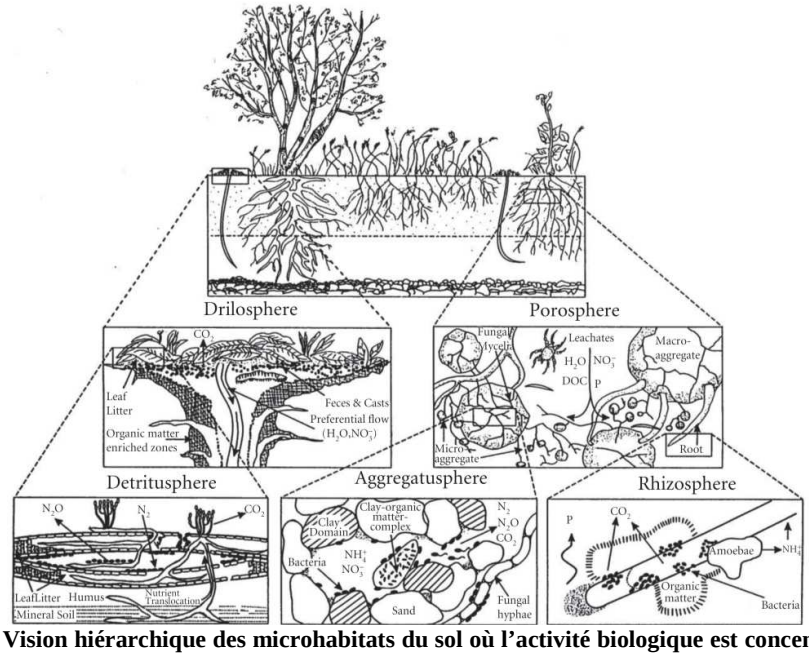

Figure 3. Vision hiérarchique des microhabitats du sol où l'activité biologique est concentrée. Tiré de **(Berg 2012)** modifié à partir de Beare *et al.* (1995).

Un des objectifs de ma thèse est de contribuer à la compréhension du rôle de la macrofaune qui attaque la litière à la surface du sol – les détritivores épigés, qui sont surtout des macroarthropodes dans les écosystèmes méditerranéens. Ces "litter transformers", dans la terminologie de Lavelle & Spain (2001), ne sont que les premiers maillons d'une chaîne qui peut se prolonger dans les horizons plus profonds du sol lorsque des vers de terre endogés ou anéciques sont présents. Les détritivores qui interviennent dans la litière ont néanmoins de nombreux effets directs et indirects sur le processus de décomposition, dont beaucoup sont encore mal compris.

Effets directs des détritivores

L'effet le plus direct de la faune détritivore sur la décomposition est la consommation de litière (Figure 4-1), qui se traduit par des transformations physiques, biochimiques et microbiologiques de la matière organique. A l'échelle de l'écosystème, la consommation de litière par l'ensemble de la communauté de détritivores représente selon les écosystèmes entre 10 et 80 % des chutes annuelles de litière (Bertrand *et al.* 1987; Hassall *et al.* 1987; Cárcamo *et al.* 2000; David & Gillon 2002; Garcia-Pausas *et al.* 2004). Le taux de consommation de litière par la faune dépend des conditions environnementales et de la biomasse de la communauté de détritivores (Fazi & Rossi 2000; Irmler 2000; David & Gillon 2002). Cependant la plupart de ces estimations sont réalisées dans des écosystèmes où les communautés de détritivores sont abondantes (en général des humus de type mull) alors que dans d'autres écosystèmes, les communautés de détritivores sont très peu abondantes et le fonctionnement du sol est principalement influencé par l'activité des champignons (humus de type mor). La plupart des schémas conceptuels et des mécanismes présentés dans ce travail se réfèrent donc à des sols ayant un humus de type mull.

La principale transformation physique due aux détritivores est la fragmentation de la litière en particules millimétriques ou inframillimétriques. Chez certaines espèces, ces particules peuvent cependant être agglomérées dans des boulettes fécales très compactes.

Les transformations biochimiques pendant la digestion varient en fonction des activités enzymatiques propres à chaque espèce. Chez le diplopode *Glomeris marginata*, la concentration de composés non-structuraux (sucres simples, amidon, protéines, acides gras...) est beaucoup moins élevée dans les boulettes fécales que dans la litière, ce qui indique qu'ils sont facilement digérés et assimilés (Jocteur Monrozier & Robin 1988; Bignell 1989; Scheu & Wolters 1991; Gillon & David 2001; Rawlins *et al.* 2006). Les macroarthropodes peuvent aussi hydrolyser ou oxyder une grande partie des tannins contenus dans la litière (Zimmer *et al.* 2002; Coulis *et al.* 2009), ce qui contribue à détoxifier la nourriture ingérée. Au contraire, la lignine est un composé très récalcitrant que l'on retrouve à des concentrations élevées dans les boulettes fécales. Quant à

la digestion des polysaccharides structuraux (cellulose, hémicellulose), elle est très variable d'une espèce animale à l'autre.

Des microorganismes sont ingérés en même temps que la litière et beaucoup sont digérés dans le tube digestif des détritivores. En général, le rapport bactéries:champignons est beaucoup plus élevé dans des fèces fraîches que dans la litière (Hassall *et al.* 1987; Maraun & Scheu 1996; Byzov *et al.* 1998). Cela s'explique d'abord par le fait que les hyphes sont plus affectés par la mastication de la litière que les bactéries. De plus, après la digestion des microorganismes dans les parties antérieures du tube digestif, le nombre de bactéries (mais pas le nombre de champignons) augmente à nouveau dans l'intestin postérieur des macroarthropodes, qui est un environnement favorable à la croissance bactérienne (Zimmer & Topp 1998; Zimmer 2002; Frouz *et al.* 2003). Selon l'équilibre entre phase de digestion et phase de croissance, il peut y avoir accroissement ou diminution de la densité de bactéries dans les fèces par rapport à la litière d'origine, et les deux cas de figure ont été rapportés dans la littérature (Hassall *et al.* 1987; Byzov *et al.* 1998; Suzuki *et al.* 2012).

Malgré les quantités importantes de litière qu'ils consomment, les détritivores n'en assimilent qu'une certaine proportion (Figure 4). Le taux d'assimilation des macroarthropodes est habituellement faible, la fourchette variant entre 5 et 30% pour les diplopodes (Köhler *et al.* 1992; David & Gillon 2002; Lawrence & Samways 2003). Les isopodes ont également des taux d'assimilation variables mais généralement plus élevés que les diplopodes, compris entre 15 et 70% (Dudgeon *et al.* 1990; Nair & Fadiel 1991; Hättenschwiler *et al.* 1999; David *et al.* 2001; Zimmer 2003). Les gastéropodes ont un système digestif encore plus efficace que les isopodes, qui leur permet d'assimiler entre 50 et 75 % des litières ingérées (Mason 1970; Jennings & Barkham 1979; Seifert & Shutov 1981; Gupta & Oli 1998). Pour évaluer l'effet direct des détritivores sur la décomposition il faut donc prendre en compte à la fois le taux de consommation et le rendement d'assimilation. Ainsi, d'après les estimations de David et Gillon (2002) en milieu méditerranéen, 109 g de litière de chêne vert sont consommés annuellement par une population de *Glomeris marginata*, ce qui correspond à 43 % des chutes annuelles de litière. Cependant dans le même lapse de temps, 103 g de boulettes fécales sont excrétées. Cet exemple montre bien que l'effet direct des détritivores sur la décomposition est parfois assez faible en termes de minéralisation de la matière organique, même si de grandes quantités de litière sont broyées et transformées en boulettes fécales.

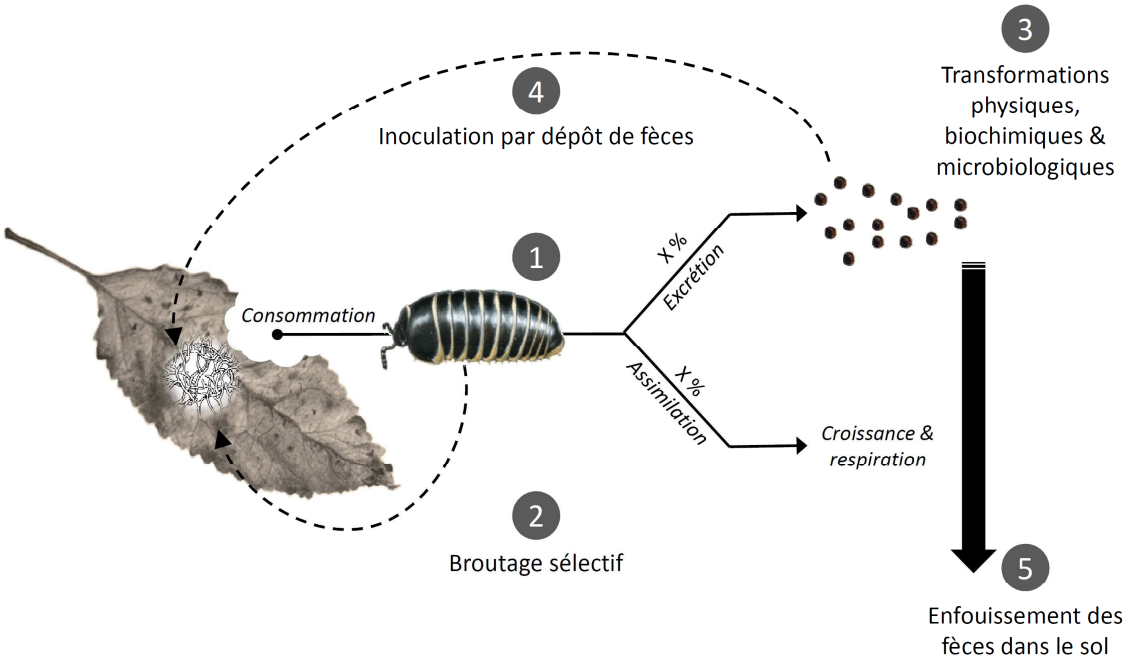

Figure 4. Schéma conceptuel regroupant les effets directs et indirects des détritivore sur la décomposition des litières. Les taux d'excrétion et d'assimilation sont variables d'une espèce à l'autre, pour plus de précision se référer au paragraphe sur le taux d'assimilation dans la section effet direct des détritivores page précédente.

Effets indirects des détritivores

Les détritivores peuvent influencer l'activité des microorganismes décomposeurs de multiples façons (Visser 1985), et ces effets indirects sur la décomposition sont souvent présentés comme les plus importants. Ce sont aussi les plus mal connus, et de nombreux mécanismes sont encore à éclaircir.

La modification de l'activité microbienne dans les fèces

Bien qu'il soit souvent admis que les détritivores stimulent l'activité microbienne dans leurs fèces, les modifications physico-chimiques subies par la litière dans le tube digestif peuvent aussi bien accélérer que ralentir le processus de décomposition. La fragmentation, qui détruit les parois végétales et rend accessible le contenu cellulaire aux microorganismes, peut favoriser la décomposition (Hanlon 1981). De plus, les litières ont une capacité de rétention en eau supérieure une fois transformées en boulettes (Webb 1977; Tajovsky *et al.* 1992), ce qui peut aussi favoriser l'activité microbienne. En revanche, la concentration accrue de composés récalcitrants comme la lignine a un effet négatif sur la décomposition (Rawlins *et al.* 2007). La compaction des fragments de litière dans les boulettes fécales peut aussi ralentir la décomposition (Webb 1977; Hanlon 1981).

Dans la plupart des études qui ont comparé la respiration des fèces de macroarthropodes et celle de la litière intacte, la respiration a augmenté dans les fèces fraîches mais seulement pendant un temps relativement court, allant de quelques heures à 2-3 semaines après leur émission (Van der Drift & Witkamp 1960; Hassall *et al.* 1987; Maraun & Scheu 1996; Frouz & Simek 2009). A plus long terme, la respiration a été similaire dans les deux substrats, ou moins importante dans les fèces que dans la litière. De même, les quelques études qui ont comparé la perte de masse des fèces de macroarthropodes et celle de la litière intacte sur des temps assez longs (allant jusqu'à 1 an) ont montré que la vitesse de décomposition était similaire dans les deux substrats, ou moins rapide dans les fèces que dans la litière (Nicholson *et al.* 1966; Webb 1977; Frouz & Simek 2009). Cependant ces études ont été réalisées à chaque fois sur une seule espèce de litière et toutes en milieu tempéré. Il serait intéressant d'étudier l'effet de la transformation en boulette fécales sur la perte de masse de litières de différentes qualités pour tester si les boulettes se décomposent de manière identique quelque soit l'origine de la matière organique consommée.

La modification de l'activité microbienne dans la litière non-consommée

Les détritivores disséminent de nombreuses propagules microbiennes en les transportant sur leur cuticule, et surtout en déposant leurs fèces dans la litière et les horizons superficiels du sol (Pherson & Beattie 1979; Visser 1985; Lilleskov & Bruns 2005). Cela influence probablement la composition des communautés microbiennes dans la litière non-consommée. Hanlon & Anderson

(1980) ont montré que l'activité de l'isopode *Oniscus asellus* augmentait considérablement et durablement les quantités de bactéries dans la litière, ce qui peut être dû, au moins en partie, au dépôt des fèces. Lorsque de grandes quantités de boulettes fécales sont déposées dans les litières par des détritivores, elles pourraient agir comme un inoculum, favoriser la colonisation microbienne des litières non-consommées et ainsi augmenter la décomposition (Figure 4-4). Ce mécanisme d'interaction entre macroarthropodes et microorganismes des litières n'a cependant jamais été étudié.

L'incorporation de la matière organique dans le sol

Contrairement aux vers de terre anéciques et endogés qui vivent et se déplacent surtout dans le sol, les autres invertébrés détritivores sont principalement actifs dans les horizons superficiels du sol au niveau de la couche de litière. Ces détritivores épigés n'ont donc pas une activité de bioturbation aussi importante que les vers de terre (Lavelle & Spain 2001). Cependant en réduisant la taille des particules, les macroarthropodes peuvent faciliter le transport passif de boulettes fécales à travers la couche de litière et dans les premiers centimètres du sol. De plus certaines espèces sont partiellement endogées (Hopkin & Read 1992). Par exemple les diplopodes de l'ordre des Julida appartiennent au type écomorphologique des « bulldozers ». Ces espèces ont un corps parfaitement cylindrique leur permettant de s'enfouir facilement dans le sol. En vivant dans le sol, même temporairement, ces espèces peuvent donc y déposer des boulettes fécales composées des résidus des litières consommées en surface. Le transport de la matière organique de surface jusque dans des microsites plus profonds où les conditions d'humidité sont plus favorables peut favoriser la décomposition de la matière organique (Figure 4-5). Cet effet indirect des macroarthropodes sur la décomposition n'a cependant pas été testé expérimentalement depuis qu'il a été suggéré par Hassall *et al.* (1987).

LES INTERACTIONS ENTRE DETRITIVORES : LE ROLE DE LA DIVERSITE

Les différences entre espèces sont plus importantes que la richesse spécifique

Nous avons détaillé précédemment comment les détritivores interagissent avec les organismes d'un autre groupe trophique (microorganismes), cependant différentes espèces de détritivores peuvent également interagir dans la façon dont elles exploitent et transforment la litière. Ce type d'interactions entre des espèces du même groupe trophique entre dans le cadre de l'étude des relations entre biodiversité et fonctionnement de l'écosystème. Bien que les relations entre la diversité des organismes et la productivité primaire, ou la résistance aux invasions aient été largement étudiées (Balvanera *et al.* 2006), il y a encore peu d'études portant sur les effets de la diversité de la faune du sol sur le processus de décomposition.

La richesse spécifique des organismes du sol ne semble pas beaucoup influencer les processus (très peu étudié, mais voir (Huhta *et al.* 1998) pour une revue des études en forêt boréales). Cependant comme la relation biodiversité-fonctionnement est basée sur des interactions entre organismes telles que la compétition ou la complémentarité – la complémentarité regroupant les mécanismes de facilitation divers ainsi que la différentiation des niches (Loreau *et al.* 2001) – le nombre d'espèces n'est peut-être pas le meilleur indicateur de diversité. Par exemple, une étude récente sur les bactéries a montré qu'augmenter la richesse sans augmenter la dissimilarité génotypique peut avoir un effet négatif sur la productivité à cause d'une augmentation de la compétition (Jousset *et al.* 2011). Le problème de la diversité taxonomique est de ne pas prendre en compte les différences ou les similitudes fonctionnelles entre les espèces, qui sont pourtant au cœur des interactions impliquées dans la relation biodiversité-fonctionnement.

L'approche fonctionnelle permet de mieux prendre en compte les différences entre espèces. A partir de mesures de traits fonctionnels[*], on peut calculer des indices de diversité fonctionnelle reflétant les différences moyennes entre les espèces au sein de la communauté (Botta-Dukát 2005; Barantal *et al.* 2011). Heemsbergen *et al.* (2004) ont manipulé la diversité des détritivores en créant différents assemblages à partir de 8 espèces de milieux tempérés. Les résultats de cette étude ont montré que les communautés de détritivores les plus dissimilaires ont un effet positif sur le processus de décomposition alors que les communautés avec des espèces semblables ont un effet négatif. Ces résultats sont attribués à un effet inhibiteur de la compétition dans les communautés les plus similaires et à un effet de facilitation dans les communautés les plus dissimilaires. La dissimilarité fonctionnelle apparait donc comme un élément important pour

[*] Selon Violle *et al.* (2007) un trait fonctionnel est défini comme toute caractéristique morphologique, physiologique ou phénologique mesurable au niveau de l'individu, de la cellule à l'ensemble de l'organisme, sans référence à l'environnement ou à tout autre niveau d'organisation.

prédire l'effet de la diversité des détritivores sur la décomposition. Cependant dans l'étude de Heemsbergen *et al.* (2004), les taux de processus issus des communautés de détritivores monospécifiques ont été utilisés pour calculer la dissimilarité dans les communautés plurispécifiques. Cette méthode pose un problème tautologique puisqu'une partie des résultats de l'expérience est utilisée pour prédire d'autres résultats de la même expérience. Hedde *et al*. (2010) ont apporté une amélioration à cette méthode en utilisant des traits fonctionnels des détritivores mesurés *a priori*, indépendamment de l'expérience dont ils cherchaient à prédire les résultats, pour mesurer la dissimilarité fonctionnelle. A l'issue d'une expérience manipulant la diversité dans des assemblages créés à partir de 4 espèces de détritivores, Hedde *et al.* (2010) ont confirmé les résultats de Heemsbergen *et al.* (2004) en montrant que la dissimilarité fonctionnelle des détritivores avait un effet positif sur le processus de décomposition.

Cependant un certain nombre de critiques sont adressées aux études portant sur la relation biodiversité-fonctionnement. Le manque de réalisme est pointé du doigt car les conditions expérimentales sont en général éloignées des conditions naturelles (Srivastava & Vellend 2005). Un des challenges de cette discipline de l'écologie est d'intégrer un certain niveau de complexité trophique dans les plans expérimentaux, ainsi que de prendre en compte la variabilité naturelle des conditions environnementales ou la variabilité induite par les activités anthropiques (Hillebrand & Matthiessen 2009; Reiss *et al.* 2009).

La diversité des litières : moteur des interactions positives ?

La relation entre la dissimilarité des détritivores et le processus de décomposition n'a jusqu'à présent été étudiée que sur un substrat simple composé d'une seule espèce de litière d'arbre (Heemsbergen *et al.* 2004; Hedde *et al.* 2010). Or la diversité végétale est importante pour le processus de décomposition puisqu'elle détermine la diversité des ressources disponibles pour les détritivores. Un assemblage de litières plus diversifié est donc susceptible de fournir une gamme plus complète de ressources nutritionnelles (balanced diet hypothesis) et de favoriser ainsi la biomasse et l'activité des détritivores . Il est également plus probable que des interactions de type complémentarité dans l'utilisation des ressources se produisent lorsque les ressources disponibles pour les détritivores sont plus diversifiées. On peut donc faire l'hypothèse que la diversité des litières a un rôle moteur dans la relation entre la diversité des détritivores et le processus de décomposition. Suivant cette hypothèse, le processus de décomposition devrait être optimale dans les conditions combinant à la fois un haut niveau de diversité des détritivores et des litières.

IMPACT DE LA SECHERESSE SUR LES INTERACTIONS ENTRE ORGANISMES ET CONSEQUENCES POUR LA DECOMPOSITION

Changement climatique et sécheresse en milieu méditerranéen

Dans son dernier rapport[†], le GIEC (IPCC) annonce pour la première fois avec certitude que l'homme est en partie responsable des changements climatiques observés depuis les années 1900. Outre l'augmentation du CO_2 et de la température de l'air, la modification du régime des précipitations risque d'affecter le fonctionnement des écosystèmes.

Le climat méditerranéen est caractérisé par une sécheresse estivale alternant avec des épisodes pluvieux violents et généralement concentrés sur de courtes périodes. Dans des écosystèmes qui sont donc déjà plus ou moins fortement limités par la disponibilité en eau, une accentuation de la sécheresse pourrait avoir des conséquences importantes pour le fonctionnement. Dans le cadre des changements climatiques, une augmentation de la sécheresse peut résulter d'une part de l'augmentation des températures qui accroît l'évaporation de l'eau, et d'autre part, des modifications de la circulation atmosphérique qui peuvent avoir d'importantes conséquences pour la quantité et la fréquence des précipitations. Dans la région méditerranéenne il est possible que les quantités de précipitations diminuent de 10 à 30% dans les 100 prochaines années (Lionello 2007). De plus la fréquence des précipitations sera également modifiée, entrainant une augmentation des risques de sécheresses et de pluies intenses (Gao *et al.* 2006).

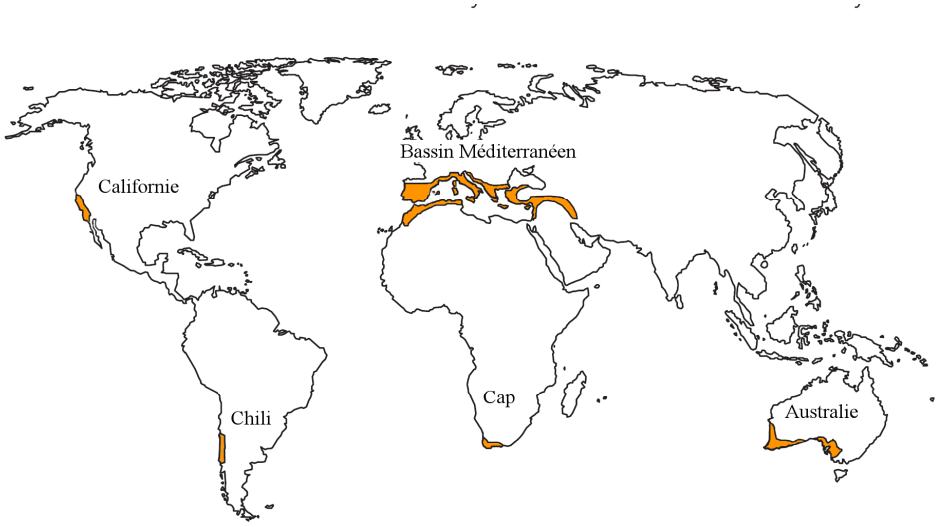

Figure 5. Les 5 régions du monde ayant un climat de type méditerranéen. Tiré de **(Cowling *et al.* 1996)**

[†] Rapport intitulé « The Physical Science Basis » publié le 30 September 2013, dont une version provisoire est accessible en ligne.

Le bassin méditerranéen est considéré comme un hotspot de biodiversité à l'échelle mondiale (Myers *et al.* 2000). Malgré sa petite superficie (Figure 5, moins de 3 % des écosystèmes terrestres selon le Millennium Ecosystem Assessment (2005), le bassin méditerranéen compte environ 25 000 espèces de plantes vasculaires dont la moitié sont endémiques (Cowling *et al.* 1996). Ces espèces seront donc particulièrement vulnérables aux changements climatiques. De plus le fonctionnement des écosystèmes méditerranéens ainsi que le rôle de la diversité dans ce fonctionnement restent très peu étudiés. Par exemple, d'importants travaux de synthèse comparant la structure des communautés et le fonctionnement du sol dans les différents biomes terrestres ne prennent pas en compte le biome méditerranéen (Petersen & Luxton 1982; Fierer *et al.* 2009; García-Palacios *et al.* 2013).

Les challenges sont donc multiples. Il s'agit dans un premier temps de mieux connaitre le rôle de la faune en milieu méditerranéen –notamment les adaptations et les acclimatations des organismes à la sécheresse– et dans un second temps, de comprendre comment une augmentation de la sécheresse pourrait affecter l'activité de la faune du sol et les interactions entre organismes qui sont au cœur du processus de décomposition.

Particularités biologiques des écosystèmes méditerranéens

Une phénologie adaptée pour éviter la sécheresse

La plupart des organismes méditerranéens évitent la sécheresse en concentrant leurs activités pendant les périodes de l'année où l'eau est disponible et où la température est clémente, c'est-à-dire au printemps et à l'automne. L'été est donc généralement marqué par une phase d'activité très réduite : les plantes réduisent leur assimilation/transpiration et souvent leur surface foliaire (Van der Molen *et al.* 2011), la faune s'enfouit dans le sol (Sharon *et al.* 2001) et l'activité microbienne est très réduite (de Dato *et al.* 2010).

Une végétation sclérophylle : la qualité des litières en pâtit

La végétation présente également des adaptations morphologiques et physiologiques lui permettant de résister à la sécheresse (sclérophyllie, pubescence, composés aromatiques, aphyllie,…). Ces adaptations se traduisent de manière générale par une mauvaise décomposabilité des litières (Gallardo & Merino 1993; Pérez-Harguindeguy *et al.* 2000).

Les communautés microbiennes dominées par les champignons

Contrairement à la plupart des bactéries, les champignons et les actinomycètes ont la capacité d'être actifs dans des sols avec une faible disponibilité en eau (Cook and Papendick, 1970 in Salamanca *et al.* 2003). De plus, les champignons possèdent des enzymes adaptées à la dégradation des substrats complexes, tels que les litières récalcitrantes produites par les arbustes

méditerranéens. Par conséquent, les champignons occupent une place importante dans les communautés microbiennes des écosystèmes méditerranéens (Wilkinson *et al.* 2002) et y jouent un rôle fonctionnel prépondérant (Collins *et al.* 2008).

Des forêts sans vers de terre ?

Dans les écosystèmes méditerranéens où les litières de surface peuvent être totalement sèches à certaines périodes de l'année, les vers de terre épigés sont quasiment absents (David 1999). D'autres espèces animales, plus résistantes à la dessiccation, telles que des macroarthropodes ou des gastéropodes jouent le même rôle dans le fonctionnement de l'écosystème en fragmentant les litières de surface. De plus les macroarthropodes tels que les diplopodes peuvent atteindre des biomasses très importantes (Iatrou & Stamou 1991; Bertrand & Lumaret 1992; David 1995) et consomment une part importante des chutes annuelles de litières (David & Gillon 2002). Les vers de terre ne sont cependant pas absents des écosystèmes méditerranéens, mais les espèces appartenant aux groupes écologiques des anéciques et des endogés dominent les communautés (David 1999). Cela suggère que, dans les écosystèmes méditerranéens, l'effet des vers de terre est principalement concentré dans les horizons minéraux du sol alors que les macroarthropodes ont un effet plus important dans les horizons superficiels au niveau de l'humus et des litières (Romanyà *et al.* 2000).

Impact de la sécheresse sur les organismes et leur activité

Effet de la sécheresse sur la décomposition microbienne

La sécheresse a un effet négatif sur la décomposition microbienne comme le montrent un grand nombre d'expériences d'exclusion de pluie sur le terrain qui ont été menées dans différentes conditions et à différentes échelles de temps. Ces résultats montrent que la décomposition peut être réduite dans des proportions allant de 9 à 78 % (Kemp *et al.* 2003; Yahdjian *et al.* 2006; Lensing & Wise 2007; Van Meeteren *et al.* 2008; Joos *et al.* 2010; Sanaullah *et al.* 2012; Allison *et al.* 2013). Les différences entre ces résultats peuvent être en partie expliquées par la quantité de précipitations exclues. Néanmoins, ce ne sont pas toujours les expériences excluant la plus forte proportion des précipitations qui engendrent la plus forte diminution de la décomposition. Par exemple Yahdjian *et al.* (2006) ont exclu 80 % des précipitations et ont observé après 80 semaines une baisse de la décomposition de 35% seulement, alors que dans l'étude de Sanaullah *et al.* (2012) une interception de 56 % des précipitations a déclenché une diminution d'environ 60 % de la décomposition en seulement 28 semaines. La relation entre le volume des précipitations et la décomposition n'est donc pas linéaire. Yahdjian & Sala (2008) ont émis l'hypothèse que la décomposition des litières de surface est contrôlée par la fréquence des épisodes pluvieux plus que par le volume des précipitations.

Effet de la sécheresse sur l'activité des détritivores

Plusieurs études montrent que la sécheresse a un effet négatif sur l'abondance des détritivores, même dans les milieux méditerranéens où les communautés sont constituées d'espèces résistantes à la sécheresse. D'après David & Handa (2010), une augmentation de la sécheresse peut avoir un impact négatif sur la survie des individus et notamment des juvéniles. Dans des sites de garrigues à *Quercus calliprinos* ayant une végétation et un sol similaires, Sharon *et al.* (2001) ont mis en évidence une relation positive entre l'abondance des détritivores et la moyenne des précipitations. Ces observations sont confirmées par des résultats expérimentaux montrant que l'irrigation d'un écosystème méditerranéen augmente de manière importante l'abondance de la macrofaune détritivore (Morón-Ríos *et al.* 2010). La sécheresse pourrait réduire l'abondance et donc *in fine* affecter négativement l'effet des détritivores sur le processus de décomposition comme le suggère l'étude de Garcia-Pausas *et al.* (2004). Cette étude de terrain portant sur trois sites méditerranéens ayant des moyennes annuelles de précipitations très contrastées, a montré que la production de boulettes fécales par la faune était beaucoup plus importante dans les sites les plus pluvieux.

La sécheresse peut aussi avoir des conséquences à court terme sur l'activité des détritivores. Dias *et al.* (2012) ont montré grâce à une expérience en milieu contrôlé qu'un passage de l'humidité relative de l'air de 80 % à 50 % diminuait entre 3 et 4 fois le taux de consommation de l'isopode *Porcellio scaber*. Plusieurs études ont montré que des macroarthropodes détritivores consommaient moins les litières sèches que les litières humides (Bertrand *et al.* 1987; David & Gillon 2002; Collison *et al.* 2013). On peut donc faire l'hypothèse que la consommation de litière par les détritivores sera négativement affectée par la sécheresse en milieu méditerrannéen, même si l'on peut s'attendre à des réponses variables d'une espèce animale à l'autre (Collison *et al.* 2013).

La sécheresse peut également modifier les interactions entre différentes espèces de détritivores. En effet des études à la fois théoriques (Cardinale *et al.* 2000) et expérimentales (Steudel *et al.* 2012) suggèrent que la relation biodiversité-fonction est dépendante du contexte environnemental. Suivant l'hypothèse des gradients de stress (SGH), les interactions positives entre espèces ont tendance à être plus fréquentes dans des conditions plus stressantes, qui favorisent la facilitation par rapport à la compétition (Bertness & Callaway 1994). Selon cette hypothèse on pourrait s'attendre à une relation entre la diversité des détritivores et la décomposition plus prononcée en conditions sèches.

Résumé des objectifs et plan de la thèse

Figure 6. Photo d'*Ommatoiulus sabulosus*

L'objectif principal de cette thèse est d'étudier l'effet des détritivores et de leur diversité sur la décomposition des litières en garrigue méditerranéene dans un contexte de sécheresse accrue. La **première partie**, comportant les deux premiers chapitres de la thèse porte sur l'effet du diplopode *Ommatoiulus sabulosus* sur la décomposition des litières de 4 espèces typiquement méditerranéennes (*Quercus coccifera*, *Cistus albidus*, *Rosmarinus officinalis*, *Ulex parviflorus*). Cette espèce de détritivore, remarquable par son abondance dans ce type d'écosystème, est apparue comme un organisme modèle évident pour étudier en détail les mécanismes directs et indirects par lesquels les macroarthropodes du sol influencent la décomposition.

Le **chapitre 1** se focalise sur les interactions entre macroarthropodes du sol et microorganismes à deux niveaux d'humidité des litières. Dans ce premier chapitre, j'ai cherché à tester l'hypothèse selon laquelle les macroarthropodes stimulent la décomposition microbienne en déposant d'importantes quantités de boulettes fécales pouvant avoir un effet d'inoculum sur les litières (H1a). L'expérience en microcosmes réalisée pour tester cette hypothèse a également permis d'étudier la variation du taux de consommation d'*Ommatoiulus* sous différentes conditions d'humidité (H1b).

Dans le **chapitre 2** je me suis intéressé, via une étude de décomposition *in situ*, à deux mécanismes par lesquels la faune peut influencer le processus de décomposition : (i) la transformation des litières en boulettes fécales, et (ii) l'enfouissement de la matière organique dans le sol. La matière organique contenue dans les boulettes fécales étant généralement plus récalcitrante que dans les litières, j'ai testé l'hypothèse que les boulettes se décomposent plus lentement que les litières (H2a). Inversement, l'enfouissement de la matière organique, en améliorant les conditions micro-environnementales pour les microorganismes, pourrait accélérer la décomposition et compenser la qualité inférieure des boulettes fécales comparé aux litières foliaires (H2b).

Dans la **seconde** partie de la thèse, développée également sous la forme de deux chapitres (respectivement 3 et 4), j'ai tenté d'améliorer la compréhension de la relation entre diversité des détritivores et fonctionnement du sol. L'objectif principal de cette partie est de tester cette relation biodiversité-fonction en faisant varier expérimentalement, non seulement la diversité des détritivores, mais aussi la diversité des litières et la disponibilité en eau. J'ai choisi 5 espèces de détritivores parmi les plus représentatives du pool régional d'espèces et de la même manière 5 espèces de litières méditerranéennes pour créer des assemblages selon un gradient de diversité fonctionnelle. Une vaste expérience en microcosmes a été réalisée à l'Ecotron de Montpellier.

Le **chapitre 3** traite des effets de la diversité fonctionnelle sur une large gamme de processus du sol (perte de masse des litières, activité microbienne du sol, lessivage) mesurés à l'échelle de la communauté (assemblage d'espèces de détritivores et de litières). Dans un premier temps, j'ai testé l'hypothèse selon laquelle la diversité fonctionnelle des détritivores et celle des litières interagit de manière positive. Selon cette hypothèse les processus du sol devraient être optimaux dans les

traitements combinant à la fois un haut niveau de diversité des détritivores et des litières (H3a). D'autre part, la sécheresse pourrait modifier la relation entre la diversité fonctionnelle et les processus du sol. Comme la relation biodiversité-fonction repose sur des mécanismes impliquant des interactions entre organismes, on peut supposer que, selon l'hypothèse des gradients de stress (SGH), la relation diversité fonction soit plus prononcée dans les conditions de stress hydrique (H3b).

Enfin, dans le **chapitre 4** la relation entre la diversité des détritivores et la perte de masse des litières a été étudiée séparément pour chacune des 5 espèces de litières. Le premier objectif a été de déterminer quels traits fonctionnels de la faune sont importants pour prédire son effet net sur la décomposition (H4a). J'ai ensuite voulu tester l'hypothèse selon laquelle la relation entre la diversité des détritivores et la décomposition est déterminée par la qualité de la matière organique, et donc que la relation biodiversité-fonction diffère suivant l'identité de l'espèce de litière (H4b).

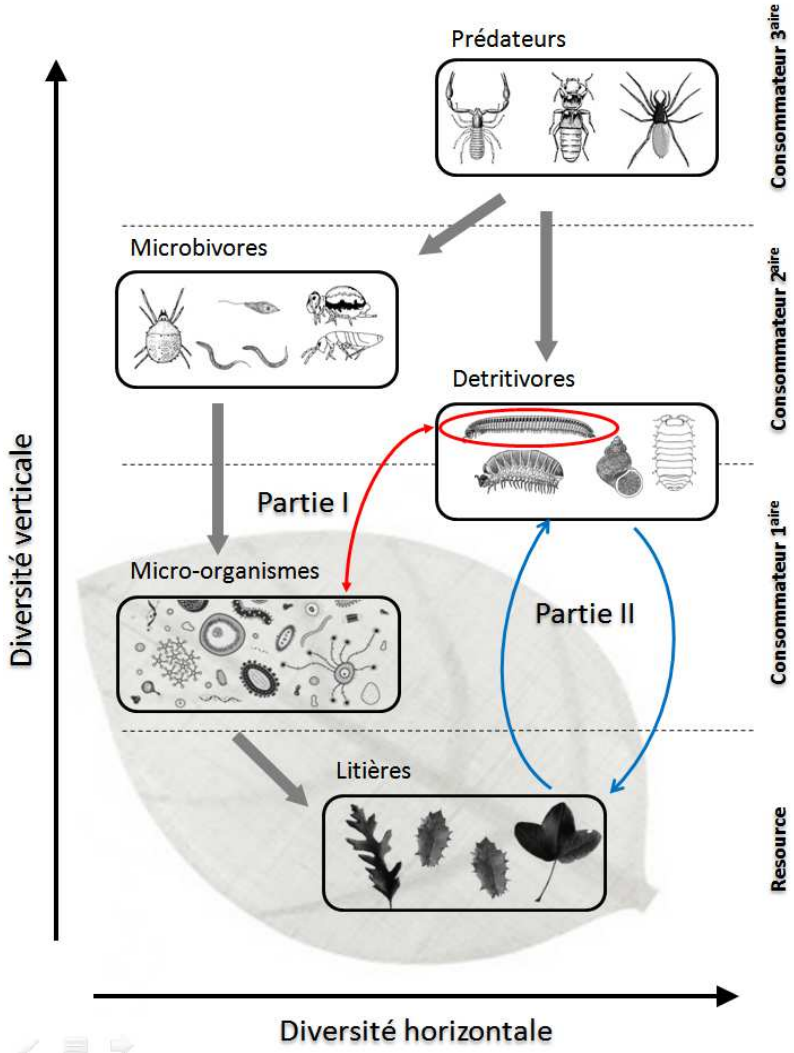

Figure 7. Schéma replaçant les interactions étudiées au cours de ma thèse dans un cadre trophique plus général. La flèche rouge indique les interactions entre détritivores et microorganismes et les flèches bleues font référence aux interactions entre la diversité des litières et la diversité des détritivores.

Présentation de l'écosystème étudié

Figure 8. Photo aérienne du site expérimental du massif de l'Etoile. Les structures carrées correspondent aux dispositifs d'exclusion de pluie.

Les travaux de cette thèse s'inscrivent dans un projet plus large, le projet CLIMED, qui étudie l'impact des changements climatiques sur la biodiversité et le fonctionnement d'un écosystème méditerranéen. Une expérience d'exclusion de pluie a débuté à l'automne 2011 dans une garrigue à chêne kermès du massif de l'Etoile à Marseille, et le projet CLIMED a pour but d'étudier les conséquences de la sécheresse sur la croissance des plantes, la macrofaune, la mésofaune et les mircoorganismes du sol, ainsi que sur le processus de décomposition. C'est sur ce site que l'expérience de terrain du chapitre 2 a été réalisée et les caractéristiques de cet écosystème ont servi de références pour préparer les expériences en microcosmes des autres chapitres.

LA GARRIGUE DU MASSIF DE L'ETOILE

Notre site d'étude fait partie du massif de l'Etoile, un petit massif montagneux culminant à 779 m et recouvrant une surface de 10 000 hectares. Ce massif est dépourvu d'habitations mais est entouré du tissu urbain dense de l'agglomération d'Aix-Marseille. Les roches sont issues de sédiments calcaires déposés pendant la période mésozoïque (de -270 à -80 Ma). C'est ensuite pendant le Paléocène et l'éocène (de -65 à -35 Ma) que des mouvements de compression ont provoqué les plis et les failles à l'origine des reliefs actuels. Le site d'étude du projet CLIMED est situé dans la partie sud du massif, sur un petit plateau de calcaire dur à 269 m d'altitude. Il appartient à la ville de Marseille.

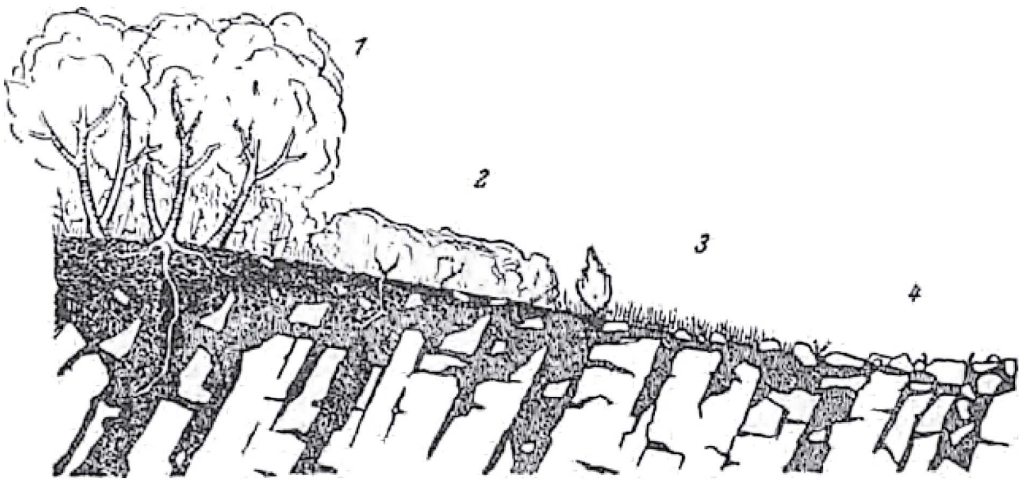

Abb. 378. Regressionsstadien und Ersatzgesellschaften des *Quercetum ilicis galloprovinciale typicum* und seines Bodenprofils auf kompaktem Kalk (aus Br.-Bl. 1936). *1 Quercetum ilicis, 2 Quercetum cocciferae brachypodietosum, 3 Brachypodietum ramosi, 4* Überweidetes *Euphorbia characias*-Stadium

Figure 9. Série régressive de la végétation méditerranéenne sur calcaire dur. La végétation du massif de l'étoile correspond dans cette classification au stade 2 ou le chêne kermès et le brachypode rameux sont les espèces dominantes (cf légende en allemand pour les noms latin des groupements végétaux). Tiré de Braun-Blanquet (1964).

La végétation est typiquement méditerranéenne : environ 60% du massif est recouvert par la garrigue. La présence humaine, qui est attestée de longue date, est marquée par de petites industries du

Moyen Age (carrières et four à chaux) ainsi que des communautés monastiques. Le massif a longtemps été utilisé par ses habitants pour le pâturage et le prélèvement de bois, l'homme a donc joué un rôle important dans la structuration de la végétation. Le dernier grand incendie, en 1997, a couvert les 3500 hectares correspondant au versant sud du massif où se trouve le site expérimental. Le feu est maintenant le seul élément qui maintient une végétation ouverte sur le massif car le pâturage n'est plus pratiqué. Si l'action combinée du feu et des activités humaines a permis l'évolution et le maintien d'une flore diversifiée, c'est probablement au détriment de la qualité des sols et de leur fertilité. En effet, le sol est aujourd'hui peu profond et comporte une grande proportion de cailloux ce qui est caractéristique d'un sol érodé. On peut supposer que l'état actuel résulte d'une série régressive de végétation due à l'érosion des couches superficielles du sol, telle que l'a décrite Braun-Blanquet (Figure 9).

LE SITE EXPERIMENTAL DU MASSIF DE L'ETOILE

Les dispositifs d'exclusion de pluie

Pour simuler une sécheresse expérimentale, des dispositifs de 4 x 4 m surmontés de gouttières en acier inoxydable couvrant 40 % de la surface, ont été installés sur le site. Ces dispositifs sont couplés à un gradient de diversité végétale. Des placettes comprenant les 4 principales espèces arbustives du site dans toutes les combinaisons de diversité possibles (une, deux, trois ou quatre espèces) ont été équipées. Pour chacune des 15 combinaisons, 3 placettes ont été installées. Comme les dispositifs perturbent le rayonnement car ils recouvrent en partie la végétation, autant de placettes ont été équipées de dispositifs témoins dont les gouttières retournées n'excluent pas la pluie. Au total 90 dispositifs ont été installés sur une superficie de 2,5 hectares.

Figure 10. Photo des dispositifs d'exclusion de pluie (arrière plan) avec les tuyaux évacuant les précipitations hors des parcelles (au premier plan).

La végétation

Sur l'ensemble des 2,5 hectares du site expérimental, 64 espèces végétales ont été identifiées en 2011 par le botaniste Daniel Pavon (cf. annexe 1). Par la suite, Natalia Rodriguez a fait des relevés d'abondance de la végétation sur les 94 placettes équipées de dispositfs. Ses résultats montrent que 5 espèces dominent la communauté végétale (Figure 11). Parmi ces 5 espèces, 4 espèces arbustives peuvent être qualifiées de pyrophytes : le chêne kermès (*Quercus coccifera*), le ciste cotonneux (*Cistus albidus*), le romarin (*Rosmarinus officinalis*) et l'ajonc de Provence (*Ulex parviflorus*). Le chêne kermès a une stratégie de « resprouter » ; sa souche résiste au feu et il émet des rejets rapidement après un incendie. Bien que leur âge n'ait pas été estimé, les chênes kermès présents sur notre site sont probablement plus vieux que l'incendie de 1997 (>26ans). Les trois autres espèces arbustives dominantes sont des « seeders », c'est-à-dire que le feu provoque la mort des individus mais favorise la germination des graines. Les individus de ces trois espèces sont donc forcément plus jeunes que l'incendie (<26ans). Enfin le brachypode rameux (*Brachypodium retusum*) est une espèce de graminée hémicryptophyte qui est, dans cette région, caractéristique des pâturages ovins abandonnés. Les 5 plantes dominantes du site traduisent bien les éléments structurants des communautés végétales que sont le feu et les pratiques anthropiques sylvo-pastorales.

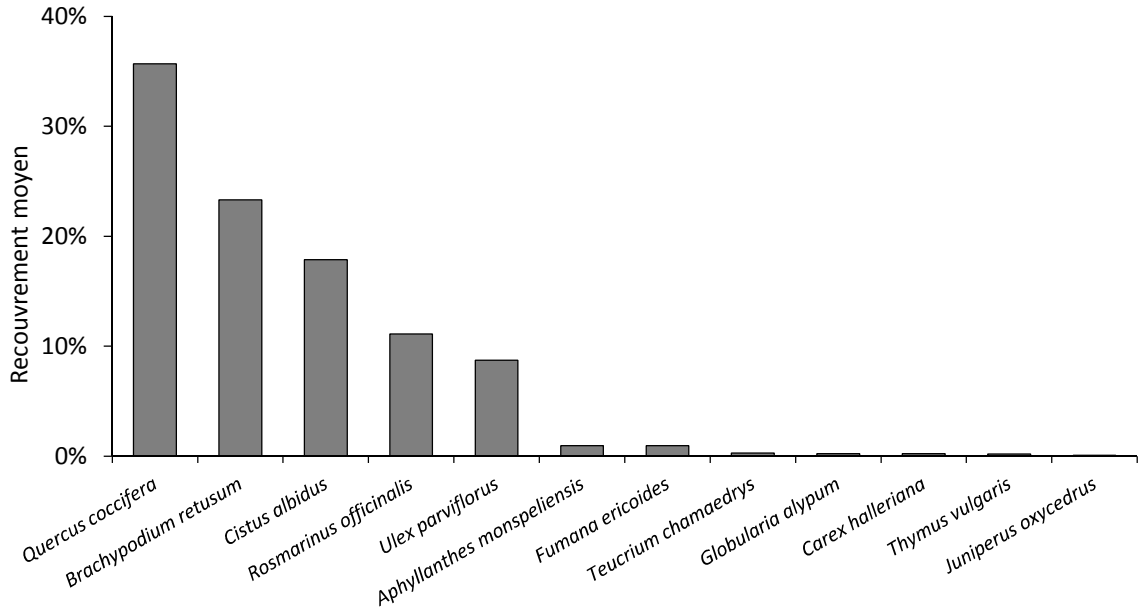

Figure 11. Recouvrements relatifs des 12 principales espèces végétales présentes sous les dispositifs d'exclusion de pluie (Données Natalia Rodríguez, Juin 2012).

Parmi les cinq espèces végétales qui ont été utilisées dans les expériences en microcosmes, quatre sont les arbustes dominants du site expérimental (*Quercus, Cistus*, *Rosmarinus* et *Ulex*). La cinquième espèce, le pin d'Alep (*Pinus halepensis*), qui s'installe fréquemment dans les garrigues à chêne kermès suite à la déprise pastorale, est très peu présente sur le site (17ème espèce en terme de recouvrement) mais est un arbre commun dans le massif de l'Etoile.

La faune du sol

La densité moyenne de la communauté de macroarthropdes du sol (détritivores, herbivores et prédateurs) a été estimée à 558 ± 101 individus/m² au printemps 2012. L'abondance relative des fourmis est de 81%, une forte proportion qui est caractéristique des écosystèmes méditerranéens (Doblas-Miranda *et al.* 2009). Les macroarthropodes détritivores ne représentent que 5 % de l'abondance totale dans cet échantillon, mais le diplopode *Ommatoiulus sabulosus*, qui représente à lui seul plus de 95% de l'abondance des détritivores, est l'espèce la plus abondante après les fourmis. Il existe des variations importantes de la densité de population d'*Ommatoiulus* entre les différentes années. En 2010, la densité de population était de 164 ± 37 individus/m² alors qu'en 2012 elle n'était plus que de 27 ± 4 individus/m². Cependant la biomasse est restée importante en 2012 (5.3 ± 0.9 g/m² contre 9.2 ± 2.0 g/m² en 2010) car la population était composée essentiellement d'adultes de grande taille (masse moyenne d'environ 200 mg). *Ommatoiulus* est l'espèce animale ayant probablement la biomasse la plus importante dans le sol (excepté peut-être les vers de terre, qui n'ont pas encore été échantillonnés). En effet les fourmis qui comptent beaucoup d'individus pèsent pour beaucoup dans l'abondance, mais comme la plupart des individus sont de très petite taille (< 2 mm), la biomasse de fourmis reste faible comparée aux *Ommatoiulus* dont les femelles atteignent facilement 35 à 40 mm.

Figure 12. Photos des macroinvertébrés du sol étudiés au cours de ma thèse. Sur la photo de gauche, trois individus d'espèces différentes observés sous la même pierre. Malgré leur distance phylognéntique, ces trois espèces ont la même aptitude à se rouler en boule (de bas en haut : *Glomeris marginata*, *Glomeris anulata*, *Armadillo officinalis*). Sur les photos de droite : *Arladillidium vulgare* (haut) et *Pomatias elegans* (bas).

Parmi les cinq espèces d'invertébrés détritivores utilisées dans les expériences en microcosmes, seul *Ommatoiulus sabulosus* est présent sur le site de l'Etoile. Cependant, les quatre autres espèces (Figure 12), le diplopode *Glomeris marginata*, le gastéropode *Pomatias elegans*, et les isopodes *Armadillidium vulgare* et *Armadillo officinalis*, sont assez communes dans les garrigues à chêne kermès du sud de la France. D'ailleurs, à l'exception d'*Armadillo*, elles ont toutes été récoltées par Bigot et Bodot (1972) lors d'une étude sur un autre site du massif de l'Etoile.

Chapitre 1 : Effets directs et indirects d'*Ommatoiulus*

Figure 13. Photo montrant un exemple de microsome utilisé au cours de l'expérience décrite dans ce chapitre. Les litières des 4 espèces (ajonc et romarin en haut, chêne et ciste en bas) étaient séparées par des petits bâtonnets en plastique empêchant les litières de se mélanger mais permettant aux détritivores de se déplacer sans difficulté. Inutile de chercher des *Ommatoiulus* sur la photo car c'est une boite sans faune qui a été prise en photo. Par contre comme c'est une boite du traitement « ajout de boulette fécales », il est possible de discerner les petites boulettes fécales qui étaient déposées sur les litières tous les deux jours pendant toute la durée de l'expérience.

Résumé du chapitre

Contexte :

Les détritivores jouent un rôle important dans le processus de décomposition car ils se nourrissent de litière. Ces organismes du sol peuvent être très abondants, en particulier dans les écosystèmes méditerranéens où les populations de diplopodes peuvent consommer jusqu'à 47% des chutes annuelles de litière (David & Gillon 2002). Cependant il est généralement admis que les détritivores ont peu d'effet direct sur la décomposition mais stimulent indirectement l'activité des décomposeurs microbiens. En effet, ils ne digèrent qu'une faible proportion des litières ingérées et rejettent de grandes quantités de boulettes fécales, dans lesquelles l'activité microbienne est généralement plus élevée que dans les litières. Ainsi, les microorganismes des boulettes fécales peuvent jouer un rôle d'inoculum dans les litières non-consommées, et accélérer leur décomposition. L'objectif de ce chapitre est donc de tester si l'ajout de boulettes fécales de diplopodes stimule la décomposition des litières et peut ainsi jouer le rôle de « fertilisant » (H1a)

Figure 14. Photos montrant les outils d'analyse microbienne utilisés pour étudier les microorganismes des boulettes fécales et des litières. A gauche, la migration des extraits de lipides membranaires à travers des billes de silice a pour but de séparer les phospholipides des autres lipides memebranaires avant leur dosage. A droite le multiplexeur permettant d'effectuer les mesures de respiration potentielle sur 30 échantillons simultanément.

Méthodes :

La principale espèce de détritivore sur le site de l'Etoile est le diplopode *Ommatoiulus sabulosus*, dont l'abondance atteint 164 individus/m² pendant les pics d'activité. Pour comprendre l'effet de l'ajout de boulettes fécales de cette espèce sur l'activité microbienne et la décomposition, nous avons réalisé une expérience en conditions contrôlées de 30 jours ; durant laquelle les litières des quatre espèces du site de l'Etoile ont été incubée au sein des mêmes microcosmes mais dans des patches distincts (Figure 13) selon trois traitements différents : (i) en absence d'*Ommatoiulus*, (ii) en présence d'*Ommatoiulus* et (iii) en absence d'*Ommatoiulus* mais en déposant régulièrement ses boulettes fécales sur les litières. Comme les écosystèmes méditerranéens sont très influencés par le manque d'eau et

qu'il est prévu que les changements climatiques augmentent la fréquence des sécheresses, nous avons simulé deux conditions d'humidité différentes. Les conditions sèches correspondaient à un arrosage deux fois moins fréquent, et donc à deux fois moins d'eau ajoutée. A l'issue de l'expérience la perte de masse des litières et la respiration potentielle (SIR) ont été mesurées dans les litières des 4 espèces (Figure 14). De plus les phospholipides membranaires ont été dosés dans ces litières de ciste (la litière la plus impactée par *Ommatoiulus*) pour caractériser l'impact du dépôt de boulettes fécales sur la structure des communautés microbiennes (Figure 14).

Résultats et discussion :

Ommatoiulus a transformé de grandes quantités de litière en boulettes fécales au cours de l'expérience, ce qui confirme l'importance de son rôle en tant que fragmenteur. De plus, des préférences alimentaires ont été mises en évidence : entre les quatre espèces proposées, le ciste cotonneux (*Cistus albidus*) a représenté 71 % des litières consommées. De ce fait, la majorité des boulettes fécales ont également été déposées sur le ciste. Cependant, le dépôt de boulettes n'a modifié ni l'activité microbienne dans les litières ni leur perte de masse, contrairement à notre hypothèse de départ. Le ciste a également été la litière où la communauté microbienne était la plus active en absence d'animaux. Ces résultats suggèrent que, dans cet écosystème, les fragmenteurs et les microorganismes recyclent plus rapidement les nutriments contenus dans les litières de ciste.

En absence d'*Ommatoiulus*, la décomposition microbienne a été affectée par la sécheresse et la perte de masse des litières a été beaucoup plus faible en conditions sèches qu'en conditions humides (-58%). A l'inverse, en présence d'*Ommatoiulus*, la perte de masse n'a diminué que de 28% en conditions sèches par rapport aux conditions humides, car la consommation du diplopode (en moyenne de 84 ± 4 mg/g) n'a pratiquement pas varié. Ce résultat suggère que la faune du sol est plus résistante à la sécheresse que les décomposeurs microbiens. Le rôle des animaux détritivores pourrait être important pour le maintien des processus de décomposition dans les écosystèmes méditerranéen où les sécheresses risquent d'être plus fréquentes et plus marquées.

Macroarthropod-microorganism interactions during the decomposition of Mediterranean shrub litter at different moisture levels

Article published in the journal « Soil Biology & Biochemistry »

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Abstract

Saprophagous macroarthropods reach high population densities in many Mediterranean terrestrial ecosystems of southern Europe but their impact on decomposition processes remains unclear. We studied the effects of the millipede *Ommatoiulus sabulosus* on the decomposition of litter from four shrub species (*Cistus albidus, Quercus coccifera, Rosmarinus officinalis* and *Ulex parviflorus*) in a 1-month laboratory experiment. Millipede effects on litter mass loss, organic matter decomposition, and substrate-induced respiration (SIR) in faecal pellets and uningested litter, were assessed in simplified systems (litter, microorganisms, detritivores). By adding freshly collected millipede faecal pellets to litter, we specifically tested their influence on mass loss rate, SIR rate and microbial community structure and biomass (using PLFA profiles). Two watering frequencies were used to study the effects of simulated drought on these processes. Millipedes consumed large amounts of shrub litter with a low assimilation efficiency. The largest effect was observed for *Cistus* that showed also the highest rate of microbial-driven decomposition. Conversion of litter into faecal pellets by millipedes did not increase organic matter decomposition and there was no evidence for a stimulation of microbial activity in faecal pellets compared to uningested litter. Faecal pellet deposition on litter, which was maximal in *Cistus*, did not change mass loss and SIR rates in the underlying litter, but significantly changed microbial community structure. Bacterial biomass was lower and fungal:bacterial ratio was higher in moist, but not in dry *Cistus* litter, after 1 month of faeces addition. Simulated drought strongly decreased microbial-driven decomposition but not millipede feeding activities. The resulting sustained production of faecal pellets, however, did not offset the lower rate of microbial organic matter decomposition in dry litter. We conclude that the transformation of large amounts of shrub litter into faeces by macroarthropods and the resultant interactions with microorganisms do not enhance carbon mineralization in the short term, regardless of litter humidity. We however surmise that faeces could be incorporated into the soil more easily than intact plant litter, with important consequences for carbon and nutrient cycling in Mediterranean ecosystems under increasing drought.

Keywords: Millipedes, Litter decomposition, Litter quality, Faecal pellets, Microbial biomass, Microbial respiration, Drought, Mediterranean ecosystem

INTRODUCTION

Litter decomposition, i.e. the gradual breakdown of dead organic material that is ultimately mineralized into CO_2 and mineral nutrients, is a key process in terrestrial ecosystems (Chapin III & Matson 2002). The activity of microbial decomposers (bacteria and fungi) depends primarily on litter quality and climatic conditions (Aerts 1997; Heal *et al.* 1997; Lavelle & Spain 2001) and, in this respect, Mediterranean ecosystems have several distinctive features. First, in spite of large differences in decomposition rates among plant species, the common and abundant evergreen sclerophyllous, coniferous and aphyllous species generally decompose slowly due to the toughness and low nutrient content of their leaves, needles or thorns (Gallardo & Merino 1993; Gillon *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Cornwell *et al.* 2008). Second, the summer is typically dry, and drought periods that affect the litter and upper soil layers exert a strong climatic control on decomposition rates (Aerts 1997; Bottner *et al.* 2000; Saura-Mas *et al.* 2012). This influence of drought is predicted to become more pronounced with climate change, due to reduced frequencies and amounts of rainfall in the Mediterranean region (IPCC 2007; Giorgi & Lionello 2008). Another feature of Mediterranean ecosystems is that saprophagous macroarthropods can reach very high abundance and biomass locally, especially in southern Europe (Iatrou & Stamou 1991; David *et al.* 1999; David 1999). These detritivores ingest large amounts of leaf litter with a typically low assimilation efficiency, resulting in the production of large amounts of faecal pellets, clearly visible in the litter and topsoil layers (Garcia-Pausas *et al.* 2004; Tagger *et al.* 2008). In a holm oak (*Quercus ilex*) forest of southern France, for example, the millipede *Glomeris marginata* was reported to consume about 109 g (dry mass) m^{-2} of leaf litter and egest 103 g (dry mass) m^{-2} of faecal pellets per year (David & Gillon 2002). Such high feeding activities have potentially important consequences for decomposition processes in these systems.

Soil invertebrates can affect decomposition directly and indirectly. Macroarthropods, as litter fragmenters, generally have little direct effect on organic matter decomposition through assimilation and respiration (Wolters 2000; Lavelle & Spain 2001). Large amounts of undecomposed plant material, especially cell wall structural constituents, are egested in their faeces (Gillon & David 2001). Therefore, a clear distinction must be made between the impact of macroarthropods on litter mass loss, which can be substantial in many types of litter, and their direct impact on organic matter decomposition, which remains marginal.

Indirect effects of macroarthropods on decomposition through interactions with microorganisms are thought to be important (Visser 1985; Wolters 2000; Lavelle & Spain 2001). Such interactions were mainly investigated in macroarthropod faeces, and large increases in bacterial counts were observed in freshly egested material compared to uningested leaf litter (Ineson & Anderson 1985; Hassall *et al.* 1987; Byzov *et al.* 1998). This has led to the widely accepted view that microbial activity

is stimulated and organic matter decomposition enhanced in macroarthropod faeces (Lavelle & Spain 2001; Coleman *et al.* 2004; Bardgett & Wardle 2010). However, other studies found that microbial respiration was not greater in faecal pellets than in uningested leaf litter (Scheu & Wolters 1991; Suzuki *et al.* 2012) and, similarly, that mass loss rates were not higher in macroarthropod faeces than in leaf litter (Nicholson *et al.* 1966; Webb 1977; Frouz & Simek 2009). This may result from the compact structure of faecal pellets that inhibits microbial decomposition (Webb 1977; Suzuki *et al.* 2012) and from the depletion of readily assimilable carbon compounds associated with increased concentrations of recalcitrant compounds such as lignin, which is not digested by macroarthropods (Gillon & David 2001; Rawlins *et al.* 2006).

Interactions between macroarthropods and microorganisms also occur in leaf litter (Visser 1985; Crowther *et al.* 2012). Some are linked to the grazing behaviour of invertebrates, which inevitably results in damage to fungal tissues. However, these interactions are complex and may have negative or positive effects on decomposition (Crowther *et al.* 2011). For example, Hanlon and Anderson (1980) showed that macroarthropod feeding activities stimulated carbon mineralization at low but not at high population densities of the woodlouse *Oniscus asellus*, which may depend on the grazing pressure on litter fungi. Macroarthropods are also good dispersers of propagules, both on their body surface and in their faeces (Lilleskov & Bruns 2005), which may accelerate microbial colonization of litter substrates. Finally, the deposition of fresh faeces, supposed to be hotspots of bacterial activity, on leaf litter may enhance decomposition (Visser 1985; Frouz & Simek 2009). This type of interaction, however, is only poorly studied and understood.

In this study, we examined the direct and indirect effects of saprophagous macroarthropods on the decomposition of plant litter from Mediterranean species, with special attention to interactions with litter microorganisms and the influence of increased drought. We investigated the effects of the millipede *Ommatoiulus sabulosus* on the decomposition of litter from four woody species (*Cistus albidus, Quercus coccifera, Rosmarinus officinalis* and *Ulex parviflorus*) in a 1-month laboratory experiment. These four shrub species are common and abundant in the garrigue ecosystem of southern France on calcareous bedrock. Due to its remarkably high abundance in this type of ecosystem, *Ommatoiulus* produces large amounts of faecal pellets in spring and autumn, which potentially leads to strong interactions with microbial decomposers. As more frequent dry spells and droughts are expected in the Mediterranean region, we carried out the experiment at two moisture levels, to study the effects of intermittent drying of litter on microbial and faunal activity. Microbial activity is known to decrease steadily with decreasing litter moisture (Manzoni *et al.* 2012). Leaf litter consumption by macroarthropods is generally reduced by low moisture contents (Bertrand *et al.* 1987; David & Gillon 2002; Collison *et al.* 2013), but Tian *et al.* (1997) suggested that fauna-mediated decomposition could be less susceptible to drought than microbial decomposition.

More specifically we assessed (1) the effects of millipedes on litter mass loss and organic matter decomposition, and their effects on microbial activity in faeces and uningested litter. For the first time, we studied the consequences of faecal pellet addition to leaf litter for decomposition and microbial biomass and activity. (2) We evaluated the consequences of low litter moisture contents for both millipede feeding activities and microbial activity in litter and faeces, and tested the notion that macroarthropods can mitigate the negative effects of drought on decomposition, i.e. have a relatively more important role when moisture conditions are less favourable (Verhoef & Brussaard 1990; Tian *et al.* 1997). (3) Finally, we took advantage of the occurrence of four litter species of contrasting quality in the same shrubland to test the notion that macroarthropods can also mitigate the negative effects of litter recalcitrance on microbial decomposition, i.e. have a relatively more important role in the decomposition of low-quality litter (Tian *et al.* 1995, 1997; Yang & Chen 2009; Riutta *et al.* 2012).

MATERIALS AND METHODS

Biological material

Leaf litter was collected in a shrubland located in the Massif de l'Etoile near Marseille, France (43°22' N; 5°25' E). A detailed description of the site was given by Montès *et al.* (2008). Litter from the four dominant plant species, *Cistus albidus* (Cistaceae), *Quercus coccifera* (Fagaceae), *Rosmarinus officinalis* (Lamiaceae) and *Ulex parviflorus* (Fabaceae), was collected on the ground in March-April 2011. Freshly fallen litter was excluded because soil macrofauna generally prefer litter with microbial conditioning (Lavelle & Spain 2001). Litter was air-dried in the laboratory, sorted into species and cleaned of adhering soil particles, fruit and flower parts or twigs. Leaves are wooly in *Cistus*, sclerophyllous in *Quercus*, tough and narrow (needle-like) in *Rosmarinus*, whereas *Ulex* litter consists of thorny stems, which are the photosynthetic organs in this aphyllous species. Litter chemical and physical characteristics were determined (Table 1). Total C and N concentrations were measured using a flash elemental analyzer (EA1112 Series; Thermo Finnigan, Milan, Italy), P concentration was measured colorimetrically using an Evolution II autoanalyzer (Alliance Instruments, Cergy, France), and lignin concentration was determined using a Fibersac 24 fibre analyzer (Ankom, Macedon, USA) (Hättenschwiler *et al.* 2008). Condensed tannin concentration was measured sprectrophotometrically using the butanol-HCl method (Coulis *et al.* 2009). To determine water holding capacity, litter was soaked in distilled water for 24 hr, drained, weighed moist and reweighed after drying at 60 °C for 48 hr.

The julid millipede *Ommatoiulus sabulosus aimatopodus* — the Mediterranean sub-species of *Ommatoiulus sabulosus* with no dorsal orange-yellow bands — was collected from the same site in April 2011. It is a very abundant species at the Massif de l'Etoile, whose population density was estimated at 164 ± 37 individuals m^{-2} in the spring of 2010, which represents a live biomass of 9.2 ± 2

g m^{-2} (J.F. David, unpublished data). Individuals in the range of 100 to 200 mg in live mass, mostly sub-adults, were selected and kept at 18 °C in a site-specific mixture of moist leaf litter before the experiment.

Table 1. Characteristics of the four species of shrub litter used in this study (means ± SE). All percentages are on a dry mass basis (CT: condensed tannins; WHC: water holding capacity).

Shrub species	*Cistus albidus*	*Quercus coccifera*	*Rosmarinus officinalis*	*Ulex parviflorus*
C (%)	43 ± 0.2	45 ± 0.3	50 ± 0.3	49 ± 0.2
N (%)	0.64 ± 0.01	1.03 ± 0.02	0.65 ± 0.02	1.08 ± 0.02
C:N ratio	67 ± 1	44 ± 1	76 ± 1	45 ± 1
P (‰)	0.56 ± 0.01	0.50 ± 0.003	0.37 ± 0.01	0.20 ± 0.01
CT (%)	0.6 ± 0.11	0.6 ± 0.02	0.1 ± 0.003	0.1 ± 0.01
Lignin (%)	25 ± 0.5	15 ± 0.4	16 ± 0.3	23 ± 1.0
WHC (%)	178 ± 5	132 ± 2	146 ± 6	97 ± 2

Decomposition experiment in the laboratory

Leaf litter was put in large (40 x 33 x 8.5 cm), lidded transparent plastic boxes, the inside of which was divided into four equal parts by 1 cm high plastic dividers to prevent litter mixing, while allowing fauna to move freely. Six grams of air-dried litter from each of the four species were moistened by submersion in distilled water for 10 min, drained and put separately in each box. Millipedes could thus feed on four monospecific litter patches randomly disposed in each box. Boxes were assigned to three faunal treatments: (1) control boxes without millipedes (n = 10); (2) boxes with six individuals of *Ommatoiulus* of similar size, representing a mean live biomass of 863 ± 12 mg per box, which was equivalent to about 70% of the field estimate of *Ommatoiulus* biomass (n = 10); (3) boxes in which only faecal pellets of millipedes were progressively added to leaf litter (n = 10). For this purpose, fresh pellets were collected every second day in an additional set of 10 boxes with the same millipede biomass as in treatment (2) (862 ± 9 mg per box), and put on the corresponding litter patches (i.e. all faecal pellets collected on a specific litter type were added to the same litter type in boxes of treatment (3). Each litter patch was watered with 1 ml of distilled water either twice a week (moist conditions in five boxes) or only once a week (dry conditions in five boxes). The resulting differences in litter water content were repeatedly assessed in two additional boxes per moisture treatment over the course of the experiment (12 times in total, at various intervals after watering). All the boxes were kept for 30 days in an open shed under Mediterranean conditions (CEFE, Montpellier, France), in which the mean air temperature over the course of the experiment was 19 °C. All

millipedes survived the 30-day period and, at the end of the experiment, they were removed and weighed. Leaf litter and faecal pellets were carefully sorted and weighed. One gram of fresh litter was freeze-dried for phospholipid fatty acid (PLFA) analysis and the remaining material was air-dried and reweighed. Some air-dried sub-samples were used to determine substrate-induced respiration (SIR) and others were oven-dried at 60 °C for 2 days to estimate the water content and final dry mass of air-dried materials. Initial oven-dry litter mass was calculated using litter species-specific conversion factors of air-dried to oven-dried mass.

Initial and final dry masses allowed calculations of the following variables under moist and dry conditions: (1) the percentage mass loss due to microbial decomposition in control boxes without animals. (2) The net effect of millipedes on litter mass loss (g per box), i.e. the difference between the total mass loss of litter observed in their presence and that in their absence in control boxes; the net effect reflects both litter consumption and millipede-microorganisms interactions in uningested litter. (3) The total amount of organic matter that decomposed in the presence of millipedes, i.e. the difference between the total mass loss of litter and the mass of faeces collected at the end of the experiment.

Substrate-induced respiration (SIR) was measured on remaining litter and faecal pellets in order to compare the potential activity of microbial communities in the different treatments. This method assesses the physiological capacity of microorganisms to catabolise glucose under optimal temperature and moisture conditions, and variations in respiration rates reflect changes in both the biomass and composition of microbial communities (Fanin *et al.* 2011). The procedure of Beare *et al.* (1990) was used and the rate of CO_2 release (μg CO_2-C g^{-1} hr^{-1}) was measured using a Varian 4900 gas chromatograph with a thermal conductivity detector (Varian, Walnut Creek, USA). To compare SIR in litter and faecal pellets, it was assumed that each litter species was consumed in proportion to the net effect of millipedes on its mass loss. Hence, litter SIR was calculated as the weighted mean (based on relative consumption of the four litter types) of litter-type specific SIR.

As our experiment showed that *Ommatoiulus* fed mainly on *Cistus* and thus also egested much more faecal pellets on this litter species, PLFA analysis was used to compare bacterial and fungal biomass in the different samples of *Cistus* litter at the end of the experiment. The ratio of fungal to bacterial PLFAs was used as an index of the relative abundance of these two groups of microorganisms (Leckie 2005). Procedures described by Zelles (1999) were used for lipid extraction and separation. After alkaline methanolysis, tridecanoic acid methyl ester (CAS number: 1731-88-0) was added as internal standard and the concentrations of ester-linked fatty acid methyl esters (EL-FAMEs) were determined using a Hewlett Packard 6890 gas chromatograph. Bacterial biomass was estimated by summing the following PLFAs: i15:0, a15:0, i16:0, 16:1ω7, i17:0, a17:0, 18:1ω7 and

cy19:0 (Wilkinson et al., 2002; Ruess and Chamberlain, 2010). Fungal biomass was estimated from the concentration of 18:2ω6,9 (Frostegård *et al.* 2011).

Statistical analyses

All statistical analyses were performed using R software version 2.12.1 (R Development Core Team, 2010). Two types of ANOVA were used: (1) In each faunal treatment, the main effects and interaction of litter species and moisture treatment on litter mass loss, SIR in litter and SIR in faecal pellets, were tested using partly hierarchical ANOVA (Logan 2011). In this design, data from moist and dry boxes were nested within moisture treatments, and litter species were crossed with moisture treatments and boxes. (2) The main effects and interaction of faunal treatment and moisture treatment on the mass loss of each litter species, SIR in each litter species, and microbial biomass data in *Cistus* litter, were tested using two-way ANOVA (3 x 2 factorial design). Homogeneity of variances was checked prior to analyses and data were log- or power-transformed where required. Tukey's HSD test was used for multiple comparisons among pairs of means. Some differences between two sample means were tested using paired *t*-tests, as indicated in the text.

RESULTS

Litter moisture conditions

The two watering frequencies significantly affected litter moisture in all four species. Measurements on 12 occasions during the experiment showed that mean water contents in *Cistus* leaf litter were 55 ± 11% and 33 ± 12% (on a litter dry mass basis) in moist and dry treatments, respectively (paired *t*-test, $P < 0.01$). Similarly, *Quercus* leaf litter had mean water contents of 29 ± 4% and 13 ± 3% in moist and dry treatments, respectively ($P < 0.001$). *Rosmarinus* leaf litter had mean water contents of 38 ± 6% and 15 ± 3% ($P < 0.001$), and *Ulex* litter had mean water contents of 28 ± 4% and 17 ± 4% ($P < 0.001$) in moist and dry treatments, respectively.

Decomposition in control boxes

Litter mass loss in animal- and faeces-free control boxes differed significantly among species ($P < 0.001$), *Cistus* decomposing much faster than the other three species under both moist and dry conditions (Figure 15a). Although correlations between litter mass loss and the measured litter quality parameters were not significant, the mass loss of moist material decreased in the same order as the water holding capacity of litter. Litter mass loss was significantly affected by the moisture treatment ($P < 0.001$). On average across all litter species, total mass loss was 5.50 ± 0.16% under moist conditions compared to 1.91 ± 0.31% under dry conditions. Although there was no significant interaction between litter species and moisture conditions, the four species tended to respond

differently to the moisture treatment. Mass loss in dry conditions was reduced by a factor of 9.6 in *Rosmarinus*, 4.6 in *Quercus*, 2.7 in *Ulex* and 1.8 in *Cistus* (Figure 15a).

Litter SIR rates in control boxes also differed significantly among species ($P < 0.001$) (Figure 15b). The highest respiration rates were recorded in *Cistus* under both moist and dry conditions, but the rank order of other species was not the same as for litter mass loss, with notably significantly higher SIR in *Quercus* than in *Rosmarinus* and *Ulex* that showed the lowest SIR of all litter types (Figure 15b). There was a marginally significant correlation between SIR rates and initial P concentrations in the four litter species under moist conditions ($P = 0.05$), a relationship that however disappeared under dry conditions ($P = 0.16$). None of the other initial litter quality characteristics was significantly correlated with litter SIR. In contrast to litter mass loss, SIR was not significantly affected by the moisture treatment. There was however a significant interaction between litter species and moisture conditions ($P < 0.05$): under dry conditions, SIR increased in *Ulex* but did not change significantly in the other species (Figure 15b).

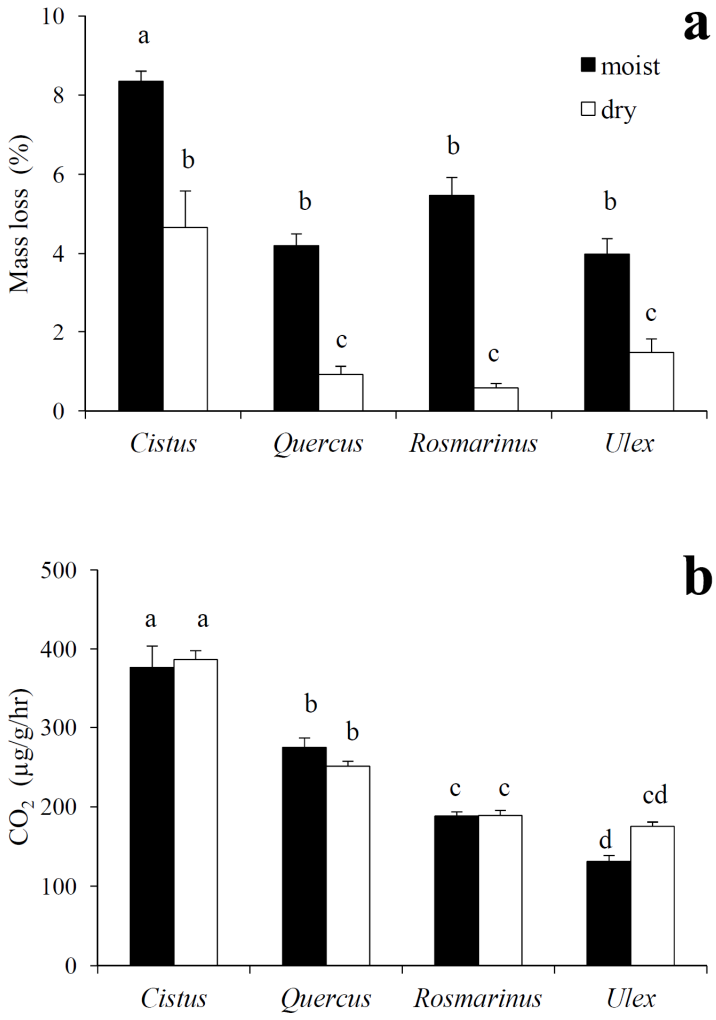

Figure 15. Mass loss as a percentage of initial dry mass (a) and substrate-induced respiration (b) of four species of shrub litter maintained for 1 month at two levels of litter moisture (means ± SE, *n* = 5).

Decomposition in boxes with millipedes

The net effect of millipedes on litter mass loss differed significantly among litter species ($P < 0.001$), with a stronger effect on *Cistus* than on any of the other species under both moist and dry conditions (Figure 16). Millipede effects on litter mass loss were not significantly correlated with the litter quality parameters reported in Table 1, but they were positively correlated with the mass loss of each litter species measured in moist control boxes ($P < 0.05$). For all species combined, the activity of millipedes led to a loss of 2.30 ± 0.17 and 2.11 ± 0.18 g litter per box under moist and dry conditions, respectively. Litter mass loss induced by millipedes was not significantly different from the mass of faecal pellets collected at the end of the experiment (2.43 ± 0.09 and 1.99 ± 0.15 g per box under moist and dry conditions, respectively; non-significant paired *t*-tests), indicating that a very large part of the litter consumed was not assimilated.. The impact of millipedes on litter mass loss was not significantly affected by litter moisture ($P = 0.46$). There was however a significant interaction between litter species and moisture conditions ($P < 0.01$). Under dry conditions, the millipede effect on *Cistus* was relatively smaller while that on *Rosmarinus* was relatively greater, indicating a shift in food preference when litter was drier.

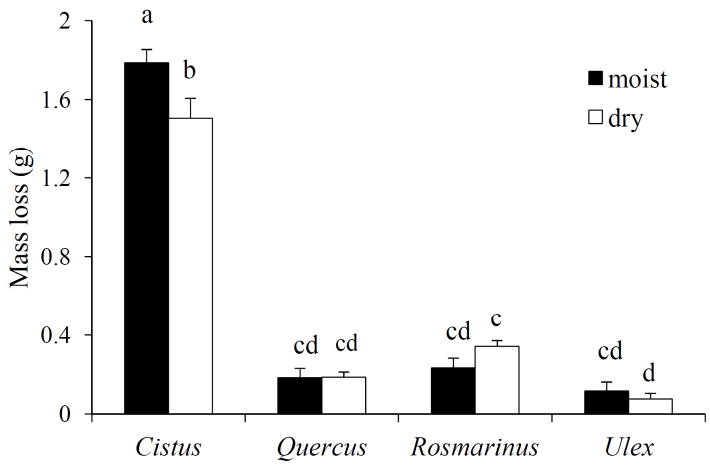

Figure 16. Net effect of millipedes on the mass loss of four species of shrub litter after incubation for 1 month at two levels of litter moisture (means ± SE, *n* = 5). The net effect of millipedes is the difference between the total mass loss of litter measured in their presence and that measured in their absence in control boxes.

Organic matter decomposition in the presence of millipedes, i.e. the difference between the total mass loss of litter and the mass of faeces collected at the end of the experiment, was on average 1.11 ± 0.11 g per box under moist conditions vs. 0.54 ± 0.07 g per box under dry conditions. This amount of mineralized litter was not significantly different from that expected from microbial decomposition alone , i.e. 1.24 ± 0.01 and 0.43 ± 0.01 g per box under moist and dry conditions, respectively (non-significant paired *t*-tests), indicating that millipede feeding activities had very little impact on organic matter decomposition over the experimental duration of one month.

SIR rates in the litter remaining in boxes with millipedes at the end of the experiment did not differ significantly from those measured in control boxes (data not shown). SIR rates in faecal pellets varied significantly depending on the litter species on which faecal pellets were egested by millipedes ($P < 0.001$) (Figure 17). The highest respiration rates were measured in pellets from *Cistus* patches and the lowest respiration rates were measured in pellets from *Quercus* patches. SIR rates in faecal pellets ranged from 204 to 310 µg CO_2 g^{-1} hr^{-1} in the moist treatment and from 147 to 298 µg CO_2 g^{-1} hr^{-1} in the dry treatment (Figure 17). These rates were consistently lower than those estimated for litter mixtures containing the four species in proportion to the amounts consumed by millipedes, i.e. 340 and 336 µg CO_2 g^{-1} hr^{-1} under moist and dry conditions, respectively. In contrast to SIR rates in litter, SIR rates in faecal pellets were significantly affected by the moisture treatment ($P < 0.01$), with lower respiration rates under dry conditions (Figure 17), indicating that microorganisms present in faeces were more sensitive to drought than those present in uningested litter.

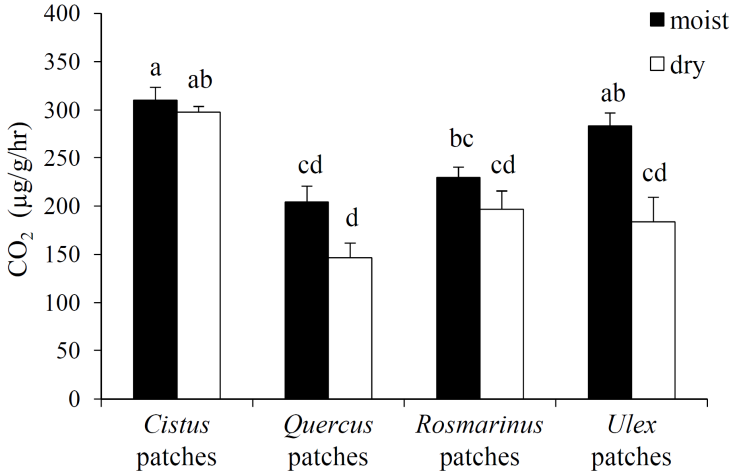

Figure 17. Substrate-induced respiration of faecal pellets egested by millipedes on four species of shrub litter under moist and dry conditions. The pellets were 2-day to 1-month old (means ± SE, $n = 5$).

Decomposition in boxes with faeces addition

The collection of fresh faecal pellets in the set of boxes intended for faeces production showed that millipedes deposited much more faecal pellets on *Cistus* litter patches than on the other three species, in accordance with their apparent preference for *Cistus* litter. The dry weight of faecal pellets added to litter in the absence of millipedes, as estimated at the end of the experiment, was on average 1.13 ± 0.06 g in *Cistus* patches and ranged between 0.14 ± 0.01 and 0.25 ± 0.03 g in other litter patches. Faecal pellet addition in the absence of millipedes did not significantly affect litter mass loss and SIR in any of the four species, the results being very similar to those recorded in control boxes under either moisture conditions (data not shown).

Microbial community structure in Cistus leaf litter

In control boxes, total microbial biomass in *Cistus* litter determined with PLFAs was not significantly different between the moist and dry treatments (Table 2). However, the effects of these two treatments differed between bacterial and fungal markers. While there was no moisture effect on fungal biomass, bacterial biomass was significantly lower under dry than under moist conditions ($P < 0.05$).

Table 2. Concentrations of characteristic PLFAs (μg g^{-1}) and fungal:bacterial ratios in *Cistus* litter subjected for 1 month to three faunal treatments under moist and dry conditions (means ± SE, $n = 4$). Different letters indicate significant differences within a row (see text for P values); asterisks indicate significant differences between moist and dry conditions ($P < 0.05$).

PLFAs		Control boxes	Boxes with millipedes	Boxes with faecal pellets
Fungal (F)	moist	263 ± 27	234 ± 6	262 ± 2
	dry	247 ± 20	220 ± 13	234 ± 17
Bacterial (B)	moist	101 ± 2 a	66 ± 4 b	69 ± 2 b
	dry	79 ± 7 *	69 ± 4	74 ± 3
Total (F+B)	moist	364 ± 26 a	300 ± 10 b	331 ± 2 ab
	dry	325 ± 27 a	289 ± 16 b	308 ± 19 a
F:B ratio	moist	2.6 ± 0.3 a	3.6 ± 0.2 b	3.8 ± 0.1 b
	dry	3.2 ± 0.1	3.2 ± 0.1	3.2 ± 0.1 *

In boxes with millipedes under moist conditions, bacterial biomass on *Cistus* litter was significantly lower than in control boxes ($P < 0.001$) (Table 2). Fungal biomass did not decrease to the same extent, which resulted in a significantly higher fungal:bacterial ratio in the presence of millipedes ($P < 0.05$). Such changes did not occur under dry conditions. Total microbial biomass, however, tended to be lower in boxes with millipedes than in control boxes under both moist and dry conditions ($P = 0.05$).

Similar changes in microbial community structure were observed in boxes with faeces addition under moist conditions. There was a significant decrease in bacterial biomass ($P < 0.001$) and a significant increase in fungal:bacterial ratio ($P < 0.05$) in comparison with control boxes (Table 2). As in boxes with millipedes, such changes did not occur under dry conditions. This indicates that, in boxes with millipedes, bacterial communities on moist *Cistus* litter were mainly affected by faecal pellet deposition and not by other millipede activities.

DISCUSSION

Faunal contribution to litter mass loss

In our study system of a Mediterranean garrigue of southern France, the four woody shrub species *Cistus albidus, Quercus coccifera, Rosmarinus officinalis* and *Ulex parviflorus* dominate the vegetation cover (Montès *et al.* 2008), and thus the litter input to the soil. Our results have shown that the most abundant species of saprophagous macroarthropods, the millipede *Ommatoiulus sabulosus*, consumes large amounts of aboveground litter produced by the four dominant species. Based on our study, the rate of litter consumption by *Ommatoiulus* in spring is at least 2.6 g (dry mass) per g animal live mass and per month. This corresponds to an estimated litter mass loss of 24 g per m^2 per month for an *Ommatoiulus* biomass estimate of 9.2 g (live mass) m^{-2} in the field, suggesting a considerable impact of this millipede species on the annual litter turnover in this system.

Ommatoiulus shows a marked preference for *Cistus* litter and consumes comparatively small amounts of the other three litter types. Other *Ommatoiulus* species have been reported to feed on *Cistus* spp. in southern Europe (Bailey & Mendonça 1990) but litter traits underpinning this apparent preference for *Cistus* remain unknown. Our analyses did not show particularly high nutrient concentrations in *Cistus* litter and it is not known whether this food is selected on the basis of other nutritional characteristics, the presence of specific microorganisms, and/or its high water holding capacity. Clearly, however, the preferred food in our study was also the litter with the highest decomposition rate in the absence of macroarthropods. The relative contribution of *Ommatoiulus* to litter mass loss, calculated using the same formula as (Tian *et al.* 1995), was larger in *Cistus* than in other species. This result does not support the view that saprophagous macrofauna, when offered litter materials of contrasting quality, have a greater relative impact on those that show less microbial decomposition (Tian *et al.* 1995, 1997). Other studies have shown that litter species preferred by saprophagous macroarthropods tend to have high activity of microbial decomposers (Köhler *et al.* 1991; Zimmer 2002; van Geffen *et al.* 2011; Collison *et al.* 2013), which is consistent with our data. Collectively, our data suggest that the combined high microbial-driven decomposition and the preference by detritivores for *Cistus* leaf litter support a rapid cycling of *Cistus*-derived nutrients, while nutrients derived from the litter of the other three dominant plant species at our study site may cycle more slowly.

Direct and indirect effects of **Ommatoiulus** *on decomposition*

Our study confirms that the direct effects of saprophagous macroarthropods on organic matter decomposition, i.e. the amount of organic material they assimilate during gut passage and transform into CO_2 through their own metabolism, are negligible. Similar to previous studies (Cárcamo *et al.* 2000; David & Gillon 2002; Ashwini & Sridhar 2005) we also found that the mass of faecal pellets

egested by millipedes was almost identical to that lost from litter due their activity, indicating very low assimilation efficiency. In such cases, indirect effects of macroarthropods on decomposition through interactions with microorganisms are assumed to be much more important (Visser 1985; Wolters 2000; Lavelle & Spain 2001).

The most widely mentioned interaction is that the transformation of leaf litter into faeces by macroarthropods stimulates microbial activity, with a higher activity in faeces compared to intact leaf litter, which ultimately should accelerate decomposition (Lavelle & Spain 2001; Coleman *et al.* 2004; Bardgett & Wardle 2010). Our results do not support this mechanism for fauna-driven increased decomposition. First, substrate-induced respiration, which gives an estimate of the catabolic capacity of the physiologically active microbial community, was lower in faecal pellets of *Ommatoiulus* than in uningested litter. Faecal pellets consisted of mixtures of *Cistus* and the other litter species consumed at lower rates, and it can be hypothesized that variation in respiration rates in faecal pellets largely reflected differences in composition (Suzuki *et al.* 2012). However, even the faecal pellets deposited in *Cistus* litter patches, presumably the richest in this litter species, respired significantly less than the average food mixture. Accordingly, there is no evidence for a stimulation of microbial activity in faeces compared to leaf litter. Although we cannot exclude the possibility that microbial respiration was stimulated in the first few days after egestion, no stimulation was detected in the faeces aged between 2 days and 1 month collected at the end of our experiment. Moreover, the insignificant difference between the litter mass loss attributed to millipedes and the mass of faecal pellets collected at the end of the experiment suggests that mass loss was not greater in pellets than in leaf litter over the duration of our study. Although our results were obtained over a relatively short period of time (1 month), they are consistent with previous findings showing that decomposition was not enhanced in faeces produced by other macroarthropod species (Nicholson *et al.* 1966; Webb 1977; Frouz & Simek 2009; Suzuki *et al.* 2012).

An additional potential indirect fauna effect on litter decomposition is the inoculation of leaf litter with faeces-derived microorganisms. Assuming that freshly produced faeces are enriched in bacteria, at least temporarily (Ineson & Anderson 1985; Hassall *et al.* 1987; Byzov *et al.* 1998), their presence on leaf litter could promote microbial colonization and influence decomposition (Visser 1985; Frouz & Simek 2009). We tested this potential interaction by adding faecal pellets to all litter patches, thus simulating the effects of *Ommatoiulus* via faeces production without the presence of the animals. Faecal pellet addition did not change the rates of litter mass loss and microbial respiration in any of the four litter species, even in *Cistus* that received the largest amounts of faecal pellets. Even though the effects of faeces deposition are assumed to be particularly strong in the first few weeks after egestion (Maraun & Scheu 1996), it would be interesting to follow any potential faeces effects over a longer period than our 1-month study to confirm this lack of effect. Faecal pellet addition, however, significantly modified microbial community structure in *Cistus* litter. In the moist treatment, bacterial

biomass in *Cistus* litter was reduced when faecal pellets were added, compared to control litter. No faeces effect was observed for fungal biomass, which consequently resulted in a higher fungal:bacterial ratio in *Cistus* litter when faecal pellets were present. A reduction in bacterial biomass following faeces addition is opposite to our initial expectation. A possible explanation for this result is that the deposition of fresh faecal pellets may have led to cascading effects on the micro-food web in leaf litter. For example, bacterivorous microfauna (protozoa, nematodes) may have been stimulated by the addition of fresh pellets, as shown by Bastow (2011) using woodlouse faeces, with possible negative effects on bacterial populations in moist leaf litter. Whatever the process involved, this points to the importance of macroarthropod faeces deposition for the structure of microbial communities in leaf litter. However, this effect of faecal pellets addition on litter microbial community structure depended on litter humidity. In the dry treatment, neither the biomass of bacteria nor that of fungi differed between litter with added faecal pellets and control litter.

The overall impact of *Ommatoiulus*, including all its direct and indirect effects on decomposition over a 1-month period in our simplified systems (litter, microorganisms, detritivores), did not increase the mass loss of organic matter. This leads to the conclusion that even high-density populations of this species that consumes important amounts of leaf litter do not enhance carbon mineralization in the litter layers of Mediterranean shrublands. Further studies are needed to clarify other possible effects of these macroarthropods on litter decomposition, such as (1) increased nitrogen mineralization, which is generally uncorrelated with the faunal impact on carbon mineralization (Anderson & Ineson 1984; Verhoef & Brussaard 1990; Frouz *et al.* 2008); and (2) a faster incorporation of dead plant material into the soil (Anderson 1988), which may be important for decomposition in Mediterranean soils subjected to drought, because the translocation of faecal pellets to deeper soil layers may provide a more favourable microclimate for decomposition compared to intact leaf litter that remains at the soil surface (Rovira & Vallejo 1997).

Drought effects

The simulated drought effect by reducing watering frequency from twice to once per week, was sufficient to strongly reduce microbial-driven litter mass loss (assuming that the effects of leaching were insignificant in both treatments given the very low absolute quantities of water added). The lower activity of microbial decomposers under dry conditions coincided with a decrease in bacterial biomass in leaf litter, at least for *Cistus* litter. Although the response of fungal biomass was less clear because of the high variability in the PLFA data, there was no apparent drought effect on fungal biomass. This is consistent with previous studies showing that fungi, which appear to be dominant in Mediterranean leaf litter (Wilkinson *et al.* 2002), are less strongly affected by drought than bacteria (Wilkinson *et al.* 2002; Yuste *et al.* 2011). In addition, our SIR measurements showed that the potential respiration of microbial communities was not altered in drier leaf litter and was at least equal to that measured under

moist conditions. This also suggests that microbial communities dominated by fungi are able to resume their activity after a temporary decrease in response to water shortage.

Feeding activities of millipedes were much less sensitive to simulated drought than microbial activity. In contrast to previous studies that showed that leaf litter consumption by macroarthropods was reduced by low moisture contents (Bertrand *et al.* 1987; David & Gillon 2002; Collison *et al.* 2013), *Ommatoiulus* continued to convert shrub litter into faecal pellets at the same rate at two levels of litter moisture. Although these contrasting results may be due to different experimental conditions, they may also indicate that typical Mediterranean macroarthropod species are better adapted to feeding on dry litter. *Ommatoiulus* slightly changed its diet in the dry treatment, with higher consumptions of *Rosmarinus* litter at the expense of the preferred litter from *Cistus*, but maintained its overall feeding rate. This supports the notion that, under dry conditions, some species of soil fauna play an increasingly important role in decomposition processes and can, to some extent, compensate for the low microbial activity (Verhoef & Brussaard 1990; Tian *et al.* 1997). On the other hand, even though litter mass loss remained high under dry conditions due to sustained consumption by *Ommatoiulus*, there was no indication that the material converted into faecal pellets decomposed at a higher rate than dry leaf litter in control boxes. Therefore any positive effect on overall decomposition by maintained millipede consumption and litter transformation into faecal pellets under dry conditions, could only be expressed in the field if these faecal pellets moved to deeper soil layers with more favourable moisture conditions.

It may seem surprising that faecal pellets of macroarthropods, which generally have a high water holding capacity (Webb 1977; Tajovsky *et al.* 1992), do not promote decomposition under dry conditions. However, our SIR data have shown that once pellets have dried after egestion in a dry environment, the microorganisms present in faecal pellets are more affected by desiccation than those present in litter, and do not return to the same activity level when replaced in optimal moisture conditions.

CONCLUSIONS

We showed that in the studied Mediterranean garrigue ecosystem, the dominant macroarthropod species transformed large amounts of above-ground litter from the dominant shrub species into faeces. These feeding activities, however, did not increase C mineralization. No direct litter consumption effects and no indirect feeding- or faeces-induced microbial stimulation effects on C mineralization were apparent, questioning the commonly assumed positive macroarthropod effects on decomposition. Moreover, the studied millipede species does not mitigate the negative effects of litter recalcitrance on microbial decomposition since it consumes primarily leaf litter that decomposes rapidly. However, we cannot exclude potential consequences on nutrient cycling or on the fate and distribution of C within

the soil resulting from feeding preferences and from the different physical structure of faecal pellets compared to intact plant litter.

Under drier conditions, the Mediterranean millipede species studied here, apparently did not reduce its consumption of shrub litter although there was a shift in the preference for certain litter types. A continued conversion of shrub litter into faecal pellets while microbial decomposition is drastically reduced in dry litter could potentially mitigate negative drought effects on C and nutrient cycling in Mediterranean ecosystems. However, such macroarthropod-driven compensation for reduced microbial activity could only result from facilitated spatial translocation of faecal pellets to deeper soil horizons compared to plant litter, because we did not observe an increased decomposition of organic matter despite unchanged fauna activity.

ACKNOWLEDGEMENTS

We especially thank Jessica Pasquet-Kok for her help in microbial analyses and throughout the experiment. We are very grateful to Bruno Buatois, Raphaëlle Leclerc and Patrick Schevin for laboratory assistance, to Jeremy Devaux for technical support and to Nicolas Fanin for helpful discussions. This research is part of the project "CLIMED" funded through the ANR grant 09-CEP-007.

Chapitre 2 : Décomposition des boulettes fécales

Figure 18. Photo montrant un exemple de sachets de litière installés sur le site du massif de l'étoile. Le grillage permet de maintenir les sachets en place et de les protéger contre les divers aléas (vent, lapins, sanglier,…). Le piquet en bois servait d'indicateur pour contrôler la profondeur d'enfouissement des sachets enterrés.

Résumé du chapitre

Contexte :

Le premier chapitre de cette thèse a montré que l'effet indirect d'*Ommatoiulus* via le dépôt de boulettes fécales n'augmente pas la décomposition des litières. Cependant, si l'échelle de temps de cette expérience (30 jours) était appropriée pour étudier l'activité microbienne, elle ne permet pas de tirer des conclusions sur l'effet d'*Ommatoiulus* sur la décomposition de litière *in situ*, qui se déroule sur des pas de temps plus importants. Dans l'étude présentée dans le chapitre précédent, *Ommatoiulus* a consommé et transformé en boulettes fécales d'importantes quantités de litière de Ciste et de Chêne, les deux espèces arbustives les plus abondantes sur le site.

Etant donnée l'importante quantité de boulettes fécales produite, il semble primordial d'étudier leur décomposition pour réellement comprendre le rôle d'*Ommatoiulus* dans le recyclage des litières de garrigue.

De plus, en milieu naturel, la matière organique peut être transportée dans le sol. *Ommatoiulus* a la capacité de s'enfouir aisément jusqu'à 10 cm de profondeur et peut ainsi rejeter des boulettes fécales dans le sol. La petite taille des boulettes par rapport aux litières peut également favoriser leur transport passif (gravité, vent, eau …) à travers les premiers horizons du sol.

L'objectif de ce chapitre est donc de tester conjointement l'effet de la transformation des litières en boulette fécales (H2a) et de leur enfouissement dans le sol (H2b) sur la décomposition de la matière organique.

Méthodes :

D'importantes quantités de boulettes fécales ont été produites par *Ommatoiulus* en conditions contrôlées à partir de litière de ciste ou de chêne. Le rapport C/N, les caractéristiques des lessivats, la capacité de rétention en eau ainsi que la qualité du C ont été mesurés dans les boulettes et les litières non consommées. Ce matériel biologique a ensuite été placé à décomposer dans des sachets à mailles fines dans la garrigue du massif de l'étoile pendant 1 an. Une moitié des sachets a été disposée à la surface et l'autre en profondeur pour tester l'effet de l'enfouissement sur la décomposition.

Résultats et discussion :

L'enfouissement de la matière organique a considérablement augmenté la perte de masse qui est passée de 28% en surface à 38% en profondeur. Cette augmentation était liée à une humidité plus importante en profondeur fournissant des conditions micro-environnementales plus favorables pour les décomposeurs microbiens. L'enfouissement de la matière organique semble donc être un mécanisme important par lequel la faune du sol stimule la décomposition.

La transformation des litières en boulettes fécales a provoquée d'importantes modifications des propriétés physico-chimiques de la matière organique. Un élément marquant en est l'augmentation importante de la quantité et de l'aromaticité du carbone organique dissout dans les boulettes par rapport aux litières. De plus les propriétés physico-chimiques des litières de ciste et de chêne n'ont pas été affectées de la même manière : les transformations étaient beaucoup plus marquées pour le chêne. De la même manière la décomposition des boulettes par rapport aux litières change en fonction de l'espèce des litières. Les boulettes issues de feuilles de chêne se décomposent plus rapidement que les litières correspondantes, alors que pour le ciste, les boulettes et les litières se décomposent à la même vitesse. Ce résultat suggère que l'effet de la faune du sol sur la décomposition dépend fortement de l'espèce de litière ingérée.

Figure 19. Photo montrant l'aspect des litières et des boulettes de chacune des deux espèces avant et après 1 an de décomposition. De haut en bas, les litières de ciste et de chêne, puis des boulettes fécales d'*Ommatoiulus* produites à partir de litières de ciste et de chêne.

Decomposition of leaf litter and macroarthropod feces at two depths in the soil of a Mediterranean shrubland

Article in preparation

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Abstract

Detritivorous macroarthropods can consume large amounts of plant-derived litter. Typically, only very small proportions of the ingested litter are actually assimilated by macroarthropods that instead produce large quantities of feces. However, the decomposition of this significant pool of organic matter remains poorly studied. Litter consumption by macroarthropods may modify the decomposition process because gut passage changes organic matter quality, but also because fecal pellets can move down the soil profile more easily than intact plant litter. Here we studied the simultaneous effects of leaf litter transformation into feces by *Ommatoiulus sabulosus*, and their position in the soil profile on decomposition. *Ommatoiulus* is a diplopod species of high abundance in Mediterranean shrublands and is dominant at our study site in Marseille, southern France. Leaf litter of *Quercus coccifera* and *Cistus albidus*, two abundant plant species at our study site, and feces produced by *Ommatoiulus* feeding on these different litter types were exposed in the field at the soil surface and buried at 5 cm soil depth over one year using fine-mesh litterbags (68 μm). Mass loss of leaf litter and feces was on average 33 % higher at 5 cm soil depth compared to the soil surface. However, the effect of the position of organic matter depended on plant species identity and the form of organic matter. At 5 cm soil depth, feces decomposed more slowly than intact leaf litter without any difference between the two plant species. In contrast, at the soil surface, *Quercus*-derived feces decomposed more rapidly than *Quercus* leaf litter, while there was no significant difference between *Cistus*-derived feces and *Cistus* leaf litter. The difference in response between the two litter species were associated to contrasted changes in the quality of organic matter during gut passage, notably an increase in the concentrations of nitrogen and dissolved organic carbon in *Quercus* feces was associated with an increase in soluble compounds and therefore of the leaching in feces compared to litter. Finally, the heterogeneity of microenvironmental conditions had large effects on organic matter decomposition. Moreover the decomposition process was less sensitive to microclimatic variability once organic matter was incorporated into the soil suggesting that this indirect effect of macroarthropod is important for insuring ecosystem functioning facing slight environmental changes.

Keywords: Millipedes, Faecal pellets, Litter decomposition, Fragmentation, Microclimatic conditions, Drought, Mediterranean ecosystem

INTRODUCTION

The important role of climate and litter quality in regulating decomposition is generally well studied and reasonably well understood (Couteaux *et al.* 1995; Parton *et al.* 2007; Cornwell *et al.* 2008). However, the relative impact of soil fauna on litter decomposition is more difficult to quantify and seems to vary considerably among different biomes (Wall *et al.* 2008). A recent meta-analysis based on a worldwide data compilation of litterbag experiments estimated that soil fauna enhances leaf litter decomposition rate by 27% (García-Palacios *et al.* 2013), suggesting that fauna effects cannot be neglected for the understanding of how litter decomposition is controlled. A challenge for the quantification of fauna effects on decomposition is the distinction between litter that "disappeared" due to fauna consumption and true decomposition, i.e. mineralization of organic material that is typically driven by microorganisms. The largest part of the soil fauna effect on litter mass loss is usually the ingestion of large proportions of the annual litter fall (Cárcamo *et al.* 2000; David & Gillon 2002) and its transformation into feces composed of mainly undigested litter material (Wolters 2000). As a result, soil macrofauna mostly converts intact leaf litter into feces with only little direct effects on decomposition in the strict sense of mineralization.

In consequence the fate of detritivore feces is very important to fully understand the decomposition process at the ecosystem level. In contrast to earthworms that mix organic matter with mineral soil, macroarthropod feces are mostly organic and are constituted of small fragments of undigested litter (Lavelle 1997; Wolters 2000). Several studies explored the decomposition dynamics of such macroarthropod feces. In the short term (from several hours to some weeks after feces egestion), the transformation of litter into feces by macroarthropods can stimulate microbial activity (Martin & Marinissen 1993), with feces having a higher respiration rate and nutrient release than intact leaf litter (Maraun & Scheu 1996; Frouz & Simek 2009). Such initial microbial stimulation would indeed lead to an overall higher decomposition rate as compared to intact leaf litter, but little is known on how long such initial stimulation may last and how important it is for the overall feces decomposition in the longer term (Nicholson *et al.* 1966; Webb 1977; Frouz & Simek 2009). Two studies on diplopod feces found no differences between litter and feces mass loss over a period of one year (Nicholson *et al.* 1966; Webb 1977) and the study comparing feces from dipteran larvae with intact leaf litter found a lower decomposition rate of feces compared to leaf litter after 11 month (Frouz & Simek 2009). After the initial flush of microbial activity, ageing macroarthropod feces can have lower mineralization and respiration rates than litter because of their compaction or as a result of the accumulating undigested recalcitrant compounds (Lavelle 1997). However, the relative change in organic matter quality of macroarthropod feces after gut transit can vary considerably among different detritivore species (Hopkins *et al.* 1998; Zimmer *et al.* 2002; Rawlins *et al.* 2006; Frouz & Simek 2009). For example Zimmer *et al.* (2002) found that different species of isopods did not have the same

capabilities to digest litter phenolic compounds. Additionally, as a result of varying assimilation efficiency of detritivores depending on the food source (David *et al.* 2001; Ashwini & Sridhar 2005), the relative difference between feces and litter quality depends on the plant species from which leaf litter is consumed by the animals.

So far, the few studies comparing subsequent decomposition of feces and the original litter they were produced from, did this either in controlled conditions in the laboratory or at the soil surface in the field. However, the comparatively small-sized macroarthropod feces do not necessarily stay at the soil surface. Instead they may be deposited by the animals away from the feeding sites, or they may sediment passively (water, wind or gravity) or be buried actively by soil animals down to deeper soil horizons (Anderson 1988). This translocation within the soil profile might be the most important consequence of litter transformation into feces (Hassall *et al.* 1987). In deeper soil horizons, the microclimatic conditions and microbial communities can differ dramatically compared to the soil surface, with important effects on decomposition of feces. Buried feces and their subsequent decomposition in more humid deeper soil layers might be especially important in water limited ecosystems such as in the Mediterranean, where litter buried in the soil was found to decompose faster than the same litter placed on the soil surface (Rovira & Vallejo 1997). This impact of burying may depend on the intensity of water stress, and may increase with the drier conditions projected in the future in the Mediterranean region. This interaction between animal activity and projected climatic change may be a key topic to understand organic matter dynamics in Mediterranean regions in the future.

Here we assessed the combined effects of the transformation of litter into feces by macroarthropods and the burying of litter and feces on decomposition in a Mediterranean sclerophyllous shrub ecosystem of southern France. In this type of ecosystem, the diplopod *Ommatoiulus sabulosus* can be remarkably abundant, with live biomass ranging between 5.3 and 9.2 g m^{-2} (David J.-F., unpublished data). Under similar climatic conditions in a Mediterranean evergreen oak forest, another species of diplopods, *Glomeris marginata* with a similar mean live biomass of 7.8 g m^{-2} consumed up to 40% of annual litter fall (David & Gillon 2002). Previous laboratory experiments indicated comparable consumption rates of *Ommatoiulus* as those observed for *Glomeris* (Coulis *et al.* 2013), suggesting a very strong impact of *Ommatoiulus* on litter turnover and nutrient cycling in Mediterranean woody shrub ecosystems, that however has never been quantified so far. We evaluated the decomposition of intact leaf litter and feces produced by *Ommatoiulus* feeding on this same leaf litter originating from *Cistus albidus* and *Quercus coccifera*, two highly abundant shrub species in this type of Mediterranean ecosystems. To test the impacts of litter transformation into feces and burial on decomposition in a climate change perspective, litterbags were placed either in plots with a rain exclusion or in control plots.

We hypothesized that potential differences in leaf litter decomposition rates between the two studied plant species diminish in feces as a result of homogenizing physical and chemical properties of the organic matter during gut passage. According to previous studies we additionally hypothesized that decomposition over several months would be similar in feces compared to intact leaf litter regardless of plant species identity. Finally, we hypothesized that both intact leaf litter and feces decompose more rapidly when buried in the top few centimeters of the soil compared to the soil surface, and that this positive effect of burying is stronger in plots with additional water exclusion. Consequently, at the scale of the ecosystem, the transformation of leaf litter into feces combined with the high probability of transfer of feces to deeper soil horizons should increase organic matter decomposition in this type of drought influenced ecosystem.

MATERIALS AND METHODS

Site description

The study was carried out 5 km north east of Marseille in the "Chaîne de l'Etoile" (43°220' N; 5°250' E). The climate is typically Mediterranean (Figure 20) with a mean annual temperature and rainfall of 14.6 °C and 552 mm, respectively. Precipitation and temperature patterns during the duration of our experiment matched well the 10-year average (Figure 20). The site is at an altitude of 275 m above sea level. The soil is classified as shallow rendzina on limestone (Montès *et al.* 2008). The soil depth can reach approximately 20 cm, but is often less due to abundant rocks accounting for about 67 % of the total volume in the top 50 cm (data not shown). The vegetation is a woody-shrub dominated "garrigue", with shrub heights ranging between 0.2 and 1.4 m (Montès *et al.* 2008) and a heterogeneous cover ranging between 25% and 95 %. Five plant species dominate the community and account for 97 % of the vegetation cover. Among those are the four woody shrubs *Quercus coccifera* (36%), *Cistus albidus* (18%), *Ulex parviflorus* (10%) and *Rosmarinus officinalis* (9%), and the grass *Brachypodium retusum* (24%) (Rodriguez, unpublished data). Regular fires occur in the type of ecosystem we studied, and at our experimental site the last fire occurred in 1997 (35 km² burnt from a total of 100 km² covered by garrigue in the area of the "Chaîne de l'Etoile").

The community of saprophagous macrofauna is dominated by the diplopod species *Ommatoiulus sabulosus aimatopodus* (the Mediterranean sub-species of *O. sabulosus* with no dorsal orange-yellow bands). Its population density can reach 164 ± 37 individuals per square meter during peak activity in spring. Depending on the season and the year live biomass ranges between 9.2 ± 2 g m^{-2} and 5.3 ± 0.9 g m^{-2} (J.F. David, unpublished data).

Experimental design

Our study was part of a larger field experiment that was set up to study the consequences of reduced precipitation on plant performance and ecosystem functioning. To this end, a total of 92 plots

have been identified to cover a diversity gradient of woody shrub species (based on the four dominant species mentioned above). Half of all plots were assigned to a rain exclusion treatment with the other half serving as control plots without rain exclusion. All plots were equipped with an aluminum frame holding stainless steel gutters 2 m above the ground. Plot size is 4 m x 4 m with gutters covering 40% of total plot area (reversely installed in the control plots). Rain exclusion and control plots were installed in October 2011. For the current study we focused exclusively on the plots with vegetation dominated by *Quercus* and/or *Cistus* shrubs because we used litter from these two species for the decomposition experiment. Litterbags were exposed in the 18 corresponding plots for one year (16 May 2012-3 June 2013).

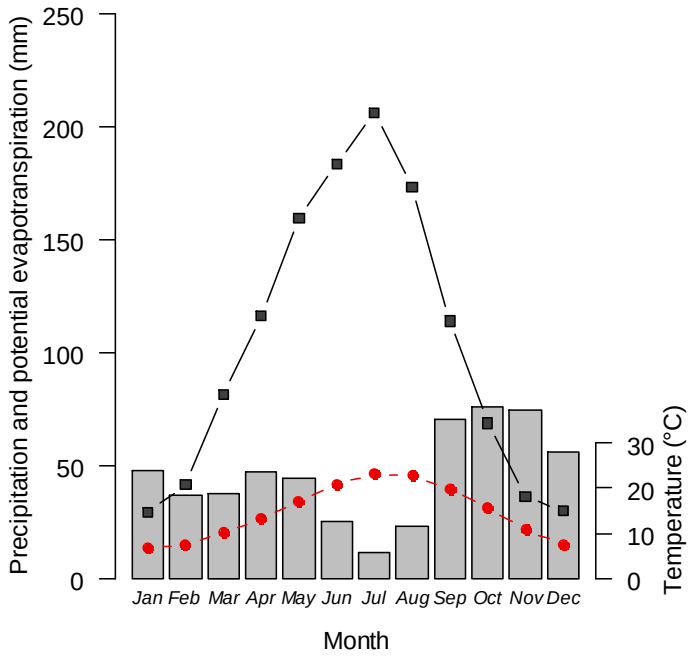

Figure 20. Monthly precipitation (grey bars, left axis), potential evapotranspiration (filled squares, left axis), and air temperature (red circles, right axis). Data are mean values over the period 2002-2012 averaged across the two meteorological stations in Marignane (43°26'12"N, 5°12'54"E) and Marseille (43°15'18"N, 5°22'48"E) closest to our experimental site (Located at 17 km and at 7 km, respectively).

Litter collection and feces production

Leaf litter of *Quercus coccifera* and *Cistus albidus* were collected on the ground near the experimental area in March - April 2011. The collected leaves that have been shed mostly during peak leaf litter fall in the summer of the previous year. This litter cohort, however, consisted still of fully intact leaves as decomposition proceeds comparatively slowly in this dry ecosystem. We decided to work with older leaf litter rather than with freshly fallen leaf litter, because litter feeding macrofauna generally prefer litter that underwent an initial stage of decomposition and is colonized with microbial communities (Lavelle & Spain 2001). Field collected leaf litter was air-dried in the laboratory, sorted into species and cleaned of adhering soil particles, fruit and flower parts or twigs in the same way as described by Coulis *et al.* (2013).

Part of this leaf litter was used to produce feces. A total of 60 g of leaf litter of each species (*Quercus* and *Cistus*) and 20 individuals of *Ommatoiulus* (average individual live weight of 103 ± 0.2 mg) per litter species were incubated at a constant temperature of 20°C in large (40 x 33 x 8.5 cm) transparent plastic boxes. Every three days, millipedes were removed and the content of the plastic boxes was sieved through a 2 mm mesh for feces collection. Litter and all *Ommatoiulus* individuals were then placed back in the respective boxes and sprayed with water to maintain optimal humidity conditions for *Ommatoiulus* activity. This procedure was repeated five times over a 15-day period. In order to have a comparable pool of leaf litter, we incubated additional plastic boxes with each leaf litter species but without fauna during the same period and in the same conditions as those used for feces production. Leaf litter from these additional plastic boxes and feces were air-dried and kept in a dark room with constant temperature until the beginning of the experiment.

Chemical analysis

We analyzed a number of quality parameters for leaf litter and feces material. Water holding capacity (WHC) was determined by soaking litter and feces for 24h in distilled water using a mass to volume ratio of 1g/50ml. After soaking, litter and feces were carefully wiped to remove surface water, weighed moist and reweighed after drying at 60 °C for 48 h. The difference between moist and oven-dry weight was used to determine the WHC (in percent of the litter dry mass). Soaking water was filtered through 0.45 μm cellulose nitrate membrane filters and then analyzed for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) with a TOC analyzer equipped with a supplementary module for N (CSH E200V, Shimadzu, Kyoto-Japan). The filtrate was also used to determine an index of DOC aromaticity following the protocol by (Weishaar *et al.* 2003). The specific UV absorbance at 280 nm ($SUVA_{280}$) was measured with an UV spectrophotometer (Helios Gamma, Thermospectronic, Cambridge, UK) and calculated as $SUVA_{280}$ = Absorbance280 nm / DOC (g l^{-1}) and is expressed in l g^{-1}.

Chemical analyses were performed on oven-dry litter and feces material ground with a Cyclotech sample mill (Foss Tecator, Höganäs, Sweden) yielding a uniform particle size of 1 mm. Total C and N concentrations were measured using a flash elemental analyzer (EA1112 Series; Thermo Finnigan, Milan, Italy). The ash content was measured gravimetrically after ignition for 3h at 550°C.

The quality of organic matter was assessed using the cross-polarization magic angle spinning ^{13}C nuclear magnetic resonance (^{13}C CPMAS NMR) following the procedure described by Alarcón-Gutiérrez *et al.* (2009). The ^{13}C chemical shifts were referenced to tetramethylsilane and calibrated with glycine carbonyl signal, set at 176.5 ppm. Chemical shift range of ^{13}C CPMAS NMR spectra of litter was designed by the following dominant forms: alkyl C (10-45 ppm), O-alkyl C (45-110 ppm), aromatic C (110-160 ppm), phenolic C (140-160 ppm), and carboxyl C (160-190 ppm). Finally, the

degree of humification was calculated as the ratio of the respective peak areas of alkyl-C to O-alkyl-C (Baldock *et al.* 1997).

Decomposition in litterbags

Litterbags of 5 x 4cm were made of 68µm nylon mesh (68PES4/135, DIATEX, St-Genis-Laval, France). Such fine mesh prevents meso- and macrofauna from entering litterbags and also prevents the loss of small fragments. Litterbags were filled with either 300 ± 10 mg of litter or 200 ± 10 mg of feces. These amounts were equivalent to about 22 leaves of *Quercus*, 13 leaves of *Cistus* and 1000 fecal pellets of *Ommatoiulus*. To compare litter and feces decomposition, two litterbags with *Quercus* and *Cistus* leaf litter as well as two litterbags with feces derived from each litter type were exposed in each experimental plot (a total of 18, see above). As many *Ommatoiulus* are frequently found at a few centimeters depth during their period of activity, litterbags containing litter and feces were placed either at the soil surface or at 5cm depth in order to mimic animal transport of their feces. During litterbag installation, the soil was dug over a square of 25 x 25cm down to 5 cm depth. Four litterbags (one of each substrate) corresponding to buried treatments were disposed horizontally. Afterwards we gently filled back the soil previously removed and placed on the top four other litterbags corresponding to the surface treatment. Litterbags were fixed on the soil surface by stainless steel wire net of 1cm mesh. A total of 144 litterbags (18 plots x 4 substrates x 2 depths) were installed on the site for the decomposition experiment.

In order to characterize microclimatic conditions at the soil surface during the relatively humid period favorable for litter decomposition we installed small data loggers (I-buttons, signal control, Gloucestershire, UK) to record air temperature and relative air humidity in each plot from October 2012 onwards. I-buttons were placed 0.5 cm above the soil surface next to the litterbags, were protected from solar radiation by a screen and recorded data every second hour until the end of the experiment. For soil moisture measurements, we took small soil cores of 1 cm width and 10 cm depth in each plot at three different dates (see Table 3). Upon harvest, the soil cores were immediately enclosed in sealed flasks, taken to the laboratory, and weighed fresh. Samples were reweighed after drying at 105°C to determine the soil water content (SWC) relative to total soil dry mass.

A set of 42 supplementary litterbags were placed in six plots (three of each control and rain exclusion treatments) to determine the water content of leaf litter and feces during the experiment. Those litterbags containing litter and feces were placed at two depths exactly like those from the decomposition experiment. All litterbags were collected in autumn (25 October 2012). Upon harvest, litterbags were enclosed in sealed flasks, taken to the laboratory, and weighed fresh. Samples were then dried at 40°C and reweighed to determine water content. At the end of the experiment (3 June 2013), water content was determined as described below on the material from decomposition experiment.

Although we used very fine mesh for litterbag construction, we measured the ash content in a subsample (n=12) of retrieved litterbags to correct for potential contamination by mineral soil. Indeed, the final ash content tended to be somewhat higher than in initial litter and feces material. However, there was no significant differences in ash content between litterbag positions (p=0.5) and between litter and feces (p=0.7). For the calculation of mass loss we corrected initial dry mass by initial litter specific ash content (Table 3) and final mass by the final average ash content (20.6 ± 1.4 %).

Table 3. Microclimatic variables in the 18 experimental plots used. All values are pooled across the control and rain-exclusion plots (no significant differences were detected between control and exclusion plots). Data are missing for 5 plots (3 exclusions and 2 controls) due to I-buttons deficiency.

Environmental variables	Minimum	Maximum	Mean
Soil water content at 0-10cm (% of water per soil dry mass, n=18)			
3rd April 2013	18.6	28.2	22.5
19th April 2013	13.2	29.5	20.6
23rd May 2013	18.1	30.0	24.0
Mean of the three dates	17.7	27.8	22.4
Air relative humidity (r.h.) (%, 0.5 cm above soil surface, n=13)			
R.h. mean	81.4	89.8	85.7
R.h. max	93.3	98.5	96.8
R.h. min	56.4	74.9	66.5
Air temperature (temp.) (°C, 0.5 cm above soil surface, n=13)			
Temp. mean	9.1	10.5	9.7
Temp. max	14.5	19.7	16.7
Temp. min	4.7	6.1	5.5

Statistical analyses

Differences in initial quality parameters of litter and feces were tested using two way ANOVA with species identity (*Quercus* and *Cistus*) and litter type (leaf litter and feces) as fixed factors. Tukey's HSD test was used for multiple comparisons among pairs of means.

Differences in mass loss were tested using a partly nested design ANOVA model. Experimental plots were considered as random blocking factor, nested within the rain exclusion treatment, which was crossed with the three other factors (i.e. litter type, location and species identity). The same ANOVA model was used to test for differences in the water content of litter and feces on two dates.

The relationships between environmental variables and mass loss were tested using ordinary least square regression (OLS). Regressions analyses were performed either (i) for each species and each type of litter separately either, or (ii) for each litter type after pooling both species.

Before ANOVAs and regression analyses, normality of residuals and homogeneity of variances were checked and data were log or power transformed if required. All statistical analyses were performed using R software version 3.0.1 (R Development Core Team, 2013).

RESULTS

Initial quality of litter and feces

Leaf litter of *Cistus* and *Quercus* had contrasted quality (Table 4). The concentration of nitrogen (N), dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were significantly higher in *Quercus* leaf litter than in *Cistus* leaf litter. *Cistus* leaf litter had a 25% higher water holding capacity (WHC) compared to *Quercus*. Leaf litter of both species had approximately the same aromaticity of dissolved organic carbon.

Leaf litter ingestion and gut passage generally led to an increase in WHC, DOC, TDN, and aromaticity of DOC in feces compared to litter. However, these changes differed between species (Table 4). The gut passage increased DOC and TDN for *Quercus* but the difference between litter and feces was not significant for *Cistus*. Moreover the increase in UV absorbance of the DOC after gut passage was more pronounced for *Quercus* than for *Cistus*.

WHC increased similarly in feces compared to litter for both species. Interestingly, N concentration in feces tended to decrease in *Cistus* while it increased in *Quercus* compared to litter. The C:N ratio was significantly higher in feces than in litter for *Cistus* but significantly lower in feces than in leaf litter for *Quercus* (Table 4Table 2).

In accordance with the larger differences between litter and feces characteristics observed in Quercus, RMN spectra differed markedly between litter and feces for *Quercus*, but were more similar for *Cistus* (Figure 21). For *Quercus,* the only region of spectra that was not affected by gut passage was the Alkyl-C region (10-45ppm), which corresponds to lipids, waxes and aliphatic carbons. In some parts of this region, the signal was even stronger in feces than in litter. The region of the spectrum that was the most affected by gut passage corresponded to O-alkyl-C (45-110 ppm), which refers to carbohydrates. The signal of this region was strongly reduced in feces compared to litter. In regions of the spectra corresponding to Carbonyl-C (160-200 ppm), Phenolic-C (140-160 ppm) and Aromatic-C (110-160 ppm), the signal decreased more slightly in feces compared to litter.

Table 4. Chemical and physical characteristics of *Ommatoiulus* feces compared to intact leaf litter (means ± SE, n=3). Different letters indicate significant differences between mean values within a row (Tukey HSD test). Numbers in brackets are litter-feces differences (in %).

Traits	*Cistus albidus*			*Quercus coccifera*		
	Litter	Feces		Litter	Feces	
Ash (%)	12.7 ± 0.4 ^{b}	16.1 ± 0.5 ^{a}	(+27)	7.9 ± 0.2 ^{c}	13.6 ± 0.8 ^{b}	(+72)
Carbon (mg/g)	453 ± 2 ^{b}	438 ± 4 ^{c}	(-3)	478 ± 1 ^{a}	451 ± 3 ^{b}	(-6)
Nitrogen (mg/g)	9.4 ± 0.2 ^{c}	8.6 ± 0.1 ^{c}	(-9)	11.7 ± 0.1 ^{b}	13.4 ± 0.3 ^{a}	(+15)
C:N	48.0 ± 0.7 ^{a}	50.9 ± 0.8 ^{b}	(+6)	40.7 ± 0.1 ^{c}	33.7 ± 0.6 ^{d}	(-17)
WHC(%)	178 ± 5 ^{b}	236 ± 3 ^{a}	(+33)	132 ± 2 ^{c}	187 ± 0.3 ^{b}	(+42)
DOC (mg/g)	3.8 ± 0.5 ^{c}	4.7 ± 0.3 ^{c}	(+24)	10.6 ± 0.8 ^{b}	17.4 ± 0.03 ^{a}	(+64)
TDN (mg/g)	0.12 ± 0.04 ^{c}	0.18 ± 0.07 ^{c}	(+50)	0.53 ± 0.03 ^{b}	1.05 ± 0.01 ^{a}	(+98)
$SUVA_{280}$(l/g)	56 ± 5 ^{c}	155 ± 7 ^{b}	(+177)	62 ± 3 ^{c}	313 ± 16 ^{a}	(+405)
Humification index	0.237 ± 0.002 ^{d}	0.275 ± 0.001 ^{c}	(+16)	0.294 ± 0.005 ^{b}	0.488 ± 0.004 ^{a}	(+66)

Litter and feces decomposition

The exclusion of rainfall had no overall effect on organic matter decomposition (dry ash-free mass loss) (Table 5). The location of litterbags at the soil surface or at 5 cm depth explained by far most of the variation in decomposition (Table 5). Averaged across the two species (*Quercus* and *Cistus*) and the two types of organic matter (leaf litter and feces), we measured a mean mass loss of 27.7 ± 0.9 % at the soil surface versus 36.7 ± 1.0 % at 5 cm depth (Figure 22). This higher mass loss in the soil was associated with substantially higher water contents in buried materials compared to surface materials in two different seasons (Figure 22). Water content was more than 3-fold, and 7-fold higher in the soil compared to the soil surface in autumn and spring, respectively (Table 6).

Species identity also significantly affected mass loss, but this species effect additionally depended on the location of litterbags (Table 5). When the organic material decomposed at 5 cm depth there was no significant difference between *Cistus* and *Quercus* (Figure 23). In contrast, when the organic material decomposed at the soil surface, mass loss was higher in *Quercus* than in *Cistus*. Moreover, there was also a significant interaction between litter type and location (Table 5). At 5 cm depth, feces tended to have a slightly lower mass loss than leaf litter. In contrast, at the soil surface, feces tended to have a slightly higher mass loss than leaf litter, due to a significantly increased mass loss in feces derived from *Quercus* (Figure 23).

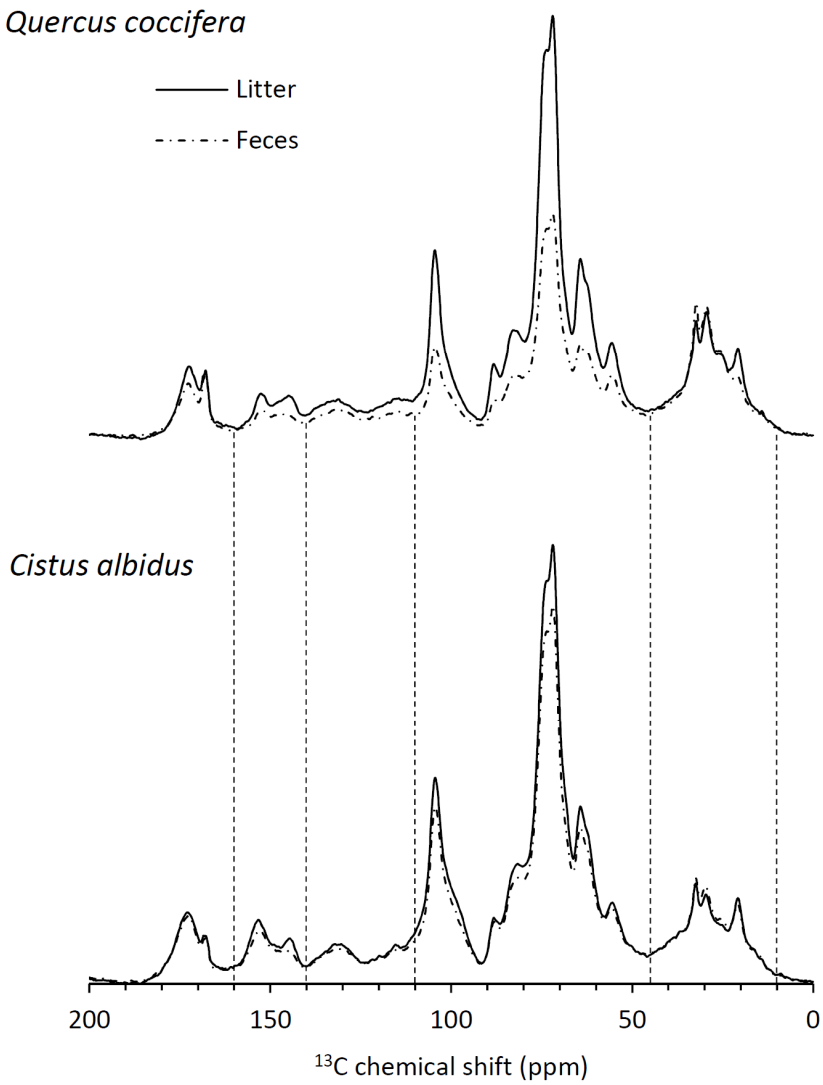

Figure 21. ^{13}C CPMAS NMR spectra of *Quercus* and *Cistus* intact litter and after transformation into feces by *Ommatoiulus*. Regions of spectra delimited by dotted lines correspond from right to left to alkyl C (10-45 ppm), O-alkyl C (45-110 ppm), aromatic C (110-160 ppm), phenolic C (140-160 ppm), and carboxyl C (160-190 ppm).

Litter and feces water content

Rain exclusion had no significant effect on water contents in leaf litter and feces at either of the two sampling dates. There was no significant interaction between the different treatments. Most of the variation in water content was explained by the location of litterbags, with significantly higher water contents in buried materials than in surface materials at both sampling dates (Figure 22, Table 6). In addition, when water content was high in autumn, the litter type and species identity also significantly influenced the water content which was 83 % higher in *Cistus* than *Quercus* and 18% higher in feces than in leaf litter (Table 6).

Table 5. Results of ANOVA to test for effects of rain exclusion and position, litter type and species identity on organic matter decomposition.

Source of variance	*Df*	*F* value	
Rain exclusion (R)	1	0.94	
Position (P)	1	24.04	***
Form (F)	1	4.25	
Species (Sp)	1	19.53	***
R x P	1	3.64	
R x F	1	1.91	
R x Sp	1	0.30	
P x F	1	18.28	***
P x Sp	1	13.91	**
F x Sp	1	3.12	
R x P x F	1	0.92	
R x P x Sp	1	0.00	
R x F x Sp	1	2.93	
P x F x Sp	1	2.45	
R x P x F x Sp	1	0.52	

Relationship between decomposition and microclimatic variables

The substantial variation in mass loss observed across the different experimental plots, in particular at the soil surface, was partially explained by differences in plot-specific micro-environmental variables. Mass loss of leaf litter correlated positively with mean soil water content, but varied independently of mean relative air humidity and mean air temperature. As regressions yielded essentially the same relationships for each species separately (r= 0.35, $p<0.05$ for the regression between *Cistus* litter mass loss and soil water content; r= 0.62, $p<0.005$ for the regression between *Quercus* litter mass loss and soil water content), the results were pooled across the two species (Table 7, Figure 24). Mass loss of feces correlated positively with mean air temperature, but did not vary with soil water content or mean relative air humidity. Again as regressions yielded similar relationships for each species separately (r=0.77, $p<0.01$ for the regression between *Cistus* feces mass loss and temperature; r=0.63, $p<0.05$ for the regression between *Quercus* feces mass loss and Tmean), the results were presented for regressions on feces mass loss pooled across the two species (Table 7, Figure 24). Eventually, mass loss of leaf litter and feces buried at 5 cm in the soil did not show any correlation with microclimatic variables (Table 7).

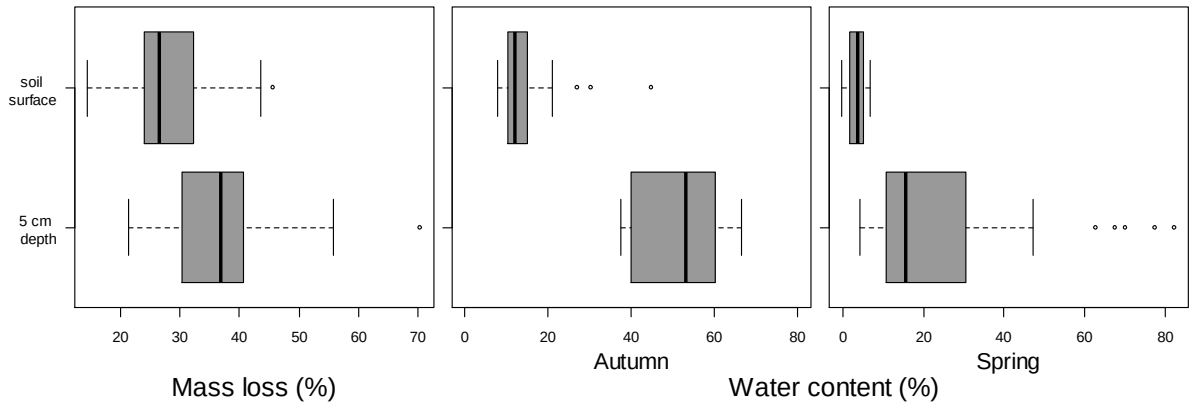

Figure 22. Mass loss and water content of organic matter at two soil depths. Water content was measured on litter and feces from a set of litterbags collected in autumn (25th October 2012) and on litter and feces collected at the end of the experiment in spring (3 June 2013).

Table 6. Results of ANOVA to test for effects of rain exclusion and position, litter type and species identity on organic matter water content at two different dates during the experiment.

Source of variance	Water content in autumn (n=42)			Water content in spring (n=144)		
	Df	*F value*		*Df*	*F value*	
Rain exclusion (R)	1	1.05		1	0.04	
Position (P)	1	165.43	***	1	26.28	***
Species (S)	1	33.94	**	1	0.19	
Form (F)	1	72.00	***	1	3.66	
R x P	1	0.14		1	0.00	
R x Sp	1	1.75		1	2.48	
R x F	1	1.07		1	0.03	
P x Sp	1	4.23		1	0.25	
P x F	1	2.11		1	2.43	
Sp x F	1	1.07		1	0.65	

DISCUSSION

Effect of organic matter burying on decomposition

Our data clearly showed that the position of organic matter at the soil surface or within the top soil strongly influenced the decomposition of leaf litter and macroarthropod feces. In line with our initial hypothesis, the average mass loss after one year of field exposure increased from 28 % at the soil surface to 38 % at 5 cm depth. This result is in accord with previous experiments reporting an increase of decomposition with soil depth (Rovira & Vallejo 1997; Withington & Sanford Jr 2007). For example Rovira & Vallejo (1997) found that decomposition of leaf litter from three evergreen Mediterranean tree species was higher at 20 and 40 cm depth than at 5 cm depth as a result of the higher drying of the upper soil horizons. By studying cellulose decomposition along an altitudinal gradient in tundra, Withington & Sanford Jr (2007) further showed that decomposition was very sensitive to the slight variations of soil moisture between surface and 6 cm depth. These former studies showed that higher decomposition within the soil matrix was mainly driven by more favorable microclimatic conditions for microbial decomposers due to higher moisture levels, which can be particularly important in ecosystems with low water availability. In line with this interpretation we measured consistently higher moisture levels in buried leaf litter and feces during a rather wet period in fall and during a relatively dry period in spring in the dry Mediterranean shrub ecosystem we studied.

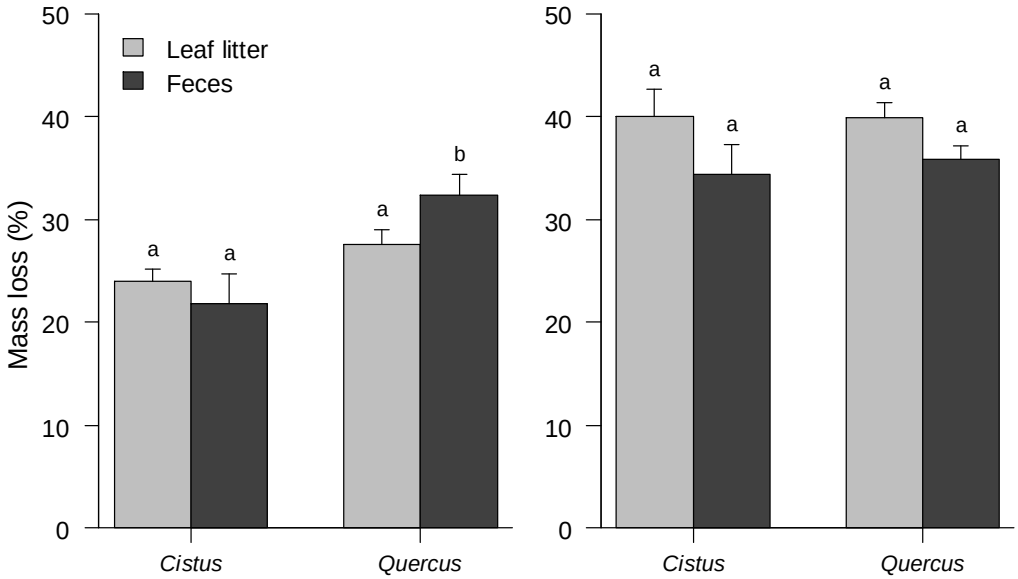

Figure 23. Leaf litter and feces mass loss of *Cistus* and *Quercus* at the surface of the soil (left) and at 5 cm soil depth (right) (means ± SE, n=18).

As the feces have a much smaller size than leaf litter (mean length and width of feces were 1.3 ± 0.13 mm and 0.6 ± 0.04 mm), they can reach deeper soil layers more easily, in basically two ways. First, as *Ommatoiulus sabulosus* was regularly observed burying into the first 10 cm of the soil, feces

can be egested *in situ* within the soil. Second, feces can be buried passively by water, wind or by gravity (Anderson 1988). Feces burial is a supposedly important mechanism by which macroarthropods indirectly affect the decomposition of plant-derived organic matter as it was first suggested by Hassall *et al.* (1987) for isopods. Transport of organic matter in soil by macroarthropods might thus play an important role in soil functioning by enhancing decomposition of organic matter and changing the location of nutrient release.

Effect of the transformation of litter into feces

The transformation of intact leaf litter into feces by *Ommatoiulus* strongly changed the quality of organic matter. For both litter species, ^{13}C NMR analysis showed that the proportion of carbohydrates decreased in feces compared to litter, indicating that these easily accessible compounds were partly assimilated by *Ommatoiulus*. Other compounds with alkyl and methyl groups (waxes or cutins, (Quideau *et al.* 2000), were not degraded by gut passage and their proportion tended to increase in feces comparing to litter. This confirms that the biochemical transformation of leaf litter by macroarthropods increases the recalcitrance of organic matter (Gillon & David 2001; Rawlins *et al.* 2007). Despite the apparent lower concentrations of carbohydrates in feces, we also measured distinctly higher concentrations of dissolved organic carbon (DOC), which however, had a higher aromaticity compared to DOC leached from litter. Gut passage therefore modifies the quantity and quality of leachates from feces compared to litter. Along, with increased DOC from feces, total dissolved nitrogen (TDN) also increased, mostly in feces produced from *Quercus* litter, and the water holding capacity (WHC) in feces was also higher by 33% for *Cistus* and by 42% for *Quercus*, compared to litter of the two species. Higher TDN and WHC both might suggest more favorable conditions for microbial decomposers in feces than in litter. The higher water holding capacity of feces was frequently observed in previous studies (Nicholson *et al.* 1966; Webb 1977; Tajovsky *et al.* 1992).

Changes in feces composition and quality were overall less pronounced for *Cistus* litter than for *Quercus* litter (Figure 21, Table 4), suggesting that the impact of transformation into feces depends on the litter species. Accordingly, subsequent decomposition of feces and their relative difference to leaf litter decomposition differed between the two species. While *Cistus* feces showed a trend for slower decomposition than *Cistus* leaf litter, *Quercus* feces decomposed clearly faster than intact litter when maintained at the soil surface for one year. Previous studies investigating macroarthropod feces decomposition under natural conditions found that feces decomposed similarly or more slowly than leaf litter (Nicholson *et al.* 1966; Webb 1977; Frouz & Simek 2009), but a stimulation of decomposition compared to intact leaf litter has not been observed so far.

Collectively, our results demonstrate that the transformation of leaf litter into feces by *Ommatoiulus* lead to an increase in organic matter recalcitrance, WHC and DOC and TDN leaching.

Within the soil, these quality changes resulted in a slower decomposition of feces than leaf litter. However, constraints for decomposition at the microclimatically less favorable soil surface differ and the consequences for litter decomposition are reversed for *Quercus* with faster mass loss of feces than litter. The high activity of *Ommatoiulus* at our study site thus accelerates organic matter turnover at the soil surface, and this more so for the litter produced by *Quercus* than by *Cistus*. This litter species-specific effect of *Ommatoiulus* may actually increase *Quercus* leaf litter breakdown compared to *Cistus* in contrast to what might be expected from higher feeding rates of *Cistus* than *Quercus* leaf litter .

Table 7. Linear relationships between mass loss and micro-environmental conditions.

Location	Litter type	Mean soil water content			Mean relative air humidity			Mean air temperature		
		slope	R^2	*p-value*	slope	R^2	*p-value*	slope	R^2	*p-value*
On soil surface	Leaf litter	**1.0**	**0.3**	**0.01**	0.0	0.0	1.0	0.4	0.0	0.9
	Ommatoiulus feces	0.9	0.1	0.1	-0.6	0.0	0.5	**12.9**	**0.6**	**0.001**
Buried at 5cm depth	Leaf litter	0.0	0.0	0.9	0.0	0.0	0.4	-0.1	0	0.6
	Ommatoiulus feces	-0.4	0.0	0.4	0.2	0.0	0.8	-0.2	0	1.0

Effects of microclimatic variability on decomposition

Mediterranean ecosystems are characterized by high temporal and spatial heterogeneity due to the combination of various abiotic (fire, drought,…) and biotic (different plant strategies, grazing pressure,…) factors (Blondel & Aronson 1999). Even with a maximum distance of 100 m between individual plots in our experiment, we documented a relatively high variability in microclimatic conditions among the study plots. Differences in air temperature just above the litter layer and in moisture of the top 10 cm of soil are likely related to the heterogeneous rock proportion in soil, and vegetation cover above ground. Variations in these microclimatic parameters among plots were relatively well correlated with the variation of decomposition determined at the soil surface. Such small-scale variation in microclimatic conditions is often neglected in studies on litter decomposition that consider rather continental or global scale variation in climate (Berg 2001, Parton et al. 2007, Cornwell et al. 2008). In our study these plot specific differences in microclimate appeared to be even more important than the exclusion of 40% of precipitation during the entire period of the decomposition study. Rain exclusion effects can be long to detect. For example (Yahdjian *et al.* 2006)

detected significant effects of rain exclusion only after 20 months of effective exclusion. On the other hand, Salamanca *et al.* (2003) found that partial rain exclusion had no effect on litter decomposition whereas total exclusion significantly reduced decomposition. The frequency of rainfall might be more important than the amount of precipitation (Yahdjian & Sala 2008; Hao *et al.* 2013) and explain why we did not find any effect of rain exclusion in the present experiment.

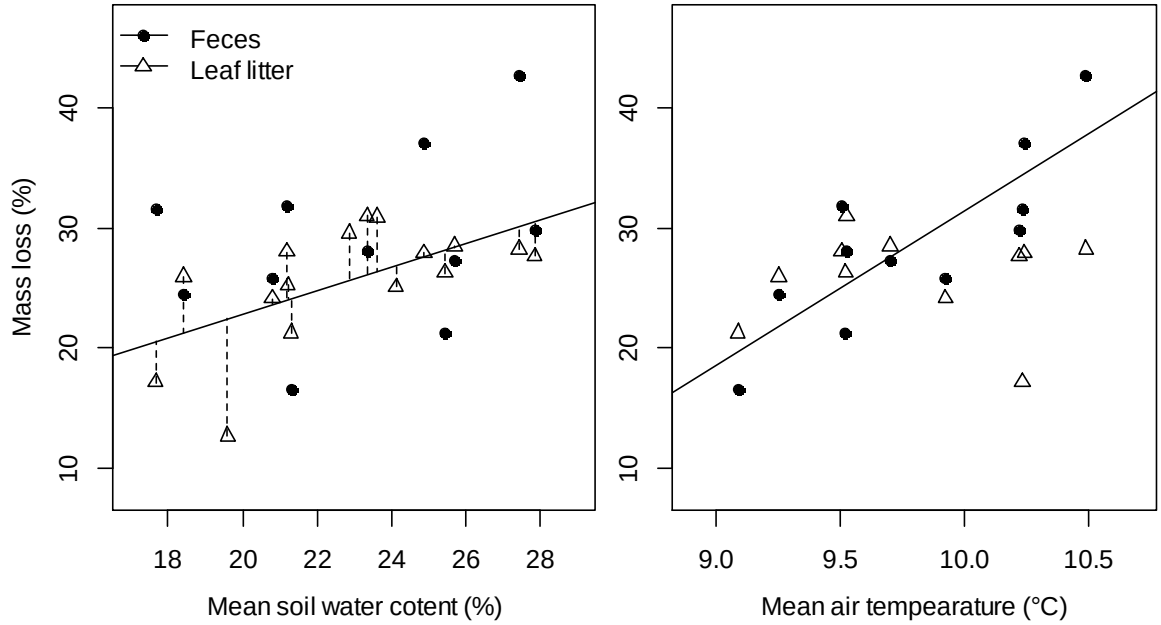

Figure 24. Relationships between organic matter decomposition and microclimatic variables. Due to missing data, n= 16 for the relation between SWC and decomposition and n=11 for the relation between mean air temperature and decomposition. When linear regressions are significant (p<0.05), regression lines are drawn.

The few other existing studies that explicitly tested for microclimatic effects on decomposition at small spatial scales are scarce (Köchy & Wilson 1997; Shaw & Harte 2001; Simpson *et al.* 2012). For example Shaw & Harte (2001) observed that variation of mean soil temperature and soil moisture at the plot scale (10 x 3 m) influenced decomposition in subalpine meadows. Furthermore (Simpson *et al.* 2012) found that decomposer activity (investigated through bait lamina sticks) varied greatly and matched variation in soil moisture content along plots disposed every 100 m from the edge to the core of the forest.

Interestingly, the decomposition of leaf litter and feces on the soil surface were not influenced in the same way by microclimatic variables. Leaf litter decomposition showed a good correlation with soil water content, while feces decomposition on the other hand correlated well with mean air temperature (from October 2012 to May 2013) but not with soil moisture. Perhaps because feces have higher WHC than leaf litter, their decomposition might depend somewhat less on soil humidity. The apparent temperature effect on feces decomposition in the Mediterranean climate might appear less obvious. However, as most of the annual rain fall is concentrated during the cooler months between

fall and spring, the most favorable conditions for decomposer activity are actually limited to this part of the year when temperatures are relatively low, and potentially limiting for process rates during decomposition (Almagro *et al.* 2009).

The absence of relation between mass loss and microclimatic conditions at 5 cm depth suggests that transport of organic matter in soil could attenuate the effect of slight variation in environmental conditions on decomposition and potentially insure the functioning of soil in fluctuating environments. However this approach is based on correlative relationships so we must be cautious about causal interpretations (Prescott 2005). Despite this limitation, our results suggest interesting insight into the interaction between environmental conditions and the complex indirect effect that macroarthropods have on decomposition process. The switch in environmental factors controlling organic matter decomposition caused by macroarthropod suggests that effects of detritivore will likely interact with environmental changes in complex ways.

CONCLUSION

In ecosystems with abundant detritivore communities, a large proportion of litter is transformed in feces but the fate of this material is rarely investigated. This study provides new data about the decomposition of macroarthropod feces, which was investigated for the first time in a Mediterranean-type ecosystem and on litter from different plant species. Our results showed that long-term decomposition of macroarhtropod feces is not systematically similar or lower than that of uningested litter. However we found that the effect of leaf litter transformation by macroarthropods depends on the litter species, the effect on decomposition being positive for *Quercus* and null for *Cistus*. Higher decomposition of *Quercus* feces was due to physical rather than biochemical organic matter transformation. The two main mechanisms likely to be involved in physical transformation are (i) the fragmentation that induced a higher leaching of dissolved organic carbon from feces and (ii) enhancement of water holding capacity, which may prolong microbial activity during drought.

Moreover, the burying of feces was an important mechanism of organic matter decomposition since it was responsible for a 33 % increase in mass loss. However mechanisms linked to physical properties of feces that apply at soil surface are not effective anymore below ground, in better moisture conditions. As a result, the indirect effects of macroarthropods on decomposition by burial and transformation into feces were not cumulative.

ACKNOWLEDGEMENTS

We are very grateful to Johanne Nahmani, Ammar Shihan and François-Xavier Joly for their help during field work and for their helpful discussions. This research is part of the project “CLIMED” funded through the ANR grant 09-CEP-007.

Chapitre 3 : Dissimilarité fonctionnelle et processus du sol

Figure 25. Photo montrant une enceinte de conditionnement (gauche), l'arrosage des microcosmes (en haut à droite) ainsi qu'un microcosme en gros plan (en bas à droite).

Résumé du chapitre

Contexte :

La communauté de détritivores du massif de l'étoile est dominée à 95% par *Ommatoiulus*. Cette forte dominance ainsi que la densité élevée de la population a permis de faire d'*Ommatoiulus* une espèce modèle pour étudier finement les effets indirects de la faune du sol sur la décomposition (Chapitre 1 et 2). Or dans beaucoup d'écosystèmes, plusieurs espèces de détritivores cohabitent et ont des effets interactifs sur le processus de décomposition. Via les interactions entre espèces, la diversité des détritivores est donc susceptible d'influencer le fonctionnement du sol. De récentes études ont mis en évidence l'importance de la dissimilarité fonctionnelle des détritivores dans le processus de décomposition. Cependant très peu de travaux ont étudié le rôle de la biodiversité à travers différents niveaux trophiques, ce qui limite fortement notre compréhension du fonctionnement de l'écosystème. L'objectif de ce troisième chapitre est donc d'étudier conjointement le rôle de la diversité des détritivores et de la diversité des litières sur une large gamme de processus du sol. Plus spécifiquement, j'ai testé l'hypothèse selon laquelle la dissimilarité fonctionnelle des détritivores et celle des litières interagit de manière positive. Selon cette hypothèse les processus du sol devraient être optimaux dans les traitements combinant à la fois un haut niveau de diversité des détritivores et des litières (H3a). D'autre part, la sécheresse pourrait modifier la relation entre la diversité fonctionnelle et les processus du sol. Comme la relation diversité-fonction repose sur des mécanismes impliquant des interactions entre organismes, on peut supposer que, selon l'hypothèse des gradients de stress (SGH), la relation diversité-fonction soit plus prononcée dans les conditions de stress hydrique (H3b).

Méthodes :

Pour tester ces hypothèses, une expérience en microcosmes a été mise en place à l'Ecotron européen de Montpellier. Cinq communautés de deux espèces de détritivores et 5 mélanges de deux espèces de litières ont été créés de manière à maximiser la dissimilarité fonctionnelle entre les espèces. Toutes les combinaisons possibles entre ces communautés de détritivores et ces mélanges de litières ont été incubées durant 11 semaines. Comme une modification de la fréquence des précipitations est attendue pour la région méditerranéenne, nous avons appliqué un traitement d'humidité caractérisé par deux fréquences d'irrigation contrastées mais un volume total d'eau ajouté identique. A l'issu de l'expérience, la perte de masse des litières, le lessivage de carbone et d'azote ainsi que la respiration potentielle et la capacité à dégrader la cellulose des microorganismes du sol ont été mesurés sur l'ensemble des microcosmes de l'expérience.

Résultats et discussion :

L'identité des mélanges de litières et des communautés de détritivores a fortement influencée les processus des sols étudiés à l'exception de la capacité à dégrader la cellulose. De plus, la dissimilarité

fonctionnelle a influencé plusieurs processus clefs du fonctionnement des sols. Par exemple, quand la diversité fonctionnelle de la faune augmentait, la perte de masse des litières augmentait et quand la diversité fonctionnelle des litières augmentait, le lessivage de carbone organique diminuait. La dissimilarité fonctionnelle n'a pas expliqué plus de 20 % de la variabilité des variables de réponse, ce qui signifie que son impact est modéré mais semble néanmoins pertinent pour comprendre l'impact de la diversité biologique sur les processus du sol.

La diversité des litières et des détritivores a affecté de manière interactive seulement la perte de masse des litières. Contrairement à notre hypothèse (H3a), cette interaction n'était pas synergique car certains mélanges de litières ayant une faible dissimilarité fonctionnelle ont été plus fortement affectés par la diversité des détritivores que d'autres mélanges de litières plus dissimilaires. Ce résultat montre que les interactions étaient dépendantes de l'identité des litières.

La sécheresse a affecté de manière significative les processus du sol mais n'a pas modifié les relations entre la diversité fonctionnelle et les processus du sol contrairement à nos attendus (H3b). Cependant la magnitude de l'effet sécheresse était plus importante dans les communautés avec un taux de processus élevé ce qui suggère que les mélanges de faune et de litières les plus performants sont plus sensibles à la sécheresse.

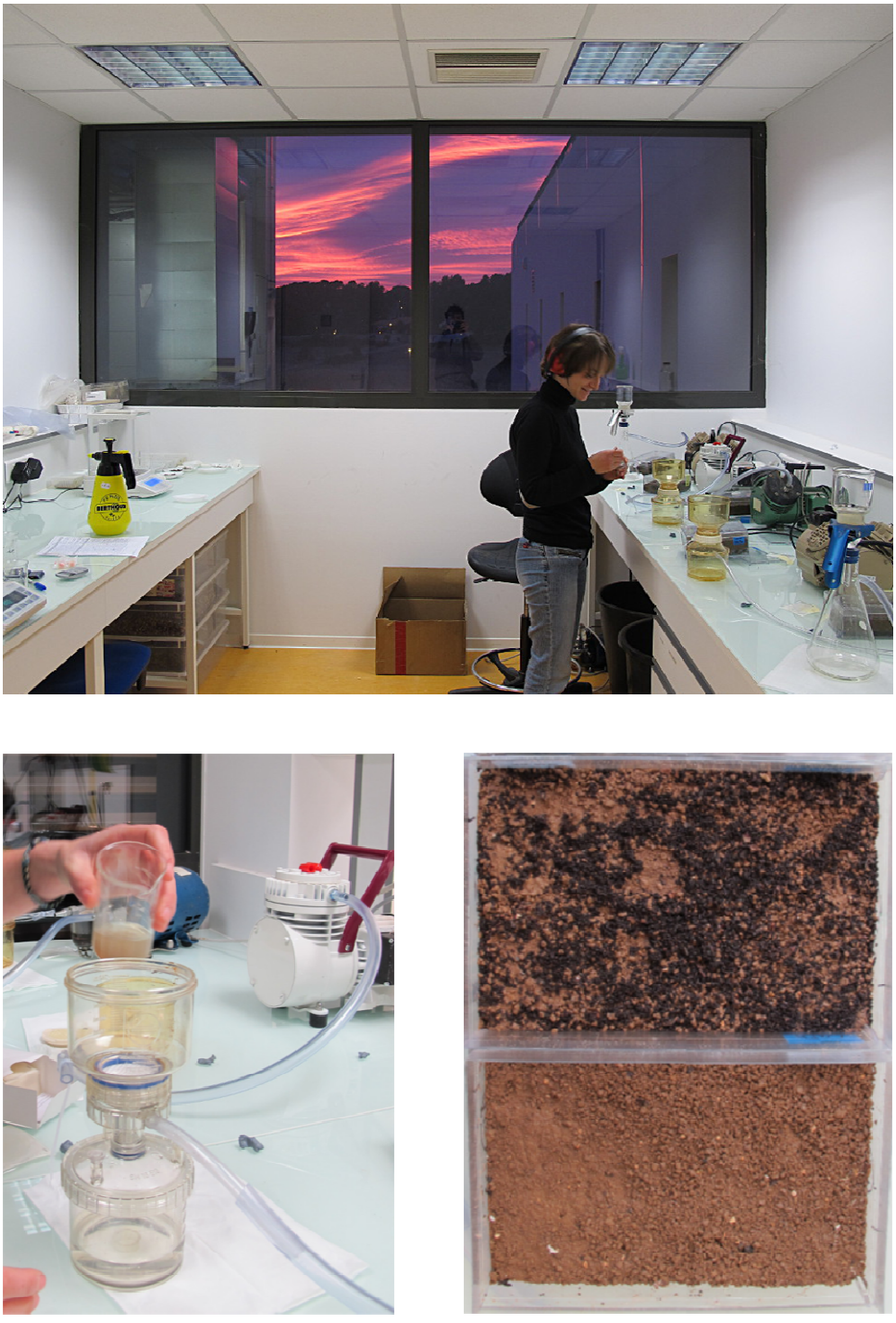

Figure 26. Photos montrant l'étape de lessivage des microcomes. En haut la salle entièrement dédiée au lessivage et à la filtration où Jordane Gavinet est en train de travailler. En bas à gauche, une unité de filtration permettant de séparer la fraction soluble de la matière organique particulaire. En bas à droite un microcosme avec faune et un sans faune, où l'on distingue bien les boulettes fécales riches en matière organique (sombre), du sol minéral (clair).

Functional dissimilarity across trophic levels as a driver of soil processes in a Mediterranean decomposer system exposed to two moisture levels

Article in preparation for the journal « Oïkos »

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Abstract

The role of biodiversity for soil processes remains poorly understood. Existing evidence suggests that functional diversity rather than species richness is relevant for soil functioning, but this has rarely been assessed at more than one trophic level. This critically limits the prediction of consequences of biodiversity loss for soil functioning, because soil organisms interact in complex food webs. In a laboratory microcosm experiment, we tested the hypothesis that functional dissimilarity of litter mixtures and litter-feeding soil fauna interactively affect five different soil processes related to litter decomposition. In a fully-crossed design, we combined five mixtures of two plant litter species and five communities of two detritivore species commonly found in Mediterranean shrubland ecosystems. Trait-based indices of functional dissimilarity were calculated for each litter mixture and detritivore community. As more intense drought periods are predicted for Mediterranean ecosystems in the future, we additionally included two different watering frequencies in our experiment to evaluate the impact of increasing drought on soil processes and their relationships with biodiversity. The different litter mixtures and soil fauna communities showed strong effects on litter mass loss, soil carbon and nitrogen leaching, as well as on soil microbial activities, but affected only litter mass loss interactively. Up to 20% of the variation in response variables was explained by functional dissimilarity, suggesting a relatively small, but ecologically relevant impact of soil functional diversity on soil process rates. Drought significantly affected several soil processes but did not modify the relationships between functional diversity and process rates. The drought effect size was higher in communities with high process rates, suggesting that better performing litter mixtures and fauna communities are more susceptible to drought. Our results indicate that trait diversity of litter mixtures and detritivore communities can predict soil process rates to some degree but that species identity effects are probably dominant.

Keywords: Detritivores, Shrub litter, Drought, Functional diversity, Mass loss, Leaching, Soil microbial activity

INTRODUCTION

Biological diversity has been recognized as a major driver of ecosystem functioning and numerous studies demonstrated its positive relationships with ecosystem processes (Balvanera *et al.* 2006; Hillebrand & Matthiessen 2009). Mechanisms underlying these relationships are multifaceted and can vary depending on the trophic level of communities of organisms and on the processes considered (Hättenschwiler *et al.* 2005; Hooper *et al.* 2005; Duffy *et al.* 2007). Moreover, biodiversity is a multidimensional concept that can be quantified in different ways (Purvis & Hector 2000). The most often used measure is species richness, which does not account specifically for functional differences among species, making mechanism-driven predictions of biodiversity-functioning relationships difficult. An increasing number of species does not necessarily reflect a parallel increase in differences among species (Epps *et al.* 2007) and can even decrease ecosystem process rates due to antagonistic (e.g. competition) interactions, as was shown in a study with bacteria (Jousset *et al.* 2011). Another widely used concept for the quantification of biodiversity is the number of functional groups, which however has the drawback of ignoring potentially important differences among species within these groups and to rely on arbitrary *a priori* decisions for group creation (Petchey & Gaston 2006). An alternative approach of functional diversity aims at defining the value and range of organismal traits that directly influence ecosystem processes at the species or individual level (Tilman 2001). Villéger et al. (2008) distinguished functional richness, functional divergence and functional evenness as distinct components of functional diversity. Each component refers to a specific attribute of the community with evenness, for example, characterizing and predicting the resistance of the community to invasion (Wilsey & Polley 2002). The choice among indices of functional diversity thus depends on the context of the study and the specific ecosystem properties to be related to functional diversity. In the case of soil processes, Hedde *et al.* (2010) found that process rates tended to saturate at low levels of soil animal species richness, suggesting that functional divergence is more relevant than functional richness of the soil animal community to capture how soil biodiversity affects soil processes. While functional richness is positively correlated with species richness, functional divergence – or equivalently functional dissimilarity (Botta-Dukát 2005) – refers to the mean functional distance between all species within a community and is independent of the number of species. Communities comprising species with similar functional attributes are more likely to undergo mutual inhibition due to competition because component species process and acquire resources in similarly ways. On the contrary, communities comprising species with dissimilar functional attributes are more likely to generate facilitation and/or to allow complementary resource use among species (Heemsbergen, *et al.* 2004). Accordingly, functional dissimilarity may correlate with process rates (Heemsbergen *et al.* 2004), suggesting that process rates could be predicted by the functional dissimilarity of the community driving these processes, and *in fine* by the functional attributes used for the calculation of functional dissimilarity.

While the importance of biodiversity for plant productivity and the underlying mechanisms have been studied in much detail (Spehn *et al.* 2005), other key ecosystem processes such as decomposition have received less attention (Gessner *et al.* 2010). During decomposition, the organically bound elements such as carbon (C) or nitrogen (N) are progressively mineralized and returned to the environment in inorganic form (Cadisch & Giller 1997). With their enzymatic capabilities, microorganisms are the key group of organisms driving decomposition worldwide (Lavelle & Spain 2001). However, microorganisms are commonly part of highly complex food webs, in which litter feeding invertebrates are major regulators of microbial activity through litter comminution and feces dispersal in the litter and top-soil layers (Lavelle & Spain 2001). A recent meta-analysis on decomposition with data from five biomes, estimated the fauna contribution to overall decomposition to be as high as 27 % on average (García-Palacios *et al.* 2013). Vos et al. (2011) clearly demonstrated that this fauna effect on decomposition depends on detritivore identity, but when different detritivore species interact the effects on decomposition and associated soil processes are often non-additive (Heemsbergen, *et al.* 2004; De Oliveira *et al.* 2010; Hedde *et al.* 2010). For example, detritivorous snails can more easily feed on fresh litter material than millipedes, and their co-occurrence leads to an overall synergistic interaction and increased decomposition (De Oliveira *et al.* 2010).

The mechanisms of facilitation or complementary resource use by a more diverse detritivore community can be particularly effective with a high diversity of available resources. Complementary resource use by detritivores is discussed as a major mechanism explaining the synergistic litter diversity effects observed in the majority of studies comparing litter mixture decomposition with that of the component litter species decomposing singly (Gartner & Cardon 2004; Hättenschwiler *et al.* 2005). The few studies that assessed decomposition of litter mixtures with and without the presence of fauna, generally found that litter-feeding animals amplified litter mixture effects on decomposition (Hättenschwiler & Gasser 2005; De Oliveira *et al.* 2010; Vos *et al.* 2011; Jabiol *et al.* 2013). These findings highlight the importance of interactions between trophic levels and the need to incorporate vertical diversity for the understanding of diversity effects on ecosystem processes (Duffy *et al.* 2007; Gessner *et al.* 2010). However, experimental manipulations of diversity across trophic levels to explore how they affect litter decomposition have been extremely rare. For an aquatic detritus-based system, Jabiol *et al.* (2013) found a synergistic interaction between fungal and detritivore species richness and demonstrated that trophic complexity is key for biodiversity effects on litter decomposition.

Here we assessed the interactive effects of changing diversity at two trophic levels on a range of soil processes related to litter decomposition in a Mediterranean garrigue ecosystem. In a fully factorial laboratory experiment, we manipulated for the first time functional diversity while keeping species number constant at both the litter (resource) and the detritivore (consumer) levels. The rationale for this approach was twofold. First, species richness *per se* usually accounts for very little or

none of the variation observed in litter diversity experiments (Gessner *et al.* 2010). Second, a clear relationship between biodiversity effects on decomposition processes and functional attributes of contributing species seems to be most promising for the establishment of a general predictive framework of how biodiversity affects decomposition and associated soil processes.

Water availability is a key factor for decomposition processes in Mediterranean ecosystems, in which the activity periods of detritivores and microorganisms typically peak in the most humid periods during fall and early spring (Doblas-Miranda *et al.* 2009; de Dato *et al.* 2010). However, these optimal periods of decomposer activity are likely to be affected by ongoing climate change. In the Mediterranean region, climate models predict a modification of the frequency of precipitation that will increase the probability of extreme events like flood or drought (Gao *et al.* 2006). Also, the coming century may be characterized by a continuous and accentuated decrease in the amount of precipitation ranging between 20 and 30 % relative to the current status (Lionello 2007). The predicted drier conditions are likely to affect decomposition processes, and they may also influence the relationships between these processes and functional diversity in the decomposer food web. The stress-gradient hypothesis (Bertness & Callaway 1994) predicts that positive interactions among species tend to increase in more stressful environments, which could result in a greater influence of functional dissimilarity under drier conditions. To address this question, we carried out our experiment at two different watering frequencies in order to simulate optimal and more limiting moisture conditions.

In brief, we hypothesized that (i) decomposition processes are positively related to the functional diversity of litter mixtures and detritivore communities, with expected highest rates when diversity is highest at both trophic levels. We further hypothesized that (ii) the relationships between process rates and functional diversity become more marked under drier conditions, because positive interspecific interactions are more likely to occur with increasing environmental stress.

MATERIALS AND METHODS

Plant and animal material

We collected leaf litter of five typical and widely distributed Mediterranean plant species: the four evergreen woody shrubs *Quercus coccifera*, *Rosmarinus officinalis*, *Ulex parviflorus* and *Cistus albidus*, and the conifer tree *Pinus halepensis* that is a pioneer species of Mediterranean forests. All five species typically co-occur in shrubland ecosystems of the Mediterranean basin. Shrub litter was collected at the Massif de l'Etoile near Marseille (5°25'E 43°22'N), and *Pinus* needle litter in the surroundings of Montpellier (3°52'E 43°40'N). All material was collected on the ground in March-April 2011, before the peak of litter fall in order to avoid confounding by freshly fallen leaf litter. Freshly fallen leaves were discarded because soil detritivores generally prefer litter that is already well colonized with microbial communities. Litter was air-dried in the laboratory, sorted into species and cleaned of adhering soil particles, twigs, and parts of fruits and flowers.

We collected five common detritivore species that are often highly abundant in the same type of garrigue ecosystem: the diplopods *Glomeris marginata* and *Ommatoiulus sabulosus*, the isopods *Armadillidium vulgare* and *Armadillo officinalis*, and the prosobranch snail *Pomatias elegans*. Three weeks before the start of the experiment, in October-November, 250 individuals of each species were collected at the Massif de l'Etoile and in the surroundings of Montpellier. All were kept in large plastic containers at constant temperature (16°C) and day length (12 h), and fed with a mixture of the five litter species chosen for the experiment.

Table 8. Litter traits used to calculate the functional dissimilarity (Rao index) of litter mixtures (mean ± SE, n = 5).

Shrub species	N (mg/g)	Lignin (mg/g)	Condensed tannins (mg/g)	Dissolved organic carbon (mg/g)	Water holding capacity (%)
Cistus albidus	6.4±0.2	249±8	5.8±1.95	3.8±0.9	178±10
Pinus halepensis	4.0±0.3	224±13	33.2±0.17	7.8±0.1	98±6
Quercus coccifera	10.3±0.3	148±8	6.0±0.27	10.6±1.3	132±5
Rosmarinus officinalis	6.5±0.3	155±6	0.7±0.06	5.2±0.5	146±12
Ulex parviflorus	10.9±0.4	230±18	0.9±0.16	5.0±1.1	97±5

Trait measurements and functional dissimilarity

The selection of functional traits is a critical step in the calculation of diversity index (Petchey & Gaston 2006; Villéger *et al.* 2008). Traits must be selected according to their relevance to the ecological process and to avoid high redundancy between traits. Five litter traits were retained among ten that were initially measured (Table 8): nitrogen (N) and lignin concentrations, as good predictors of litter decomposition rates (e.g. Zhang et al., 2008); condensed tannin concentration, due to its importance for both microbial decomposers (Kraus *et al.* 2003) and detritivores (Coq *et al.* 2010).; water-soluble carbon concentration, which is a critical energy source for decomposers and has a strong influence on how decomposing litter affects soil processes (Fanin et al. 2012); and water holding capacity of litter, a potentially important trait for detritivores when water is limiting, and a good predictor of decomposition, especially in Mediterranean ecosystems (Makkonen *et al.* 2012). We used standard methods to determine the litter traits as described in Coq *et al.* (2010) and Coulis *et al.* (2013).

Five functional traits were also selected among six that had been measured on each detritivore species (Table 9). All were related to the ability of detritivores to transform leaf litter and influence its subsequent decomposition in their feces: consumption rate and assimilation efficiency, which are directly related to the expected impact of detritivores on litter mass loss and mineralization; outer surface area of fecal pellets and size of litter particles within fecal pellets, which mirror the surface available for microbial colonization in feces (Lavelle & Spain 2001; Hedde *et al.* 2007); and hygroscopicity of feces, due to the importance of water availability in this material for subsequent microbial activity. All traits were determined using a single leaf litter species, *Cistus albidus*, which was found to be the preferred food of the five detritivore species studied (unpublished results). Consumption rates (mg of dry litter consumed per g of live animal per day) and assimilation efficiencies were calculated according to (David & Gillon 2002). Width, length and height of 50 fecal pellets from each species were measured and used to estimate the mean surface area. The mean particle size in feces was calculated according to Hedde *et al.* (2007). The water content of feces was measured after enclosing 50 fecal pellets for five hours in a water saturated atmosphere.

Table 9. Traits of the five detritivore species used to calculate the functional dissimilarity (Rao index) of detritivore communities (mean ± SE, n = 5). Mean individual biomass was not used for distance measurements but for weighting individual species traits.

Shrub species	Consumption rate (mg/g/d)	Assimilation efficiency (%)	Feces surface area (mm^2)	Feces hygroscopy (%)	Feces mean weighted particule size (mm)	Individual biomass (mg)
Armadillidium vulgare	77±1	50±1	7±0.3	29±1.8	0.26±0.001	195±0.8
Armadillo officinalis	88±7	65±3	9±0.4	28±1	0.2±0.01	149±0.9
Glomeris marginata	126±34	12±3	40±1.2	15±0.9	0.27±0.004	259±0.8
Ommatoiulus sabulosus	117±12	23±4	8±0.1	30±0.7	0.16±0.008	93±0.2
Pomatias elegans	26±4	43±5	8±0.5	20±0.7	0.1±0.001	475±4.6

Most previous studies did not formally distinguish between species richness and functional diversity or varied both components of biodiversity at the same time. We chose here to vary functional diversity across two trophic levels while keeping the number of species constant. For this purpose, we first calculated Rao's quadratic entropy as an index of functional dissimilarity (Botta-Dukát 2005) for all possible combinations of two species of plant litter and soil animals. At each trophic level, there were ten possible combinations of two species and we chose five that matched the following criteria: (i) to maximize the functional diversity gradient, i.e. the range of Rao index values, and (ii) to include each species exactly twice in the five combinations. The five litter mixtures retained were, in increasing order of functional dissimilarity, *Quercus*/*Rosmarinus* (0.33), *Rosmarinus*/*Ulex* (0.40), *Cistus*/*Ulex* (0.43), *Cistus*/*Pinus* (0.69) and *Quercus*/*Pinus* (0.81); and the five detritivore communities retained were *Armadillidium*/*Armadillo* (0.03), *Armadillidium*/*Ommatoiulus* (0.21), *Pomatias*/*Armadillo* (0.37), *Glomeris*/*Ommatoiulus* (0.58) and *Pomatias*/*Glomeris* (0.70). At the end of the experiment, Rao's index was recalculated for each microcosm and weighted by the relative abundance of species expressed in terms of biomass (Barantal *et al.* 2011). Litter biomass values were similar in all microcosms but invertebrate biomass values varied slightly at the start of the experiment, and even more at the end of the experiment due to mortality in some microcosms (the overall death rate was 5 %). The average of the initial and final biomass was worked out for each detritivore species in all microcosms, taking into account the approximate date of death when needed, and these biomass values were used to weight the dissimilarity indices.

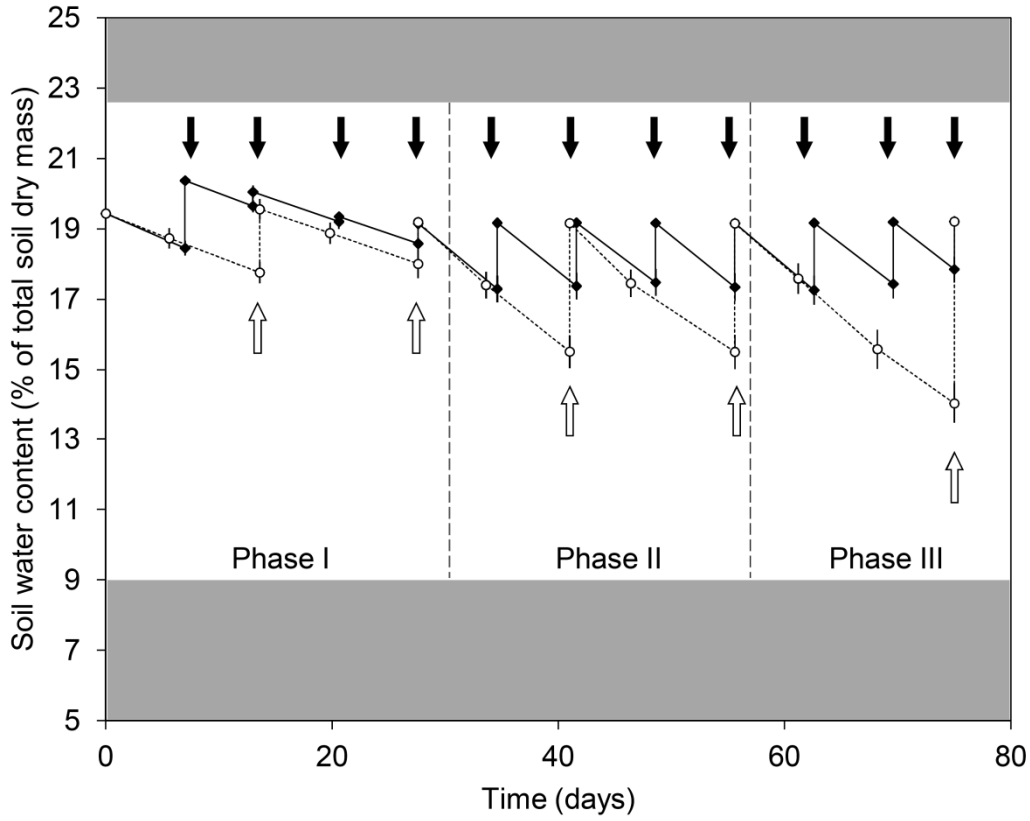

Figure 27. Dynamics of soil water content (means ± SE, n = 150) in microcosms from the dry treatment (open circles) and the moist treatment (filled circles). Arrows indicate rewetting events. Zones corresponding to water contents above the field capacity and below the wilting point are darkened. .

Experimental design

Microcosms were constructed in lidded boxes of transparent polystyrene (175 x 115 x 65 mm, LAB4 © CAUBERE). The bottom of each box was lined with 1 cm thick inert plastic composite (polyamide and polyethylene terephthalate, Enkadrain®) to improve drainage of the system. This drainage layer was covered by 700 g of air-dried soil sieved through a 2 mm screen, resulting in a 3-cm deep soil layer within each box. The soil used for the experiment was collected from the top layer (top 10 cm) of an experimental agricultural field at Grignon, France (1°56'E, 48°50N). We chose this particular soil because the field had been cultivated with C_4 plants for 40 years and we intended to take advantage of the difference in isotopic labeling between soil organic matter and the C_3 litter species used, to distinguish between soil and litter respiration (data not shown here). The soil was a Luvisol developed on loess over limestone, with a total C content of 13.9 g kg^{-1} and a total N content of 1.27 g kg^{-1}. Eight grams of leaf litter (4 g of each of the two species) were laid on the soil layer. At the start of the experiment each microcosm was watered with deionized water to reach 80% of field capacity in the soil and to approach water holding capacity of litter (see below for actual litter water content).

After watering, two individuals of each of the two animal species, previously starved for 24 h and weighed, were added in each microcosm.

In addition to the two fully crossed parameters of litter functional dissimilarity (five litter mixtures) and detritivore dissimilarity (five detritivore assemblages plus a treatment without fauna), we included two different watering regimes. Each treatment combination was replicated five times resulting in a total number of 300 microcosms (5 litter treatments x 6 animal treatments x 2 watering regimes x 5 replicates). An additional five replicates per watering regime without any litter and fauna were included, yielding a grand total of 310 microcosms. Each of the five replicates per treatment combination was kept in one of five incubators, with microcosms distributed randomly within incubators and positions changed every 3 days according to a randomized complete block design.

Microcosms were incubated at the European Ecotron facility for 11 weeks, at constant temperature (20°C), relative air humidity (50%), and day length (12h) in the incubators. Two watering frequencies were used in the microcosms. Microcosms of the humid treatment were remoistened weekly, whereas those of the dry treatment were remoistened every two weeks or after a three-week interval during the last drying-rewetting cycle (see Figure 27). Microcosm lids were initially pierced with five 1.3 mm diameter holes to allow CO_2 and water vapor exchanges (Phase I, Figure 27). As the desiccation rate was rather low, an additional 14 holes were pierced (a total of 19) during phases II and III (Figure 27). The amount of water added when watering compensated for evaporation losses and reset litter and soil moisture to initial conditions. Consequently, the same total amount of water was added to microcosms of the humid and dry treatments (96.6 ±1.8 and 95.5 ± 2.2 ml, respectivley) over the course of the experiment. However, soil water content was on average 81 ± 0.1% of field capacity in the humid treatment, vs. 77 ± 0.1% in the dry treatment ($p < 0.001$). Additionally, soil moisture content in the dry treatment decreased to 67% and even 58% of the field capacity during the last drying-rewetting cycle, while it never dropped below 75 % in the humid treatment (Figure 27). Litter water content just after watering was on average 120% for *Cistus*, 72% for *Quercus*, 71% for *Rosmarinus*, 67% for *Pinus*, and 54% for *Ulex*. These values decreased rapidly within two days and, after six days, water content was 26% for *Cistus*, 24% for *Quercus*, 25% for *Rosmarinus*, 24% for *Pinus* and 19% for *Ulex*. Litter water content remained at similar levels during the second week of dry treatment (see Fig. A. in Annexe 2 for more details).

Response variables

At the end of the 11-week experiment, animals were taken out of the boxes and weighed. The remaining litter material was collected and rinsed in 200 ml distilled water for five minutes to remove soil particles, and immediately freeze-dried before weighing for mass loss determination (expressed in % of initial litter dry mass).The water used for litter rinsing was added to the corresponding microcosm in order to simulate a heavy rain shower (i.e. 10 mm of precipitation in less than an hour). Soil was allowed to drain for 20 min and leachates were collected underneath the drainage layer, filtered at 0.45 µm (cellulose nitrate membrane, Sartorius) to remove microorganisms and particulate soil matter, and immediately stored at -80°C until analysis. Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) in leachates were determined using a TOC analyzer equipped with a supplementary module for N detection (TOC-V CSH E200V and TNM-1, Shimadzu, Tokyo, Japan).

Microcosms were then kept at 25°C for 48 h to allow moderate drying before the soil was sieved through a 2 mm screen and dried at 25°C for 5 days. Air-dry soil of each microcosm was then automatically split into ten equal samples using a sample divider. From these subsamples, we measured substrate induced respiration (SIR) following Beare et al. (1990). Further measurements included the capacity of the soil microbial community to degrade cellulose paper according to Wardle et al. (1999). Briefly, cellulose paper disks (filter paper qualitative 410, VWR, 55 mm diameter) were enclosed between two nylon 2 mm mesh nets and incubated with 20 ± 0.5 g of soil watered to 80% of field capacity in Petri dishes. After three weeks at 25°C in the dark, cellulose disks were recovered, gently cleaned with a brush in deionized water, and oven dried (65°C) to determine remaining cellulose dry mass and cellulose mass loss (expressed in % of initial cellulose mass).

Statistical analyses

The main effects and interactions of litter mixture identity, detritivore community idendity and watering frequency on the response variables were tested using ANOVA. Incubators were included in the analyses as a blocking factor and the main effects and interactions of the three fixed factors were tested over their interactions with blocks. Post-hoc pairwise comparisons were performed using Tukey's method. The linear relationships between response variables and functional dissimilarity of litter mixtures or detritivore communities were determined by ordinary least squares (OLS) regression, with litter and detritivore dissimilarity indices as continuous explanatory variables. We used ANCOVA to test the relationships between functional dissimilarity (co-variable) and process rates with the moisture treatment as a categorical variable. Interaction terms between functional dissimilarity and moisture treatment were used to compare the slopes of the regression lines at the two moisture levels.

In order to assess the magnitude of drought effect for each treatment combination, we calculated the standardized difference between mean process rate in humid (μ_{humid}) and dry (μ_{dry}) conditions (drought effect size) using Cohen's d formula (Cohen 1992):

$$d = \frac{\mu_{humid} - \mu_{dry}}{\sqrt{\left((\sigma_{humid})^2 + \left(\sigma_{dry}\right)^2 \right)/2}}$$

Drought effect size was calculated for each process. Its relationship with mean process rates in humid conditions was tested by ordinary least squares (OLS) regression.

RESULTS

Impacts of litter mixture and detritivore community identity on process rates

Three processes (litter mass loss, organic carbon leaching and total nitrogen leaching) were significantly affected by both litter mixture and detritivore community identity (Table 10). Moreover, SIR of the soil differed significantly among detritivore communities, and cellulose decomposition differed significantly among litter mixtures (Table 10).

Litter mixture identity strongly affected litter mass loss, which ranged from 14.7 ± 1.0 % in *Quercus/Pinus* to 23.1 ± 1.0 % in *Quercus/Rosmarinus* when no detritivores were present. The presence of detritivores nearly doubled these values but also changed the ranking of litter mixtures in terms of mass loss rates. Fauna effects were more substantial in *Cistus*-comprising mixtures and, across all detritivore and moisture treatments, litter mass loss ranged from 29.0 ± 0.6% in *Quercus/Pinus* to 43.9 ± 1.3% in *Cistus/Ulex* (Figure 28). Detritivore community identity also significantly affected litter mass loss, which ranged from 31.0 ± 0.7 % with *Pomatias/Armadillio* to 46.1 ± 1.5% with *Glomeris/Ommatoiulus* (all litter and moisture treatments combined) (Figure 28). However, the relative impact of each detritivore community on mass loss differed among litter mixtures, as shown by the significant litter-fauna interaction (Table 3). The *Pomatias/Armadillo* community, in particular, had a comparatively weaker impact on *Cistus/Ulex* and a stronger impact on *Quercus/Romarinus* than other detritivore communities.

Table 10. Results of ANOVAs to test for the effects of litter mixture identity, detritivore community identity, and moisture treatment on the five variables measured at the end of the experiment.

	Litter mass loss				DOC leaching				TDN leaching				Soil SIR				Soil PCD			
	D.f.	M.Sq.	F value		D.f.	M.Sq.	F value		D.f.	M.Sq.	F value		D.f.	M.Sq.	F value		D.f.	M.Sq.	F value	
Block (B)	4	0.020	-		4	0.25	-		4	3.01	-		4	1.36	-		4	294	-	
Litter mixture identity (L)	4	0.243	183	***	4	28.34	267	***	4	3.84	21	***	4	0.79	2		4	71	5	*
L x B	16	0.001	-		16	0.11	-		16	0.19	-		16	0.34	-		16	15	-	
Detritivore community identity (D)	4	0.178	50	***	4	1.94	9	***	4	0.75	5	**	4	0.74	9	***	4	10	1	
D x B	16	0.004	-		16	0.22	-		16	0.15	-		16	0.08	-		16	11	-	
Watering frequency (W)	1	0.028	12	*	1	4.12	8	*	1	2.23	2		1	2.84	12	*	1	158	3	
W x B	4	0.002	-		4	0.53	-		4	1.23	-		4	0.23	-		4	58	-	
L x D	16	0.009	7	***	16	0.20	1		16	0.23	1		16	0.14	1		16	29	2	
L x D x B	64	0.001	-		64	0.23	-		64	0.29	-		64	0.14	-		64	19	-	
L x W	4	0.002	1		4	0.23	1		4	0.06	0		4	0.29	4	*	4	21	2	
L x W x B	16	0.002	-		16	0.20	-		16	0.14	-		16	0.07	-		16	12	-	
D x W	4	0.002	2		4	0.19	1		4	0.21	1		4	0.14	1		4	10	0	
D x W x B	16	0.001	-		16	0.13	-		16	0.17	-		16	0.15	-		16	25	-	
L x D x W	16	0.002	1		16	0.23	1		16	0.33	1		16	0.07	0		16	13	1	
L x D x W x B	64	0.001	-		62	0.19	-		63	0.23	-		61	0.18	-		58	21	-	

Dissolved organic carbon (DOC) leaching from the entire microcosms at the end of the experiment was mostly driven by decomposing leaf litter, as shown by the roughly 6-fold higher amount of carbon leached in microcosms with litter additions (on average 2.7 ± 0.1 mg kg^{-1} in the absence of detritivores) compared to control microcosms without any litter material and detritivore (0.4 ± 0.1 mg kg^{-1}, $p < 0.001$). Litter mixture identity significantly affected the amount of DOC, which ranged from 1.7 ± 0.1 mg kg^{-1} in *Cistus/Ulex* to 3.5 ± 0.1 mg kg^{-1} in *Quercus/Rosmarinus* (all fauna and moisture treatments combined) (Figure 28). Although the presence of detritivores only slightly decreased carbon leaching in comparison with control microcosms without addition of fauna, the amount of DOC differed significantly depending on the type of community, ranging from 2.3 ± 0.1 mg kg^{-1} with *Pomatias/Glomeris* to 2.8 ± 0.1 mg kg^{-1} with *Armadillidium/Armadillo* (all litter and moisture treatments combined) (Figure 28)

Litter mixture identity significantly affected the total dissolved nitrogen (TDN) content in leachates at the end of the experiment (Table 10). Across all fauna and moisture treatments, TDN ranged from 1.34 ± 0.07 mg kg^{-1} in *Quercus/Rosmarinus* to 2.06 ± 0.09 mg kg^{-1} in *Quercus/Pinus* (Figure 28). Although the presence of detritivores did not significantly affect nitrogen leaching in comparison with control microcosms without fauna, again, the amount of TDN differed significantly depending on the type of community, ranging from 1.42 ± 0.07 mg kg^{-1} with *Pomatias/Glomeris* to 1.72 ± 0.08 mg kg^{-1} with *Armadillidium/Armadillo* (all litter and moisture treatments combined) (Figure 28).

Soil microbial processes (SIR and PCD) responded differently to changes in biotic components. Soil SIR was slightly but significantly affected by the presence and identity of detritivores, while PCD was only affected by the identity of litter mixtures (Table 10). Soil SIR was higher in microcosms with detritivores (4.46 ± 0.03 µg CO_2 g^{-1} hr^{-1}) compared to microcosms in which only litter was added (3.97 ± 0.07 µg CO_2 g^{-1} hr^{-1}, $p < 0.001$). Moreover, soil SIR varied significantly depending on the detritivore community, ranging from 4.32 ± 0.05 µg CO_2 g^{-1} hr^{-1} with *Pomatias/Armadillio* to 4.61 ± 0.07 µg CO_2 g^{-1} hr^{-1} with *Glomeris/Ommatoiulus* (all litter and moisture treatments combined) (Figure 28). By contrast, soil PCD varied depending on the litter mixture, ranging from 20.0 ± 0.6 % for *Rosmarinus/Ulex* to 22.9 ± 0.7 % for *Cistus/Ulex* (all fauna and moisture treatments combined) (Figure 28).

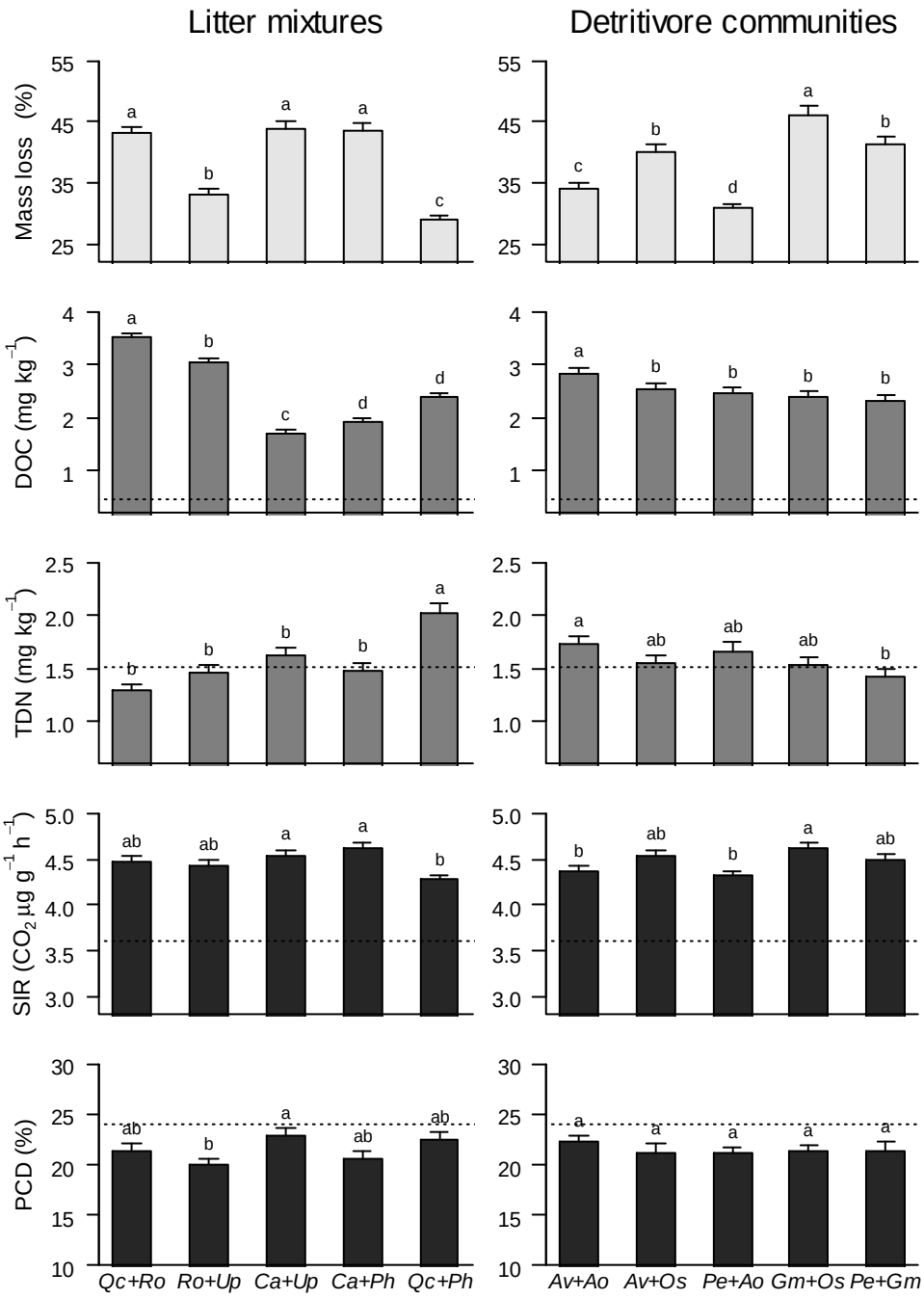

Figure 28. Effects of litter mixtures and detritivore communities on litter mass loss (mean ± SE, n=50, pooled across the two humidity treatments). Tukey's post hoc tests were performed to evaluate pairwise differences between litter mixtures across all detritivore communities (left). The same tests were run to evaluate pairwise differences between detritivore communities across all litter mixtures (right). The different letters indicate significant differences among groups of bars. Dotted lines indicate mean process rates in microcosms without leaf litter.

The impact of functional dissimilarity on process rates

There were significant linear relationships between three processes (litter mass loss, organic carbon leaching and total nitrogen leaching) and the functional dissimilarity of litter mixtures and/or detritivore communities (Figure 29). Litter mass loss decreased with increasing litter dissimilarity and increased with detritivore dissimilarity. Although opposite, the slopes of these relationships were of similar magnitude and explained a similar amount of variation. DOC leaching showed broadly a similar negative relationship with litter dissimilarity as was observed for litter mass loss but, in contrast to litter mass loss, DOC leaching was also negatively, though weakly correlated with detritivore dissimilarity. Unlike DOC leaching, TDN leaching was positively correlated with litter dissimilarity and showed no significant correlation with detritivore dissimilarity (Figure 29). We detected no relationships between the soil microbial parameters (SIR and PCD) and litter or detritivore dissimilarity (data not shown).

Comparisons between the sums of squares calculated in these linear regressions and those calculated in ANOVAs performed on the same data set (see above) showed that linear models based on functional dissimilarity accounted for a much smaller proportion of the total sum of squares than differences among groups in the ANOVAs (e.g. 16 and 20% in the linear regressions of DOC on litter dissimilarity under humid and dry conditions, respectively, vs. 74 and 61 % for the litter treatment effects on DOC in the ANOVAs). This indicates that differences in process rates observed among litter mixtures or detritivore communities were only partly explained by functional dissimilarity.

Moisture effects

Reduced watering frequency significantly affected litter mass loss, carbon leaching and soil SIR, but not total nitrogen leaching and potential cellulose decomposition (Table 10). Drier conditions significantly decreased litter mass loss, on average from 19.7 % to 17.7 % in the absence of detritivores and from 39.6 % to 37.5 % when detritivores were present (Figure 29). In contrast to litter mass loss, microcosm DOC leaching increased significantly from 2.4 ± 0.1 mg kg^{-1} under humid conditions to 2.6 ± 0.1 mg kg^{-1} under dry conditions (all litter and fauna treatments combined). Similarly to DOC, the average TDN (across all fauna and litter treatments) increased from 1.50 ± 0.04 to 1.69 ± 0.06 mg kg^{-1} with reduced watering. Reduced watering frequency also increased soil SIR from 4.36 ± 0.04 µg CO_2 g^{-1} hr^{-1} under humid conditions to 4.57 ± 0.04 µg CO_2 g^{-1} hr^{-1} under dry conditions. In contrast, the PCD decreased from 21.9 ± 0.4% under humid conditions to 20.3 ± 0.4% under dry conditions.

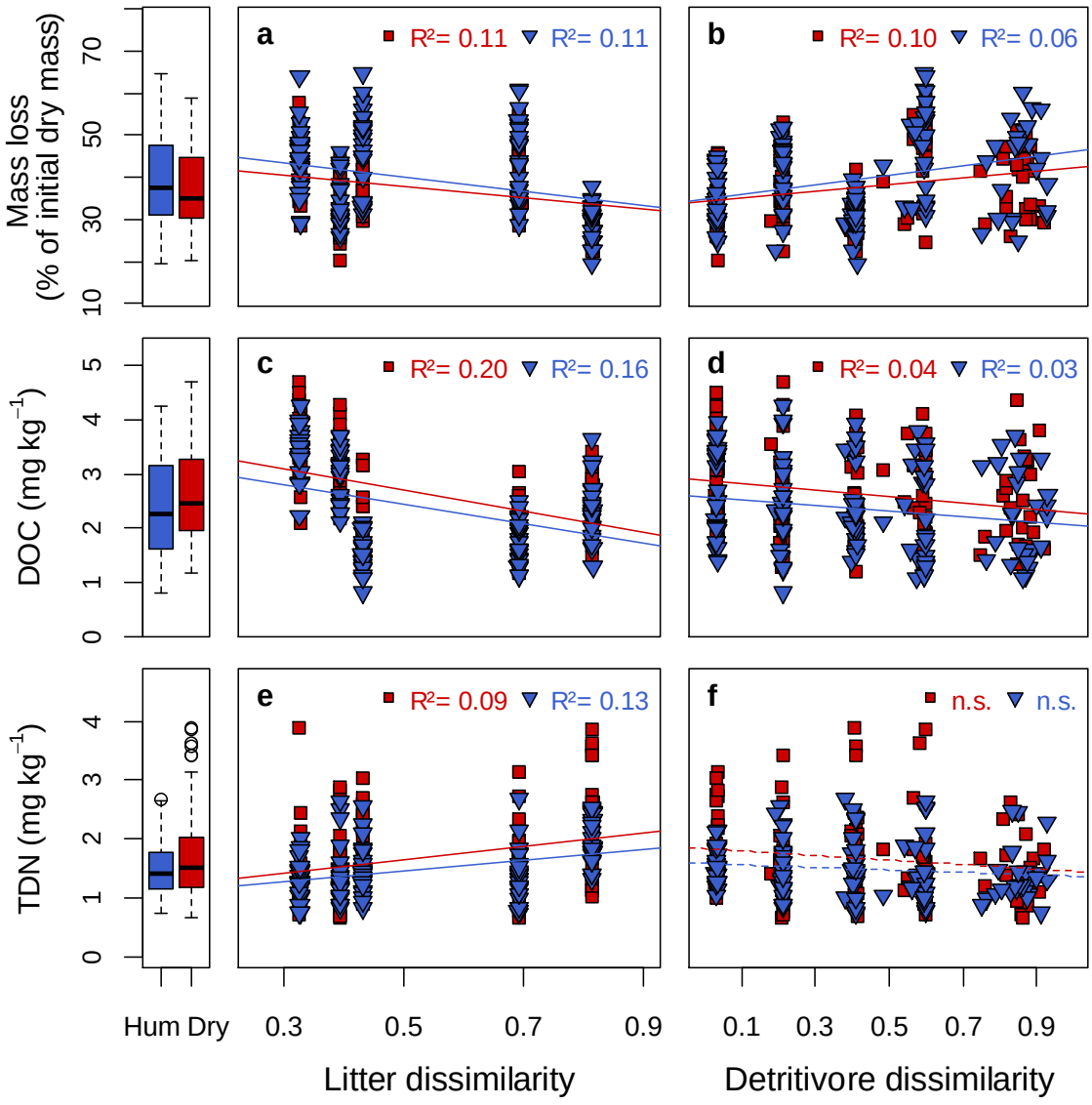

Figure 29. Relationships between functional dissimilarity of litter mixtures or detritivore communities and mass loss (a, b), leaching of dissolved organic carbon (DOC) (c, d), and leaching of total dissolved nitrogen (TDN) (e, f). For each process, data are shown either grouped by humidity treatment in a boxplot (left), expressed as a function of litter mixture dissimilarity (center) or as a function of detritivore community dissimilarity (right). When linear regressions are significant ($p < 0.05$), regression lines are drawn with their respective R^2 values.

The drought effect size for litter mass loss, DOC leaching and PCD significantly increased with increasing process rates under humid conditions (Figure 30). In contrast, there was no change in drought effect size for TDN leaching and SIR with increasing process rates under humid conditions (Figure 30).

Finally, the slopes of the linear regressions of litter mass loss, DOC leaching, and TDN leaching on functional dissimilarity did not differ significantly under humid and dry conditions (Figure 29), indicating that reduced watering frequency in microcosms did not change the relationships between litter or detritivore dissimilarity and rates of any of the quantified processes.

DISCUSSION

By manipulating biodiversity equally across the two trophic levels of plant leaf litter and litter feeding soil animals, we showed that changing biodiversity in the decomposer system has important consequences on a range of soil processes of a Mediterranean woody shrub ecosystem. Water availability as a critical environmental factor in the studied ecosystem additionally changed soil processes, but did not appear to modify the observed relationships between functional diversity and process rates.

Importance of the identity of interacting organisms for soil processes

A first important result of our study is that the species compositions of litter mixtures and detritivore communities have major effects on belowground ecosystem processes such as decomposition and nutrient cycling. The results not only confirmed that changes in litter and detritivore identity interactively affect rates of litter mass loss (De Oliveira *et al.* 2010), but further showed that these changes have potentially important consequences for the transfer of soluble nutrients in the underlying soil and soil microbial functioning.

Decomposing litter apparently was an important source of the C transferred to the soil in the form of DOC, with a 6-fold higher amount of DOC from soil with litter compared to bare soil. This is as such not surprising because leaf litter was a supplementary source of organic matter with a higher relative amount of labile C compared to soil C (Lavelle & Spain 2001), which can be leached more easily. However, changes in litter mixture composition resulted in a 2.1-fold variation in C leaching and a 1.5-fold variation in N leaching. These variations did not correlate with litter mass loss, in line with previous findings showing that rates of mineralization and DOC leaching are independent (Hagedorn & Machwitz 2007). Moreover, changes in detritivore community composition also affected leaching, with a 1.2-fold difference for C and N leaching between the communities with the lowest (*Pomatias/Glomeris*) and the highest (*Armadillidium/Armadillo*) leaching. Interestingly, these effects were not correlated with the fauna impacts on litter mass loss, indicating that different litter-feeding

invertebrates did not influence the flux of elements by comminuting plant litter to varying degrees, but had more complex effects probably linked to species-specific functional traits, such as digestive capacity and characteristics of feces. Finally, the influence of litter mixtures on cellulose decomposition and that of detrivore communities on SIR in the soil, although less pronounced, were also significant. It is clear from our results that changes in the composition of plant and soil invertebrate communities play a crucial role in the functioning of the studied Mediterranean ecosystem.

Functional dissimilarity as a predictor of process rates

Originally we hypothesized that the community identity effects discussed above are related to and thus predictable from trait dissimilarity expressed by the different communities. Unlike previous experiments that included species richness gradients, we exclusively varied functional dissimilarity defined on the basis of five well-described functional plant and detritivore attributes. Functional dissimilarity as a specific component of biodiversity has been suggested to better predict biodiversity effects in the decomposer system than species numbers (Heemsbergen, *et al.* 2004). By keeping species number constant at two species at both trophic levels with the same abundances and similar biomass, we standardized across a number of parameters that are known to affect decomposition and associated soil processes in order to evaluate specifically the importance of functional dissimilarity as a driver of ecosystem processes.

In line with our initial hypothesis, increasing functional dissimilarity of detritivore communities correlated positively with litter mass loss – and negatively with DOC leaching, which may also reflect better resource use. Functional dissimilarity of soil animals has been proposed to predict soil processes before (Heemsbergen, *et al.* 2004; Hedde *et al.* 2010). In a laboratory microcosm experiment Heemsbergen et al. (2004) manipulated detritivore diversity by constructing 18 different detritivore communities using eight temperate species of litter-feeding macrofauna with *Alnus glutinosa* leaf litter as a food source. Similar to our results, they observed a positive relationship between mean functional dissimilarity of detritivore communities and the net diversity effect on litter mass loss and soil respiration. They concluded that communities with functionally more dissimilar species should generate facilitation and thus have stronger effects on process rates than communities with functionally similar species, which should inhibit each other because of competition. In another laboratory microcosm experiment with 4 temperate detritivore species, (Hedde *et al.* 2010) also observed that dissimilarity was positively correlated with the net diversity effect on mass loss of *Fagus* leaf litter and respiratory CO_2 efflux. The few existing explicit tests on the role of functional diversity of detritivore communities from temperate forest ecosystems and our study using a different set of species from a Mediterranean woody shrub ecosystem, all suggest that trait dissimilarity of litter-feeding soil animal communities is an important component of soil biodiversity that can predict

some of the variation in soil process rates. However, all the existing studies have been conducted under controlled laboratory conditions and documented a relatively small amount of variation in process rates explained by detritivore functional dissimilarity. It remains to be shown whether this relationship still is relevant under field conditions with fluctuating and non-optimal environmental conditions. By varying the moisture conditions, our results indicate that the relationship may still hold when environmental factors are somewhat more stressful, suggesting that the relationship between detritivore functional dissimilarity and process rates may be quite robust.

Functional dissimilarity of litter mixtures also correlated with litter mass loss, and the leaching of DOC and TDN. However, in contrast to our initial hypothesis, litter mass loss decreased with increasing litter functional dissimilarity. This negative relationship between functional litter dissimilarity and mass loss also explains in part why we could not confirm the hypothesis that increasing functional diversity at both the resource and consumer trophic levels leads to the highest process rates. The different detritivore communities had an especially strong effect on the three litter mixtures *Cistus/Ulex*, *Cistus/Pinus* and *Quercus/Rosmarinus*, which include all five litter species used for our tests and were quite evenly distributed along the litter dissimilarity gradient. Moreover, the most dissimilar *Glomeris/Pomatias* detritivore community, and the least dissimilar *Armadillidium/Armadillo* community, had the same effect on litter mass loss of *Quercus/Pinus*, the litter mixture with the highest functional dissimilarity. Consequently, instead of increasing the litter dissimilarity effect on mass loss, detritivore presence attenuated this effect, which in our case means a less negative correlation between litter dissimilarity and mass loss when detritivores were present. As far as we know there exists no other published study that tested the interactive effects of changing functional dissimilarity of litter mixtures and detritivore communities on terrestrial decomposition. The few previous studies that specifically evaluated the impact of litter functional diversity on decomposition reported mixed results. Using leaf litter from 16 tropical rainforest tree species, Barantal *et al.* (2011) constructed 28 different litter mixtures containing between 2 and 4 different litter species, that decomposed in the natural environment. Although they observed strong non-additive litter mixture effects, these were not significantly related to any of the three functional diversity components (richness, evenness, and divergence). Barantal *et al.* (2011) concluded that interactions among different litter species depend on the presence of particular species driving the mixture effects on decomposition, independently of the number and characteristics of other species present in the mixture. In a different study, Hättenschwiler & Jørgensen (2010) composed litter mixtures from tropical rainforest species to specifically create a dissimilarity gradient in C:N:P stoichiometry, assuming that resource stoichiometry critically determines decomposer activity. In the presence of litter-feeding macrofauna, they observed increased C, N, and P loss from litter mixtures with increasing stoichiometric dissimilarity, but this significant correlation disappeared when fauna was excluded and microorganisms were dominating decomposition. In line with this result, a recent

laboratory study with temperate species demonstrated that dissimilarity in litter nutrient content was a strong driver of litter mixture effects, especially in presence of detritivores (Vos *et al.* 2013).

Both increasing dissimilarity of litter mixtures and detritivore communities reduced DOC leaching, suggesting that functional diversity of decomposing litter and litter-feeding soil fauna leads to reduced C transport within the soil profile, with potentially important consequences for soil C fluxes and long term C storage (Kalbitz & Kaiser 2008). Moreover, as litter mass loss increased with increasing detritivore dissimilarity, a higher functional diversity of soil fauna may modify the balance between C mineralization and DOC leaching as two important pathways of soil C fluxes. Any detritivore effect on C mineralization would rather be indirect by stimulating microbial activity (Lavelle & Spain 2001), which concurs with our results of higher soil SIR in the presence of detritivores compared to microcosms without detritivores. However, this detritivore effect on SIR was not correlated to the dissimilarity of detritivore communities.

The litter traits chosen to calculate functional diversity indices vary from one study to another, which impacts the value and range of the indices. How the traits are chosen and how many are combined is apparently an important question. On the basis of eight distinct litter traits, Barantal *et al.* (2011) tested a large number of trait combinations for the calculation of their different functional diversity indices, but found very little differences in the resulting correlations with litter mass loss. In spite of determining the five litter traits to be used in our calculations *a priori*, we also included additional traits and tested different trait combinations and their effect on the dissimilarity index and the correlation with process rates *a posteriori*. Similar to Barantal *et al.* (2011), the results differed very little. This can mean two things, (1) that the process relevant traits were not measured, or (2) that trait-based functional dissimilarity does not explain much more variation in process rates than what was observed in our and previous studies, whatever the traits used for dissimilarity calculations. The species entity comprises all potentially measurable traits and the selection of appropriate traits is a tricky issue. In order to be as close to the process to be evaluated as possible, Heemsbergen *et al.* (2004), for example, used process rates measured *a posteriori* in single species treatments as functional attributes to calculate functional dissimilarity of multispecies communities. While this approach assures that the relevant traits are being used, it can be criticized because it confounds predictor variables with response variables. It is preferable to use traits that differ from response variables and that are determined *a priori*, based on literature data or on specific measurement as it was done here and in other studies (Hedde *et al.* 2010; Barantal *et al.* 2011; Vos *et al.* 2013). Such an *a priori* choice is relatively simple for litter traits, because of the intensively studied litter quality impacts on decomposition. However, the choice of pertinent fauna traits is more difficult, because there are only few data available and, unlike dead leaves, traits of live fauna such as litter consumption rates can vary with environmental conditions. In future research, the integration of intraspecific trait variability will be an important step in measuring functional diversity (Petchey & Gaston 2006).

The impact of drought

Although all microcosms received virtually the same amounts of water during the experiment, reduced frequency of watering in half of the microcosms clearly resulted in drier conditions, which caused significant changes in several of the processes we measured. As expected, litter mass loss was significantly lower in the dry treatment. This result is in line with earlier studies that showed that the frequency rather than the quantity of precipitation is important for litter decomposition, because the soil surface dries out at the same rate after large or small rain events, and differences in soil moisture at greater depth are less relevant for leaf litter decomposing at the soil surface (Yahdjian & Sala 2008). Litter mass loss also decreased in the dry treatment when detritivores were present, but the results suggest that their activity attenuated the negative effects of drought on microbial decomposition. Overall, reduced watering frequency decreased litter mass loss by 5% in the presence of detritivores, vs. 10% in microcosms without addition of fauna. The same fauna-driven attenuation of negative effects of drought on decomposition was observed in a previous experiment applying even harsher drought conditions, which reduced microbial-driven decomposition by as much as 58% (Coulis *et al.* 2013). In order to remain active, both microorganisms and detritivores require a certain humidity of their substrates and activity ceases below a threshold value. For Mediterranean ecosystems it has been suggested that soil microorganisms become inactive below 13 to 20 % of volumetric soil water content (Sardans & Peñuelas 2013). To our knowledge such threshold values have not been determined for litter-feeding fauna, but our results suggest that they will be lower for detritivores than for microorganisms.

Microcosms from the drier treatment leached more DOC than those maintained at a consistently high humidity. This result might appear counterintuitive, but it reflects well the pulse of DOC that is expected when microorganisms subjected to drought release osmolites upon rewetting (Schimel *et al.* 2007). Such drought-induced pulses of easily available compounds might have a positive feedback on soil microbial activity, as indicated by the higher SIR that we measured in soils from the dry treatment. The increase in SIR in response to increased drought documented here, has typically been observed after a rewetting event following drought, both under laboratory conditions (Butenschoen *et al.* 2011) and in the field (Sherman *et al.* 2012). However, in our study, the increase in SIR was associated to a decrease in potential cellulose decomposition (PCD) by the soil microbial communities that were exposed to increased drought. Without detailed data on microbial community composition, it is difficult to interpret this drought-induced decrease in PCD.

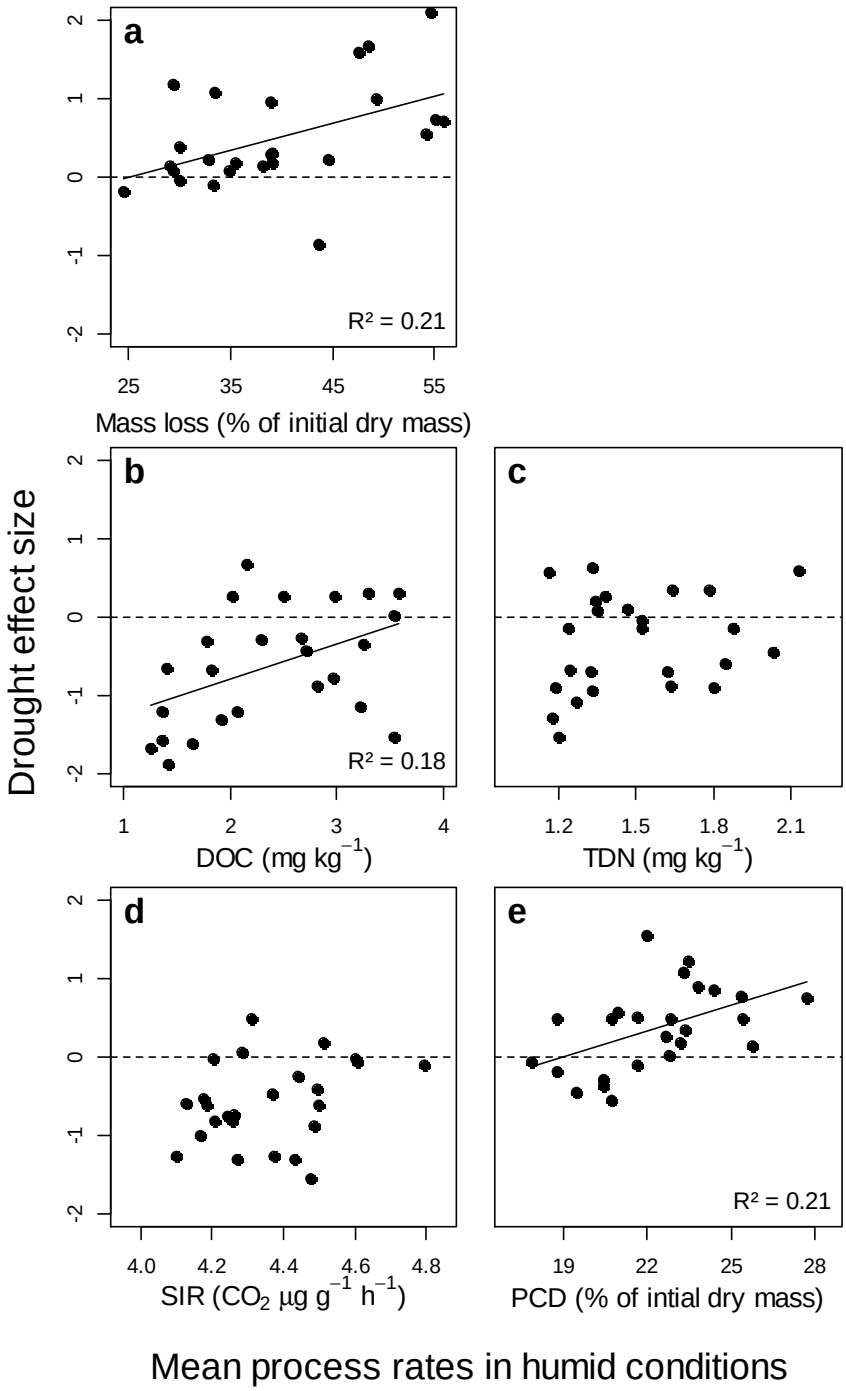

Figure 30. Drought effect size as a function of mean process rates in humid conditions. Each point represents the mean of a particular combination of litter mixture and detritivore community. Treatments without detritivores are not shown. When linear regressions are significant ($p < 0.05$), regression lines are drawn with their respective R^2 values.

Despite these significant impacts of the dry treatment on soil processes, our data did not confirm the initial hypothesis that drier conditions would change the relationships between functional dissimilarity and process rates. The stress gradient hypothesis states that as stress increases in an ecosystem, positive interactions between species, such as facilitation, tend to increase and negative interactions, such as competition, tend to decrease (Bertness & Callaway 1994). Such modifications of species interactions could in turn affect biodiversity effects on ecosystem functioning and we hypothesized that functional diversity would increase in importance under more limiting humidity conditions. This hypothesis has recently been tested in an aquatic detritivore community by (Fugère *et al.* 2012) who found a switch from negative to neutral interactions with increasing resource quality stress. Furthermore, (Collison *et al.* 2013) investigated detritivore diversity effects on litter decomposition at different moisture levels and net diversity effects tended to be higher in dry conditions, in line with the stress gradient hypothesis. In the present work, there were no changes in the relationships between functional dissimilarity of detritivore communities and process rates due to increasing drought.

However, we did observe that the drought effect increased with increasing process rates measured under optimal humidity conditions. This shows that litter and detritivore assemblages resulting in high process rates under undisturbed conditions were more sensitive to reduced water availability. This result agrees with the suggested higher sensitivity to drought of higher productive plant communities (Pfisterer & Schmid 2002). Similar to studies on plant productivity, our results for a different ecosystem process also suggest a trade-off between high performance and resistance to perturbation (Pfisterer & Schmid 2002; Wang *et al.* 2007; Van Ruijven & Berendse 2010). In the type of Mediterranean ecosystem we studied, which is predicted to suffer even more severe drought periods under future climate scenarios, poorer performing communities might actually ensure more stable process rates in the long term.

Collectively, our data indicate that a relatively subtle change in the frequency of precipitation leads to clear and predictable changes in soil processes even in the drought adapted Mediterranean ecosystem studied here. The decrease of litter mass loss associated to higher C loss by leaching suggests important changes in soil C-cycling in response to shifts in precipitation frequency. Litter feeding fauna could buffer these drought effects on soil C-cycling to some degree. However, beyond some threshold values that need to be determined in field studies, fauna populations could crash, leading to marked and longer term changes in soil processes.

CONCLUSIONS

In conclusion, by manipulating community composition and functional diversity at two trophic levels, but keeping species richness constant, we showed that litter decomposition, soil C and N

leaching as well as soil microbial activity were modified with changing leaf litter mixtures and detritivore communities. Part of the variation in process rates we observed could be explained by functional dissimilarity of litter mixtures and detritivore communities, suggesting that the trait diversity of these communities can predict soil process rates to some degree. However, most of the variation in process rates was unrelated to functional dissimilarity, indicating that species identity effects are overall more important in determining soil processes in the studied Mediterranean ecosystem.

The intensity of drought simulated in our experiment did not alter the relationship between functional dissimilarity and soil processes, suggesting some robustness of this relationship under changing environmental conditions. However, the best performing litter mixtures and detritivore communities under optimal humidity conditions were distinctively more affected by drought, suggesting a trade-off between performance and resistance to perturbations for soil organisms.

ACKNOWLEDGEMENTS

We thank all the Ecotron team for their technical support during the course of the experiment as well as Sandra Barantal, David Degueldre, Jeremy Devaux, François-Xavier Joly, Johanne Nahmani and Anaïs Rancon for their help during the setting up and the dismantling of the experiment. SIR and PCD and functional traits were measured at the Plateforme d'Analyses Chimiques en Ecologie, technical facilities of the LabEx Centre Méditerranéen de l'Environnement et de la Biodiversité, with the help of Raphaëlle Leclerc and Patrick Schevin. We are grateful to Joelle Toucet and the BioSolTrop lab (Eco&Sols, Montpellier) for TOC analyses. We would further like to thank Pascal Mirleau and the BioFlux team for helpful discussion. This research is part of the project "CLIMED" funded through the ANR grant 09-CEP-007.

Chapitre 4 : Effets relatifs de l'identité et de la dissimilarité fonctionnelle des détritivores sur la décomposition

Figure 31. Photo montrant des microcosmes provenant de l'expérience réalisée à l'écotron de montpellier les 5 mélanges de litière et le témoin sol nu sont représentés. A partir de la vignette en haut à gauche : le mélange *Cistus*/*Pinus*, *Quercus*/*Rosmarinus*, *Quercus*/*Pinus*, *Cistus*/*Ulex*, *Rosmarinus*/*Ulex* et le témoin sans litière.

Résumé du chapitre

Contexte :

Dans le chapitre précédent, j'ai montré que la dissimilarité fonctionnelle a un effet significatif sur les processus impliqués dans le fonctionnement du sol, mais que l'identité des espèces a un pouvoir explicatif plus important. Cependant ces deux composantes (identité et dissimilarité) ont été étudiées via des analyses séparées, ce qui a permis de comparer le pouvoir explicatif de chacune des composantes séparément mais ne renseigne pas sur l'effet relatif de chacune sur le fonctionnement du sol.

En utilisant les traits fonctionnels des espèces, il est possible de quantifier le rôle de l'identité des espèces. Selon l'hypothèse du « biomass-ratio » (Grime 1998), l'effet de chaque espèce dans la communauté est proportionnelle à sa biomasse. Les traits moyens des espèces pondérés par leur biomasse dans la communauté (en anglais le « community weighted mean » CWM) sont donc définis comme l'identité fonctionnelle d'une communauté. A partir de cette mesure de l'identité fonctionnelle ainsi que des indices de dissimilarité tels que le Rao, Díaz *et al.* (2007) ont proposé un cadre méthodologique et conceptuel permettant de tester dans une même analyse l'importance de l'identité et de la diversité fonctionnelle. Or ce type d'analyse a pour le moment très peu été utilisé. De plus, la plupart des études ont été menées sur des communautés de plantes pour expliquer leur effet sur la productivité primaire.

L'objectif de ce quatrième chapitre est donc d'étudier l'effet relatif de l'identité fonctionnelle et de la dissimilarité des détritivores sur la perte de masse des litières (H4a). De plus comme il a été montré dans le chapitre précédent qu'il y a une interaction entre l'identité des litières et l'identité des détritivore, on peut donc s'attendre à ce que la relation entre la dissimilarité fonctionnelle des détritivores et la perte de masse change selon l'espèce de litière (H4b).

Méthode :

Pour tester ces deux hypothèses, nous avons utilisé les données de perte de masse des espèces individuelles présentes dans les mélanges provenant de l'expérience menée à l'écotron[1] (cf. chapitre précédent pour les détails méthodologiques).

Pour tester l'effet relatif de l'identité et de la dissimilarité fonctionnelle des détritivore sur la perte de masse des litières (H4a), les traits moyens des communautés de détritivore ont été calculés pour 5 traits fonctionnels différents. Avec ces 5 mêmes traits, l'indice de dissimilarité fonctionnelle de Rao a également été calculé. Dans un premier temps l'effet de chaque variable sur la perte de masse a été étudié individuellement. Dans un second temps l'identité fonctionnelle et la dissimilarité fonctionnelle

[1] Ce chapitre est donc dédié à l'étude des pertes en masse espèce par espèce alors que le chapitre précédent se focalisait sur la perte de masse à l'échelle des mélanges

ont été intégrées dans un même modèle de régression linéaire multiple dans le but de hiérarchiser l'importance de chaque variable. Les analyses ont été réalisées pour chaque espèce de litières séparément. Nous avons donc pu étudier la relation entre la dissimilarité fonctionnelle des détritivore et la perte de masse pour 5 espèces de litières différentes, ce qui a permis de tester l'hypothèse (H4b).

Résultats et discussion :

L'identité fonctionnelle des détritivores a eu un effet très fort sur la perte de masse de toutes les espèces de litière étudiées, excepté sur les litières d'*Ulex* qui semblent évitées par les détritivores. Globalement l'effet relatif de l'identité fonctionnelle des détritivores est beaucoup plus important que celui de la dissimilarité fonctionnelle. Concernant les 4 espèces influencées par les détritivores, l'identité fonctionnelle a contribué en moyenne à 85 % de la variabilité expliquée par les modèles alors que la dissimilarité n'a contribuée qu'à 13%.

L'analyse détaillée trait par trait montre que se sont principalement les traits fonctionnels liés aux stratégies alimentaires (taux de consommation, rendement d'assimilation) des détritivores qui sont importants pour prédire l'effet sur le processus de décomposition. Globalement cette approche basée sur les traits moyens des espèces de détritivore s'est montrée efficace pour prédire l'effet des détritivore sur la perte de masse des litières. Cependant nos résultats sont le fruit d'expérience en laboratoire, il serait donc très intéressant de vérifier ces résultats *in situ*.

Cependant l'efficacité des traits à prédire l'effet des détritivores sur la perte de masse a varié selon les espèces de litières. Les relations entre la dissimilarité fonctionnelle des détritivores et la perte de masse étaient soit négative (*Quercus*), soit nulle (*Cistus*), soit positives (*Rosmarinus* et *Pinus*). Ce qui montre que la relation diversité-fonction est fortement dépendante de l'identité des litières. Nous n'avons pas réussi à mettre en évidence, ni au sein de notre jeu de donnée, ni en comparant avec des études similaires (Zimmer *et al.* 2005), des traits des litières qui semblent favoriser une relation positive entre la dissimilarité des détritivores et le processus de décomposition.

The relative importance of functional identity and diversity of detritivore communities for litter mass loss of Mediterranean shrub species

Article in preparation

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INTRODUCTION

Biodiversity is a major driver of ecosystem functioning (Balvanera *et al.* 2006). Initially, the efforts towards understanding the relationships between biodiversity (BD) and ecosystem functioning (EF) focused mostly on the importance of species richness for ecosystem processes such as primary productivity (e.g. Hector et al. 1999). Later studies showed that beyond the number of species the consideration of their functional characteristics further improves the understanding and prediction of BD-EF relationships (Petchey & Gaston 2006; Reiss *et al.* 2009). A functional characterization of communities is based on functional attributes of the species composing that community which are defined as any morphological, physiological or phenological features measurable at the individual level and which affect ecosystem properties (Violle *et al.* 2007). Two main aspects of functional characteristics have been identified in the context of BD-EF research, the functional identity and the functional dissimilarity (e.g. Mouillot et al., 2011). The functional identity refers to the biomass-ratio hypothesis (Grime 1998) by stating that the effect of a species on an ecosystem process is proportional to the relative abundance of that species in the community. Extended by the trait framework, the effect of each species would be proportional to the relative abundance of the trait value of that species. The community as a whole is then described by the sum of each species' relative trait value, resulting in the community-weighted mean (CWM) trait value (Garnier et al., 2004). Functional community identity has been demonstrated to be a good predictor of various ecosystem processes such as primary productivity, or litter decomposition in grassland ecosystems (Mokany *et al.* 2008). On the other hand, the functional diversity insists on the diversity of traits within a community rather than community-weighted mean trait values. The trait-based definition of diversity or dissimilarity indices explicitly allows accounting for the functional heterogeneity of organisms within the community (Petchey & Gaston 2006). Functional identity and functional diversity are not mutually exclusive for the understanding of how community characteristics affect ecosystem properties, however their relative effects on ecosystem processes are poorly tested (but see Díaz et al., 2007; Mouillot et al., 2011; Roscher et al., 2012; Schumacher and Roscher, 2009).

While the measurement of plant traits has a long tradition and is widely used in the ecological literature (e.g. Kattge et al., 2011), animal traits are more rarely determined and less generally used to describe functional aspects of communities (but see Dumay et al., 2004; Hedde et al., 2013, 2012; Mason et al., 2008; Mouillot et al., 2007). For example, a series of morphological traits of co-occurring fish species have been used to characterize the functional diversity of fish communities in order to explore community assembly rules (Mouillot *et al.* 2007). In terrestrial ecosystems, Hedde et al. (2013) described the responses of soil macrofauna communities to land use change using a trait-based approach. However, these trait-based approaches for the characterization of animal communities were mainly used to assess the responses of animal communities to environmental constraints and only

few studies attempted to quantify animal community effects on ecosystem processes using functional traits (Heemsbergen, *et al.* 2004; Hedde *et al.* 2010). These two studies compared decomposition process rates of different communities with variable numbers of detritivore species with those expected from the calculated CWM trait values based on individual species effects. Both studies reported significant deviations from CWM predictions suggesting species interactions beyond purely additive effects which would be predictable from CWM. Moreover, these deviations correlated better with functional dissimilarity of detritivore communities expressed with a series of traits determined for each detritivore species than with detritivore species richness (Heemsbergen, *et al.* 2004; Hedde *et al.* 2010). The greater importance of functional dissimilarity than of species richness suggests that communities with increasingly dissimilar traits use resources more complementary leading to higher decomposition rates.

The previous studies on detritivore diversity and their impact on process rates used a homogeneous resource of a single leaf litter species (Heemsbergen, *et al.* 2004; Hedde *et al.* 2010). However, in their natural environment, detritivores typically have diverse food sources at their disposal and their impact on resource use and consequently on rates of organic matter decomposition can vary substantially in response to resource identity (e.g. Rouifed *et al.* 2010; Vos *et al.* 2011) and resource diversity (Hättenschwiler & Gasser 2005). Knowing that trophic complexity and interacting horizontal and vertical diversity are likely modifying diversity effects on ecosystem processes (Duffy *et al.* 2007; Gessner *et al.* 2010), it is important to introduce such complexity in the design of experiments along with environmental variability in order to gain in realism for the assessment of how biodiversity and ecosystem functioning are related (Hillebrand & Matthiessen 2009; Reiss *et al.* 2009).

In the present study we aimed for such more realistic higher complexity by assessing the impact of varying detritivore dissimilarity and litter dissimilarity under two contrasting humidity conditions on litter mass loss. Our study system is a Mediterranean shrubland, also known as "garrigue", with a typically highly abundant detritivore community. In view of the anticipated climate change leading to decreasing precipitations in the Mediterranean area (Alley *et al.* 2007), we additionally included a humidity treatment in our experiment. Decreasing water availability is likely to change the diversity-functioning relationship, with a hypothesized increasing importance of biodiversity under more stressful conditions according to the stress gradient hypothesis (Bertness & Callaway 1994). With a fully factorial laboratory experiment we manipulated the functional dissimilarity of detritivores and their resources, while keeping species number constant at two species at both trophic levels. We aimed particularly at quantifying the relative importance of functional identity and functional dissimilarity of detritivore communities for litter decomposition. We hypothesized that (i) both functional identity and functional dissimilarity of detritivore communities have an effect on decomposition, but that functional identity overrides the impact of functional dissimilarity. Moreover, it was shown that BD-EF relationships are context dependent (Cardinale *et al.* 2000; Fridley 2003), hence we expected this

relation to vary. According to the results of Zimmer et al. (2005), we expected that (ii) the effect of detritivore dissimilarity will be modified by the identity and the diversity of litter and more specifically that the positive effect of detritivore functional dissimilarity will increase with improving litter quality. Finally we hypothesized that (iii) the effect of functional identity will remain unchanged under dryer conditions, but that the effect of detritivore dissimilarity will increase under dryer conditions because species interactions are likely to be intensified under more stressful conditions (Bertness & Callaway 1994).

MATERIALS AND METHODS

Plant and animal material

N. B. This paragraph is the same as that of chapter 3, because both chapters refer to the same experiment.

We collected leaf litter of five typical and widely distributed Mediterranean plant species: the four evergreen woody shrubs Quercus coccifera, Rosmarinus officinalis, Ulex parviflorus and Cistus albidus, and the conifer tree Pinus halepensis that is a pioneer species of Mediterranean forests. All five species typically co-occur in shrubland ecosystems of the Mediterranean basin. Shrub litter was collected at the Massif de l'Etoile near Marseille (5°25'E 43°22'N), and Pinus needle litter in the surroundings of Montpellier (3°52'E 43°40'N). All material was collected on the ground in March-April 2011, before the peak of litter fall in order to avoid confounding by freshly fallen leaf litter. Freshly fallen leaves were discarded because soil detritivores generally prefer litter that is already well colonized with microbial communities. Litter was air-dried upon harvest, sorted into species and cleaned of adhering soil particles, twigs, and parts of fruits and flowers.

We collected five common detritivore species that are often highly abundant in the same type of garrigue ecosystem: the diplopods Glomeris marginata and Ommatoiulus sabulosus, the isopods Armadillidium vulgare and Armadillo officinalis, and the prosobranch snail Pomatias elegans. Three weeks before the start of the experiment, in October-November, 250 individuals of each species were collected at the Massif de l'Etoile and in the surroundings of Montpellier. All were kept in large plastic containers at constant temperature (16°C) and day length (12 h), and fed with a mixture of the five litter species chosen for the experiment.

Measurements of detritivore functional traits

N. B. This paragraph is the same as that of chapter 3, because both chapters refer to the same experiment.

The selection of functional traits is a critical step in the calculation of diversity index (Petchey & Gaston 2006; Villéger et al. 2008). Traits must be selected according to their relevance to the ecological process and to avoid high redundancy between traits. Five litter traits were retained (Table 8) among ten that were initially measured: nitrogen (N) and lignin concentrations, as good predictors of litter decomposition rates (e.g. Zhang et al., 2008).; condensed tannin concentration , due to its importance for both microbial decomposers (Kraus et al. 2003) and detritivores (Coq et al. 2010).; water-soluble carbon concentration, which is a critical energy source for decomposers and has a strong influence on how decomposing litter affects soil processes (Fanin et al. in prep); and water holding capacity of litter, a potentially important trait for detritivores when water is limiting , and a good predictor of decomposition, especially in Mediterranean ecosystems (Makkonen et al. 2012). We used standard methods to determine the litter traits as described in Coq et al. (2010) and Coulis et al. (2013).

Five functional traits were also selected among six that had been measured on each detritivore species (Table 9). All were related to the ability of detritivores to transform leaf litter and influence its subsequent decomposition in their feces: consumption rate and assimilation efficiency, which are directly related to the expected impact of detritivores on litter mass loss and mineralization; outer surface area of fecal pellets and size of litter particles within fecal pellets, which mirror the surface available for microbial colonization in feces (Lavelle & Spain 2001; Hedde et al. 2007); and hygroscopicity of feces, due to the importance of water availability in this material for subsequent microbial activity. All traits were determined using a single leaf litter species, Cistus albidus , which was found to be the preferred food of the five detritivore species studied (unpublished results). Consumption rates (mg of dry litter consumed per g of live animal per day) and assimilation efficiencies were calculated according to (David & Gillon 2002). Width, length and height of 50 fecal pellets from each species were measured and used to estimate the mean surface area. The water content of feces was measured after enclosing 50 fecal pellets for five hours in a water saturated atmosphere. Finally the mean particle size in feces was calculated according to Hedde et al. (2007).

Most previous studies did not formally distinguish between species richness and functional diversity or varied both components of biodiversity at the same time. In a novel approach, we chose here to vary functional diversity across two trophic levels while keeping the number of species constant. For this purpose, we first calculated Rao's quadratic entropy as an index of functional dissimilarity (Botta-Dukát 2005) for all possible combinations of two species of plant litter and soil animals. At each trophic level, there were ten possible combinations of two species and we chose five that matched the following criteria: (i) to maximize the functional diversity gradient, i.e. the range of Rao index values, and (ii) to include each species exactly twice in the five combinations. The five litter mixtures retained were, in increasing order of functional dissimilarity, Quercus/Rosmarinus (0.33), Rosmarinus/Ulex (0.40), Cistus/Ulex (0.43), Cistus/Pinus (0.69) and Quercus/Pinus (0.81); and the

five detritivore communities retained were Armadillidium/Armadillo (0.03), Armadillidium/Ommatoiulus (0.21), Pomatias/Armadillo (0.37), Glomeris/Ommatoiulus (0.58) and Pomatias/Glomeris (0.70). At the end of the experiment, Rao's index was recalculated for each microcosm and weighted by the relative abundance of species expressed in terms of biomass (Barantal et al. 2011). Litter biomass values were similar in all microcosms but invertebrate biomass values varied slightly at the start of the experiment, and even more at the end of the experiment due to mortality in some microcosms (the overall death rate was 5 %). The average of the initial and final biomass was worked out for each detritivore species in all microcosms, taking into account the approximate date of death when needed, and these biomass values were used to weight the dissimilarity indices.

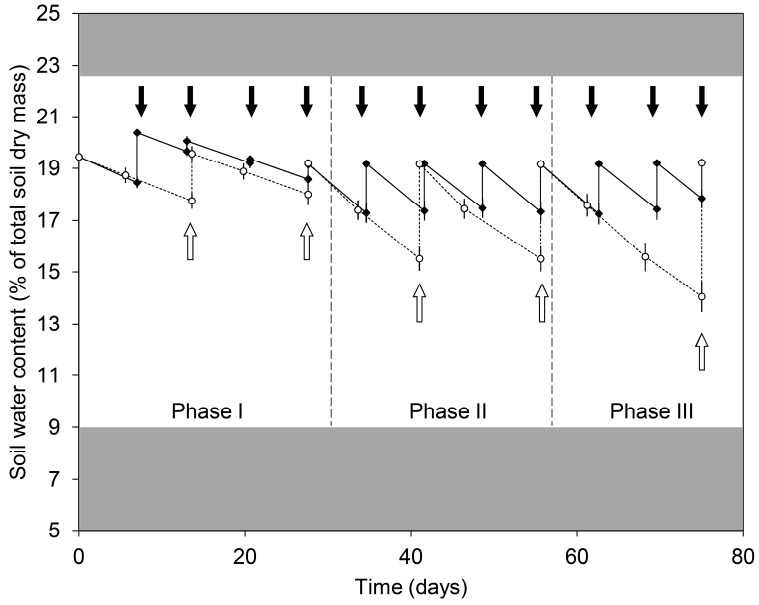

Figure 32. Dynamic of soil water content in microcosms from dry treatments (open circles) and humid treatments (filled circles). Arrows indicates rewetting events. Zones corresponding to water content above field capacity and below wilting point are darkened. Water content was estimated by gravimetric method hence it is expressed in % of water per soil dry mass (mean ± SE, n=150).

Experimental design

N. B. This paragraph is the same as that of chapter 3, because both chapters refer to the same experiment.

Microcosms were constructed in lidded boxes of transparent polystyrene (175 x 115 x 65 mm, LAB4 © CAUBERE). The bottom of each box was lined with 1 cm thick inert plastic composite (polyamide and polyethylene terephthalate, Enkadrain®) to improve drainage of the system. This drainage layer was covered by 700 g of air-dried soil sieved through a 2 mm screen, resulting in a 3-cm deep soil layer within each box. The soil used for the experiment was collected from the top layer (top 10 cm) of an experimental agricultural field at Grignon, France (1°56'E, 48°50N). We chose this

particular soil because the field had been cultivated with C_4 plants for 40 years and we intended to take advantage of the difference in isotopic labeling between soil organic matter and the C_3 litter species used, to distinguish between soil and litter respiration (data not shown here). The soil was a Luvisol developed on loess over limestone, with a total C content of 13.9 g kg^{-1} and a total N content of 1.27 g kg^{-1}. Eight grams of leaf litter (4 g of each of the two species) were laid on the soil layer. At the start of the experiment each microcosm was watered with deionized water to reach 80% of field capacity in the soil and to approach water holding capacity of litter (see below for actual litter water content). After watering, two individuals of each of the two animal species, previously starved for 24 h and weighed, were added in each microcosm.

In addition to the two fully crossed parameters of litter functional dissimilarity (five litter mixtures) and detritivore dissimilarity (five detritivore assemblages plus a treatment without fauna), we included two different watering regimes. Each treatment combination was replicated five times resulting in a total number of 300 microcosms (5 litter treatments x 6 animal treatments x 2 watering regimes x 5 replicates). An additional five replicates per watering regime without any litter and fauna were included, yielding a grand total of 310 microcosms. Each of the five replicates per treatment combination was kept in one of five incubators with microcosms distributed randomly within incubators and positions changed every 3 days according to a randomized complete block design.

Microcosms were incubated at the European Ecotron facility for 11 weeks, at constant temperature (20°C), relative air humidity (50%), and day length (12h) in the incubators. Two watering frequencies were used in the microcosms. Microcosms of the humid treatment were remoistened weekly, whereas those of the dry treatment were remoistened every two weeks or after a three-week interval during the last drying-rewetting cycle (see Figure 32). Microcosm lids were initially pierced with five 1.3 mm diameter holes to allow CO_2 and water vapor exchanges (Phase I, Figure 32). As the desiccation rate was rather low, an additional 14 holes were pierced (a total of 19) during phases II and III (Figure 32). The amount of water added when watering compensated for evaporation losses and reset litter and soil moisture to initial conditions. Consequently, the same total amount of water was added to microcosms of the humid and dry treatments (96.6 ±1.8 and 95.5 ± 2.2 ml, respectivley) over the course of the experiment. However, soil water content was on average 81 ± 0.1% of field capacity in the humid treatment, vs. 77 ± 0.1% in the dry treatment ($p < 0.001$). Additionally, soil moisture content in the dry treatment decreased to 67% and even 58% of the field capacity during the last drying-rewetting cycle, while it never dropped below 75 % in the humid treatment (Figure 32). Litter water content just after watering was on average 120% for Cistus, 72% for Quercus, 71% for Rosmarinus, 67% for Pinus, and 54% for Ulex. These values decreased rapidly within two days and, after six days, water content was 26% for Cistus, 24% for Quercus, 25% for Rosmarinus, 24% for Pinus and 19% for Ulex. Litter water content remained at similar levels during the second week of dry treatment (see Fig. A. in Annexe 2 for more details).

Response variables

Soil water content (SWC) was monitored by weighing each microcosm once a week before treatment-specific watering in order to reach the initial total microcosm weight (see Figure 32). These weekly values of SWC were used to calculate the mean, the standard deviation and the range of SWC for each individual microcosm during the entire course of the experiment.

At the end of the experiment, the remaining litter material was collected and rinsed in 200 ml distilled water for five minutes to remove soil particles. Litter were sorted by species and immediately freeze-dried before weighting for mass loss determination. The net effect of detritivore communities on litter mass loss (g) was calculated as the difference between the total mass loss of litter observed in their presence and that in their absence (the treatment where we added only litter) for the respective litter and humidity treatment. The net effect reflects both litter consumption by animals and potential indirect detritivore effects on microbial decomposition of uningested litter.

Detritivore biomass during the entire experiment was determined for each species by averaging their initial and final biomass. During the eleven weeks of the experiment, we recorded 55 dead animals. We replaced 32 of them during the first eight weeks, and stopped doing so afterwards. Given the overall on thousand individuals used for the whole experiment, this yields a survival rate of 95%. In case of dead animals, the integrated biomass value was obtained by averaging the biomass of the death individual and that of the new one weighted by their respective time spent within the microcosm. For example if animal α die at the 2nd week and was replaced by the animal β, the mean biomass (B) was:

$$B = \frac{\left[(B_\alpha \times 2/11) + \left(B_\beta \times 9/11\right)\right]}{2}$$

Finally, in the few cases for which the date of death was unknown and the dead individual has not been replaced, the individual was considered alive up to mid-term of the experiment and the total detritivore biomass was calculated accordingly.

Functional characterization of detritivore communities

The functional identity of each detritivore community was determined using the community weighted mean (CWM) for each functional trait. CWM value was calculated by weighting the species average trait value by the mean species biomass during the experiment as follows:

$$CWM = \sum_{i=1}^{n} B_i \times trait_i$$

In order to calculate integrated indices of functional identity using all five traits we determined for each detritivore species, we performed a principal component analysis. Together, the two first axis of the PCA explained 79% of variability (see Annexe 3). The coordinates of the barycentre of each species on the two PCA axis (PCA-1 and PCA-2) were extracted, and used to calculate species-specific biomass weighted community indices of functional identity (similar to the CWM of single traits).

The functional dissimilarity of detritivore communities was expressed with the Rao's quadratic entropy (Botta-Dukát 2005). This index represents the average dissimilarity between pairs of species (Epps *et al.*, 2007). It was computed using the standardized Euclidean distance weighted by the relative abundance of component species expressed in terms of biomass (Barantal *et al.* 2011).

Statistical analysis

We first analyzed litter mass loss in control microcosms (i.e. without detritivore) before detailed analyses of detritivore effects. Differences in litter mass loss of individual litter species within the five distinct litter mixtures without detritivores were analyzed using ANOVA with species identity (fixed factor) and humidity (fixed factor) as crossed factors and litter mixture identity as a nested factor within species identity (fixed factor). No blocking factor was included in this analysis.

The differences of absolute values of litter mass loss with and without detritivores were defined as net detritivore effects for each litter species from each mixture individually. The net detritivore effect was tested for each litter species separately using a model for fully randomized block design. The five incubators we used (each incubator contained one replicate of each treatment combination) were considered as blocks (random factor) and the effect of identity of detritivore community, identity of litter mixture and humidity treatments (fixed factors) were tested against the mean squares of their respective interactions with block (Quinn & Keough 2002).

Finally relative net detritivore effects on each of the two litter species in a given litter mixture (i.e. the proportion of net detrivore effect on each litter species relative to the total net detritivore effect on the mixture) were analyzed separately for each litter mixture using a model for a fully randomized block design. Incubators were considered as blocks (random factor) and the effect of identity of detritivore community and humidity treatments (fixed factors) were tested against the mean squares of their respective interactions with block (Quinn & Keough 2002).

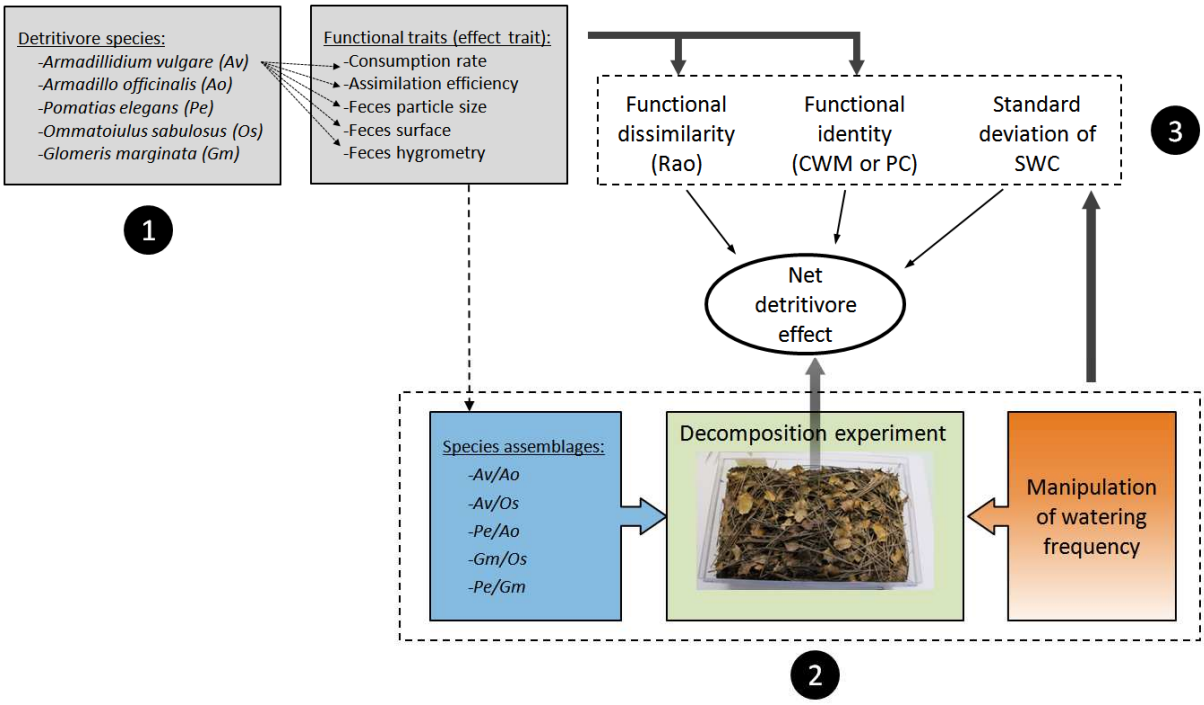

Figure 33. A schematic representation of the experimental design. Five functional traits were measured for each of the five detritivore species and used to determine species assemblages (1). Five different leaf litter mixtures were created based on the same trait-approach as for the detritivores. All possible combinations of detritivore communities and litter mixtures were exposed to two different watering frequencies for 80 days (2). Net detritivore effects on litter decomposition as response variable was analyzed for the relative effects of functional dissimilarity, functional identity and standard deviation of SWC using multiple regression analyses (3). CWM = community-weighted mean of single traits, PC = principal component axis, SWC = soil water content.

For testing net detritivore effects, we used the methodological framework proposed by Díaz et al. (2007) ; i.e. we proceed gradually by fitting in a first step the potential parameters affecting net detritivore effects separately and in a second step by integrating them in a multiple regression analysis (Figure 33).

The first step consisted in testing for the effect of each main factor separately, using Ordinary least square regressions. The effect of the abiotic factor (watering frequency) was assessed by testing for the relationship between net detritivore effect and three different metrics of SWC: the mean, the standard deviation and the range of SWC. The effect of functional identity of detritivore community was assessed by testing for the relationship between net detritivore effect and CWM of each functional trait as well as the two axes from PCA (PCA-1 and PCA-2). The effect of functional dissimilarity was taken into account by testing for the relationship between net detritivore effect and the Rao index.

In a second step, we used multiple regressions for prioritize the main factors explaining net detritivore effect. These models were run/implemented with the variables of each group of main factors that correlated best with net detritivore effects, i.e. standard deviation of SWC for the factor of soil humidity, PCA axis for functional identity and the Rao index for functional dissimilarity. A backward selection procedure was used to select the more parsimonious model by removing the

variables that did not add supplementary information. Moreover, in order to quantify the relative importance of each variable in the model, we calculated an estimator of relative importance of each variable. Proportional marginal variance decomposition (PMVD) was chosen according to Grömping (2007). PMVD is expressed in % of the variance explained by the model (R^2).

For all statistical analyses, normality and homogeneity of variance in residuals were checked, and data transformed (log or arcsin) if assumptions were violated. For multiple linear regressions, co-linearity among variables was checked using the Variation Inflation Factor (VIF) and approved (VIF < 2). All analyses were performed using R software version 3.0.1 (R Development Core Team, 2010) with the package "relaimpo 2.2".

RESULTS

Effect of litter species identity on litter mass loss without fauna

Mass loss of litter without the presence of fauna differed among the five litter species. *Rosmarinus* leaf litter decomposed much faster than all other species. *Cistus* and *Quercus* decomposed at similar rates with an intermediate mass loss, and *Ulex* and *Pinus* also decomposed at similar but lowest rates compared to the other species (Figure 34). In addition to the strong litter species identity effect, mass loss was also affected by the humidity treatment (Table 11). Reduced watering frequency resulted in an average 11 % lower litter mass loss (data not shown). Litter mixture identity had no effect on litter mass loss of either species (*i.e.* individual litter species decomposed similarly in both litter mixtures in which they were present) (Table 11).

Net effect of detritivore communities on litter mass loss

Across all litter species, mass loss due to the net detritivore effect (0.73 ± 0.03 g on average) was similar to that due to microbial driven decomposition (0.69 ± 0.03 g on average), indicating that detritivore activity approximately doubled overall mass loss compared to purely microbial-driven decomposition. However, the net detritivore effect differed strongly among the five litter species (Figure 34), and the ranking of net detritivore effects across litter species differed from that of microbial decomposition (Figure 34). We observed the highest net detritivore effect for *Cistus* litter that was three times higher than that for *Rosmarinus* litter. The net detritivore effect on *Ulex* litter was low, but significantly different from zero (p<0.001). With the exception of *Ulex* litter, detritivore community identity generally explained most of the variance in the net detritivore effect on litter mass loss (Table 12). For example, the net detritivore effect on *Cistus* litter varied from 1.15 ± 0.03 g with *Pomatias*/*Armadillo* to 2.58 ± 0.05 g with *Glomeris*/*Ommatoiulus* (data not shown).

Table 11. Results of ANOVA to test for the effect of species identity, litter mixture and humidity on microbial decomposition.

source of variance	Df	*F* value	*p* value
Species identity (Sp)	4	88.5	<0.001***
→Litter mixture (Mix)	5	1.2	0.323
Humidity (Hum)	1	9.2	0.003**
Sp x Hum	4	1.9	0.121
Mix x Hum	5	0.9	0.456
Residuals	80		

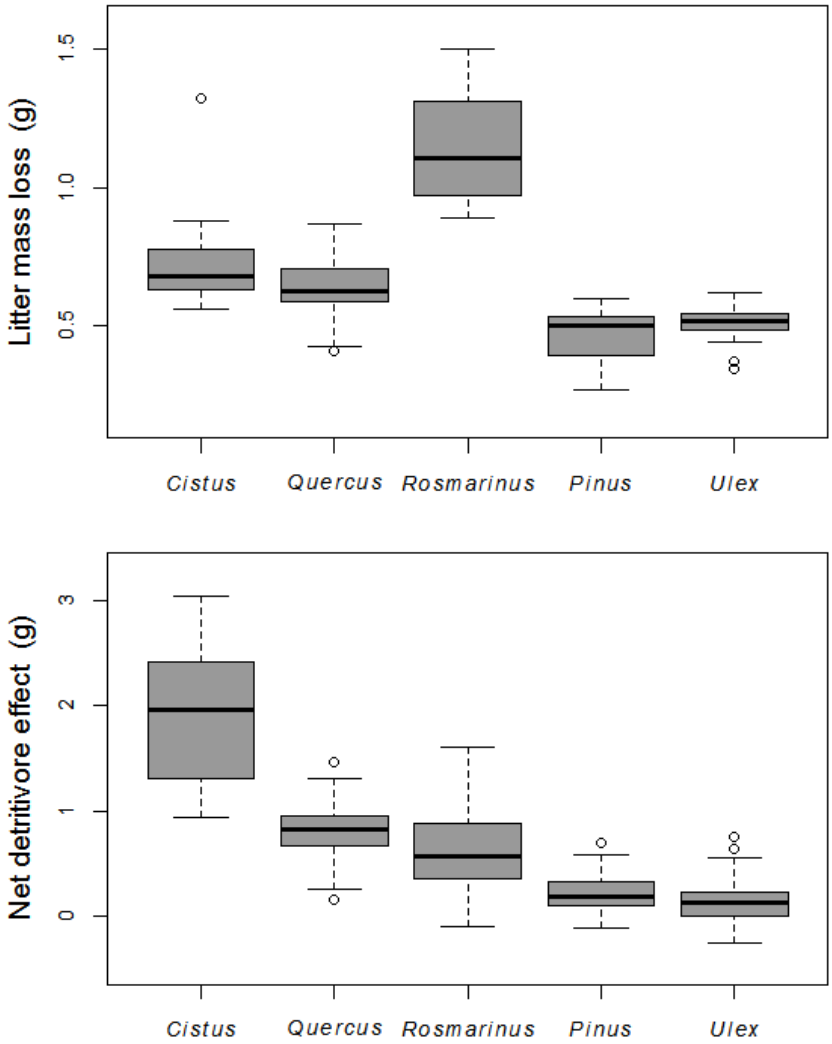

Figure 34. Litter mass loss due to microbial activity only (top), and net detritivore effect on mass loss (bottom) for leaf litter of the five different plant species used in the experiment.

The two litter species within a litter mixture were distinctively affected by different detritivore communities (Figure 35). For instance, within the mixture of *Quercus*/*Rosmarinus* 75% of the net detritivore effect was due to *Quercus* when the detritivore community was composed of *Armadillidium*/*Armadillo*, while *Quercus* accounted for only 44% of the net detritivore effect when the detritivore community was composed of *Glomeris*/*Ommatoiulus*. However, despite an important variability, the relative effect of detritivores on *Ulex* mass loss did not significantly vary across the five detritivore communities for the two litter mixtures that included this species.

While the identity of litter mixture did not influence individual litter species litter mass loss within the mixtures in the absence of fauna, the net detritivore effects on *Cistus*, *Rosmarinus* and *Ulex* litter mass loss differed significantly between the two different litter mixtures containing these species (Table 12). Overall, different watering frequencies had only little impact on the net detritivore effects. Only *Ulex* mass loss was negatively affected by reduced watering.

The relative importance of functional identity and functional dissimilarity for net detritivore effects

In accordance to ANOVA results, regressions analyses also showed small effects of differing watering frequency on net detritivore effects (data not shown). The only litter species that showed reduced net detritivore effect with less watering was *Ulex*. Standard deviation of SWC correlated negatively with the net detritivore effect on *Ulex* litter mass loss ($r = -0.33$, $p>0.001$).

In contrast, total detritivore biomass was an important driver of the net detritivore effect on litter mass loss with a significantly negative effect on mass loss of *Cistus*, *Quercus*, *Rosmarinus* and *Pinus* with increasing detritivore biomass (Table 13, Figure 36). Community-weighted mean trait values (CWM) of detritivores were generally well correlated with net detritivore effects on *Cistus*, *Quercus*, *Rosmarinus* and *Pinus* litter mass loss. However, the traits that correlated best with litter mass loss varied depending on litter species. For *Cistus* and *Rosmarinus*, the CWM of assimilation efficiency explained the net detritivore effect best, whereas for *Quercus* and *Pinus* the CWM of consumption rate correlated best. The overall functional identity of the detritivore community expressed by the coordinates on PCA axes (PCA-1 and PCA-2) explained at least as much variation as the best CWM of single traits (Table 13). For *Cistus* and *Quercus*, PCA-1coordinates showed the best correlation with the net detritivore effect, reflecting the strong contribution of assimilation efficiency and feces surface to this axis. The net detritivore effect on *Pinus* litter was relatively well correlated to PCA-2, but the correlation coefficient was lower than the best CWM single trait value (consumption rate). Functional dissimilarity was significantly correlated with the net detritivore effect only for *Cistus* and *Rosmarinus* litter, but not for the other three species (Table 13).

Table 12. Results of ANOVAs to test for the effects of identity of detritivore community, identity of litter mixture and humidity on the net detritivore effect on litter mass loss.

Source of variance	*Cistus*		*Quercus*		*Rosmarinus*		*Pinus*		*Ulex*	
	Df	*F*	Df	*F*	Df	*F*	Df	*F*	Df	*F*
Identity of detritivore community (Det)	4	62.4 ***	4	11.4 ***	4	40.4 ***	4	14.7 ***	4	0.7
Identity of litter mixture (Mix)	1	29.7 **	1	1.3	1	12.9 *	1	3.3	1	24.7 **
Watering frequency (Wat)	1	0.0	1	0.1	1	0.0	1	5.0	1	13.4 *
Det x Mix	4	3.1 *	4	2.3	4	0.7	4	0.3	4	2.5
Det x Wat	4	1.5	4	2.5	4	0.2	4	2.2	4	0.6
Mix x Wat	1	0.0	1	3.3	1	7.8 *	1	4.5	1	0.2
Det x Mix x Wat	4	0.8	4	2.3	4	2.2	4	0.2	4	1.5

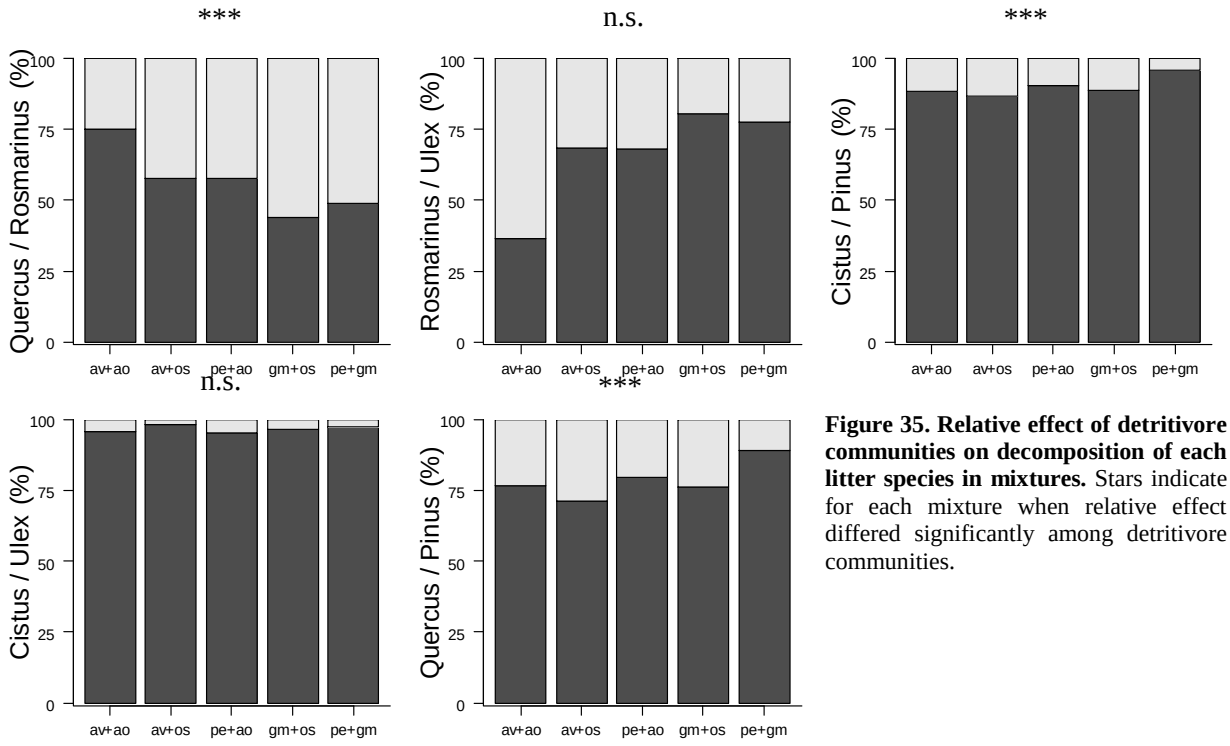

Figure 35. Relative effect of detritivore communities on decomposition of each litter species in mixtures. Stars indicate for each mixture when relative effect differed significantly among detritivore communities.

Multiple regressions including watering frequency, functional identity, and functional dissimilarity of detritivore communities accounted for a large part of variation in the net detritivore effect on *Cistus* (76%) and *Rosmarinus* (51%) mass loss. Variation in *Quercus* and *Pinus* mass loss was less well explained by the same model and that of *Ulex* was only poorly explained (Table 14). Functional identity was characterized using PCA-1 for *Cistus*, *Quercus Rosmarinus* and *Ulex* whereas PCA-2 was used for *Pinus*. Generally, functional identity of the detritivore community accounted for most of the variation in the net detritivore effect on litter mass loss in all species, except in *Ulex* that was more affected by watering frequency. However, functional dissimilarity significantly improved model predictions for the net detritivore effect on *Rosmarinus*, *Quercus* and *Pinus* litter mass loss accounting between 12 % and 23 % of the variation explained by models (Table 4). *Cistus* was the only species for which functional dissimilarity did not explain any further variation. .

DISCUSSION

The relative impact of functional identity and functional dissimilarity of detritivore communities on litter mass loss

Community-weighted mean (CWM) trait values of plant communities have been shown to predict ecosystem processes such as productivity (Garnier *et al.* 2004; Vile *et al.* 2006) and decomposition (Kazakou *et al.* 2006) quite well. This is in agreement with the biomass-ratio hypothesis, stating that the contribution of each species to an ecosystem process equals the species' relative abundance in the community (Grime 1998). The relative contributions of CWM traits and community trait diversity for the prediction of ecosystem processes, however, have rarely been assessed conjunctively. The few studies that did so, were all looking at primary productivity in grassland ecosystems (Mokany *et al.* 2008; Schumacher & Roscher 2009; Roscher *et al.* 2012). In all of these studies, community trait diversity significantly affected primary productivity; however CWM traits always had a greater relative importance for the prediction of primary productivity. The CWM approach is not often used in the assessment of how animal communities affect ecosystem processes. Moreover, the relative contribution of community functional identity, i.e. trait-based CWM, and community functional diversity, i.e. trait-based functional dissimilarity, in the prediction of ecosystem processes driven by animals remains essentially untested. Here we addressed this question for Mediterranean detritivore communities and the process of litter decomposition. Based on the available literature from plant studies, we hypothesized that both aspects of functional community composition are important, but that functional identity has a greater predictive power for ecosystem process rates than functional dissimilarity.

Table 13. Relationships between functional characteristics of detritivore communities and net detritivore effects for each of the five litter species. Relationships were tested using OLS regression, Pearson coefficients are given and stars indicate significant relationships (p<0.05).

Functional characteristic of detritivore community	*Cistus*	*Quercus*	*Rosmarinus*	*Pinus*	*Ulex*
Biomass	-0.58*	-0.34*	-0.41*	-0.44*	-0.10
Detritivore community weighted mean (CWM):					
Consumption rate	0.54*	0.46*	0.48*	0.54*	0.11
Assimilation efficiency	-0.83*	-0.45*	-0.76*	-0.22*	-0.08
Feces surface	0.78*	0.41*	0.64*	0.02	0.04
Feces hygroscopy	-0.38*	-0.05	-0.31*	0.39*	0.05
Feces mean weighted particle size	0.08	0.30*	-0.03	0.44*	0.07
PCA-1	0.88*	0.54*	0.70*	0.15	0.08
PCA-2	-0.18	0.09	-0.14	0.47*	0.06
Detritivore functionnal dissimilarity:					
Rao	0.47*	0.08	0.54*	-0.16	-0.01

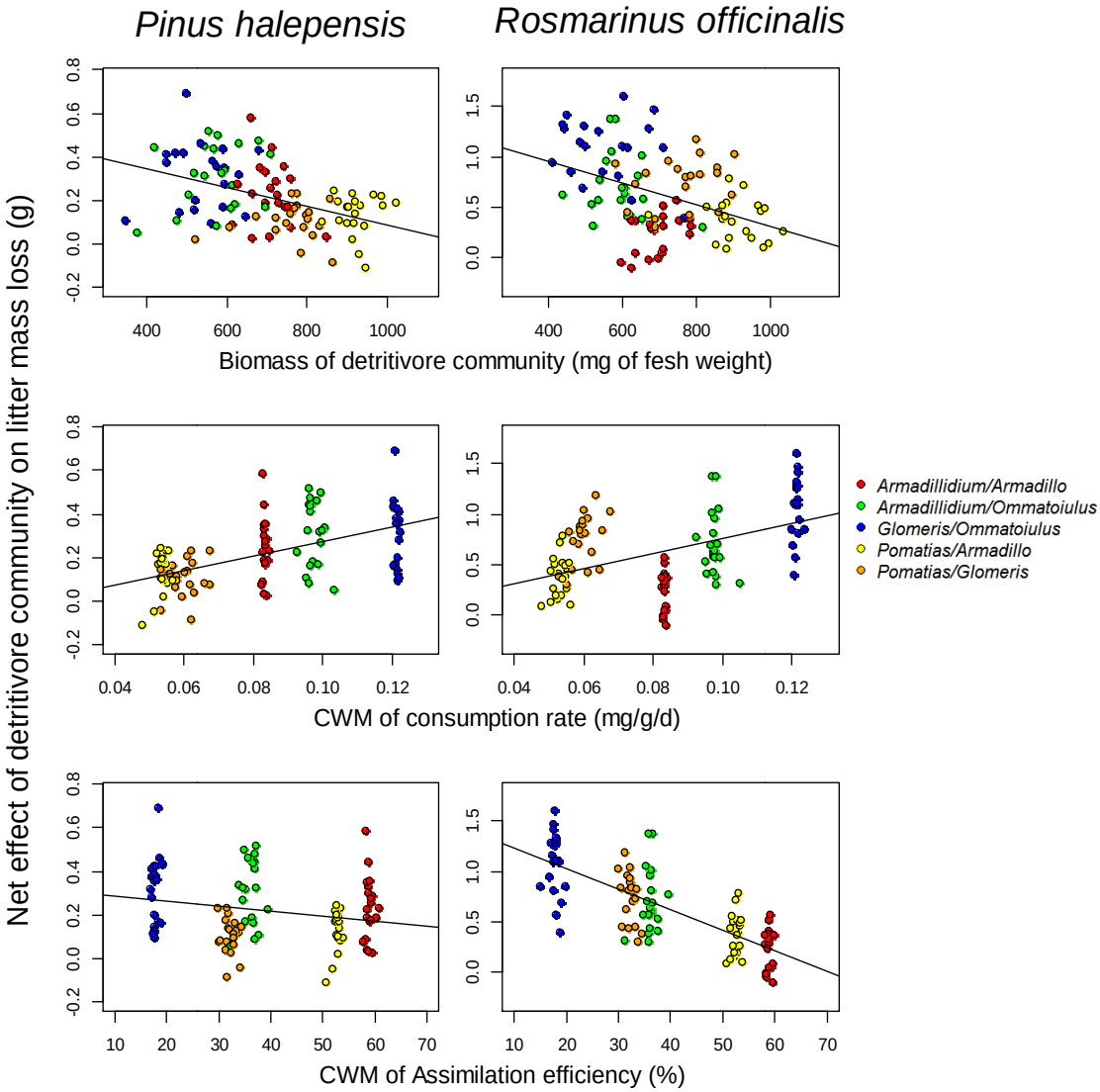

Figure 36. Examples of regressions between detritivore functional traits and net detritivore effect on decomposition of *Pinus halepensis* and *Rosmarinus officinalis* litter (see Table 3 for regression coefficients).

Table 14. Results of multiple regression analysis between net detritivore effect (response variable) and standard deviation of soil water content (Watering frequency), functional identity and functional dissimilarity of detritivore communities (explanatory variables). The « t-values » are indicated for each explanatory variables and adjusted R^2 as well as *p*-values are indicated for each model. Explanatory variables written in bold are significant. pmvd is a measure of the relative importance of each explanatory variable and is expressed in percent of variability explained by each model (R^2).

	Cistus		*Quercus*		*Rosmarinus*		*Pinus*		*Ulex*	
	t-value	*pmvd (%)*	*t-value*	*pmvd (%)*	*t-value*	*pmvd (%)*	*t-value*	*pmvd (%)*	*t-value*	*pmvd (%)*
Explanatory variables:										
Watering frequency	-0.53	(0)	-0.35	(0)	-0.85	(1)	1.36	(4)	**-3.77**	(92)
Functional identity	**15.18**	(100)	**7.40**	(82)	**6.82**	(87)	**6.50**	(73)	0.99	(4)
Functional dissimilarity	-0.82	(0)	**-3.49**	(18)	**2.41**	(12)	**3.68**	(23)	-0.94	(4)
models statistics:										
R^2	0.76		0.35		0.51		0.31		0.11	
p-value	<0.001		<0.001		<0.001		<0.001		0.006	

In line with this hypothesis, our data showed that functional identity of detritivore communities had a clearly higher impact on litter mass loss than their functional dissimilarity, irrespective of leaf litter species. Across the five different litter species, multiple regression analyses showed that functional identity accounted for 34 % of the variation while that of functional dissimilarity accounted for 4 %. Functional identity can be expressed in different ways. In the multiple regression approach, we included functional identity as PCA coordinates in the model. In order to explore the different components contributing to the functional identity of detritivore communities in more detail, we fitted a series of single regressions for each functional trait and the combination of these traits determined as the coordinates of PCA (Table 3). Surprisingly and counter intuitively, detritivore community biomass was negatively correlated to the net detritivore effect on litter mass loss. This result is in contrast with most previous results, that generally reported positive relationships between either density or biomass of detritivores and litter consumption (Bolton & Phillipson 1976; Dangerfield & Milner 1993; Fazi & Rossi 2000; David & Gillon 2002). However, these contrasting results are not necessarily contradictory. Previous studies quantified litter consumption as a function of animal biomass at the level of individuals or of populations. Community level data are rare and results are mixed, Irmler (2000), reported that litter mass loss in a temperate forest tended to decrease with increasing earthworm biomass whereas litter mass loss increased with increasing macroarthropod biomass. Here, we were interested in how the whole community biomass was affecting litter mass loss, and community biomass was obviously determined by the identity of detritivore species For example, communities containing the snail *Pomatias elegans* showed smaller effects on litter mass loss (Figure

36). Despite having a comparatively high biomass, *Pomatias* has a low consumption rate but high assimilation rate which contributes to the apparent negative relationship between community biomass and litter mass loss. However, this relationship was not exclusively driven by the presence of *Pomatias* since the isopod *Armadillo officinalis* also had a comparatively high biomass but low consumption rate. Even if this result is a consequence of the artificially composed communities in our experiment which are not necessarily found under natural conditions, it still makes the important point that increasing community biomass may not automatically increase rates of litter mass loss or other process rates. The CWM of consumption rate correlated well and positively with the net detritivore effect on litter mass loss, and the assimilation efficiency on the other hand was negatively correlated with mass loss. These relationships indicate that lower assimilation efficiency leads to higher consumption rates and therefore as a logical consequence to higher rates of litter mass loss, which reflects a physiological necessity of the respective detritivore communities. The significant correlations between CWM of feces characteristics and net detritivore effects on litter mass loss are less straightforward to interpret. As it is frequently discussed in the literature, litter transformation into feces and their physical and chemical characteristics can indirectly influence decomposition. However the hypothesis that feces could stimulate litter decomposition was not confirmed in a recent experiment with *Ommatoiulus* sabulosus feeding on litter from the same shrub species that we used here (Coulis *et al.* 2013). It is thus unlikely that feces stimulated litter decomposition in the present experiment; however feces characteristics could reflect detritivore digestive capabilities. Köhler et al. (1991) related the tooth density on mandibles to assimilation efficiency of diplopods and found that animals having higher density of teeth could fragment litter in smaller particles and thus assimilate litter more efficiently. In our experiment, the feces particle size as well as feces surface tend to decrease with increasing detritivore assimilation efficiency (see PCA in Annexe 3 for traits inter-relations). As those feces traits are often more easily measurable in the field than assimilation efficiency, feces characteristics could be used as a good proxy of detritivore feeding and its consequences on litter mass loss.

Despite the fact that functional identity accounted for more variation observed in litter mass loss, functional dissimilarity of detritivore communities improved predictions for detritivore effects in the majority of litter species tested. Taking into account detritivore functional diversity can thus improve the prediction of detritivore effects on decomposition. Similar to what Heemsbergen, *et al.* (2004) and Hedde *et al.* (2010) proposed, the complementarity in resource use between dissimilar detritivore species is likely to be involved in this relationship. Moreover our results are in line with the recent findings from grassland biodiversity-productivity experiments (Mokany *et al.* 2008; Schumacher & Roscher 2009; Roscher *et al.* 2012) showing that trait values of the dominant species and functional trait diversity at the community level predict effect on ecosystem processes best.

Conclusively, our results suggest that the characterization of macroarthropod detritivore communities based on functional traits is well suited for predicting detritivore effects on litter mass loss. The functional trait approach allows the use of unified and relatively easily measureable metrics for a functional description of communities composed of contrasted taxonomic groups such as gastropods, terrestrial crustacean and diplopoda. A combination of functional identity and functional dissimilarity based on the same set of traits appears to predict community effects on ecosystem processes particularly well. It would be interesting to apply the same approach for different detritivore communities, particularly naturally established communities, and from other ecosystem types to test the generality of the demonstrated relationship between functional community composition and ecosystem processes.

Litter species dependent effects of detritivore communities

In our second hypothesis we stated that the effect of functional identity and dissimilarity of detritivore communities depend on resource identity/quality. In the very few previous studies assessing the importance of detritivore functional dissimilarity for decomposition processes single litter species have been used (Heemsbergen, *et al.* 2004; Hedde *et al.* 2010). However, a relatively important diversity of different litter species occurs in most ecosystems, and litter feeding fauna is known to prefer certain litter species over others (Cárcamo *et al.* 2000; Hättenschwiler & Bretscher 2001). In addition it has been demonstrated that fauna effects on mass loss of a specific litter species depends on the presence of other litter species (Hättenschwiler & Gasser 2005). For a thorough test of how functional identity and functional dissimilarity of detritivore communities affect litter mass loss, it is important to include a range of different litter species and allowing a choice for litter feeding animals. We did this in the present study by including five different litter species in five different two-species litter mixtures.

While the general pattern of detritivore community effects on litter mass loss was quite robust across the different litter types as discussed above, there were also some important differences among the five litter species included in our test. The most conspicuous litter species was *Ulex* that apparently was very little consumed and that consequently showed no significant effect of any CWM trait or functional dissimilarity of the detritivore community. This result may appear surprising as *Ulex* showed the highest N concentration of all litter species, which is usually considered as a key trait for detritivore consumption (Curry & Schmidt 2007). On the other hand, *Ulex* is an aphyllous species and the litter produced from its photosynthetic stems is hard and dense and is not very palatable for detritivore consumers. The CWM of detritivore traits affected mass loss of the remaining four litter species differently. These differences however remain moderate since only the relative importance, but not the general trends changed between litter species. Also, the direction of the relationships remains unchanged, indicating that functional identity of detritivore influenced litter decomposition rather

uniformly across litter species. However, the effect of functional dissimilarity on litter mass loss was significant for only three species of the four. Moreover, functional dissimilarity had positive effect on *Rosmarinus* and *Pinus* litter mass loss, whereas it had a negative effect on *Quercus* litter mass loss. The relationship between detritivore dissimilarity and litter mass loss thus depends on the identity of litter species on which detritivore feed. In a microcosm experiment over 8 weeks, Zimmer et al. (2005) reported similarly that the interaction between an earthworm and an isopod species is modified depending on litter identity. Detritivore interactions were positive, negative or simply additive depending on litter substrate. Such changes in detritivore interactions depending on litter quality could also be at the origin of the modification of the relationship between detritivore dissimilarity and decomposition that we observed in our study. Zimmer et al. (2005) suggested that interactions are more likely to be positive on high-quality litter and negative on low-quality litter. Our results do however not support this hypothesis since the effect of detritivore dissimilarity was high on *Pinus* litter (a low-quality litter) and null on *Cistus* litter (a high-quality litter).

In conclusion, litter type and detritivore community composition interact on litter decomposition in a complex way. As it was emphasized by De Oliveira et al. (2010), different mechanisms such as complementarity and facilitation can be involved in these interactions. In addition, the relative importance of each mechanism can change dynamically depending on litter identity and the decomposition state of the litter. Detritivore interactions as well as the effect of detritivore diversity on litter decomposition thus appear to be a function of litter identity and it seems very difficult to pinpoint litter trait or traits that may drive such changing detritivore interactions.

The impact of drought on detritivore dissimilarity effects

According to previous studies that showed that the frequency of rainfall events rather than the total amount of precipitation influenced surface litter decomposition (Yahdjian & Sala 2008), we manipulated the frequency of water addition in our experiment. Reduced frequency of watering clearly resulted in drier conditions which caused an overall decrease of 11% of litter mass loss measured in microcosms without detritivores. Based on the stress gradient hypothesis (Bertness & Callaway 1994), we expected that the relative impact of functional dissimilarity of detritivore communities increases with drier conditions.

Our data did not confirm this hypothesis because changing watering frequencies did not influence net detritivore effects on all but one litter species. *Ulex* as a single litter species showed a reduced net detritivore effect under drier conditions. As mentioned above, litter from this species was avoided by detritivores. Hence the net detritivore effect, that was already very low in humid, still have been reduced in drier conditions. This could point towards a higher preference of higher quality litter species under drier and thus more stressful conditions. However, this result has to be interpreted cautiously as *Ulex* was actually mostly avoided by detritivore (see above). Overall it seems that

detritivores are more resistant to a reduction in water availability than microbial decomposers, a result that has previously been shown for one of the detritivore species (*Ommatoiulus s.*) used in our test (Coulis et al. 2013). In the type of Mediterranean ecosystem we studied, which is predicted to be exposed to even more severe drought periods under future climate change scenarios, the relative importance of detritivore could increase as a result of buffering drought effects on decomposition to some degree.

However little is known about how detritivore resist to increasing drought and maintain their activity. Detritivores could have consumed more litter in dryer conditions in order to absorb the water contained in litter (Cruz-Rivera & Hay 2000). This compensatory feeding could thus allow detritivores to maintain their activity in drier conditions but may in the long term have a negative effect on detritivore fitness and thus on detritivore population densities. Further and more detailed studies on detritivore responses to a reduction in precipitation are needed for a more comprehensive understanding of detritivore effects on litter decomposition.

ACKNOWLEDGEMENTS

We thank all the Ecotron team for their technical support during the course of the experiment as well as Sandra Barantal, David Degueldre, Jeremy Devaux, François-Xavier Joly, Johanne Nahmani and Anaïs Rancon for their help during the setting up and the dismantling of the experiment. We would further like to thank Mickaël Hedde and Xavier Morin for helpful discussion about statistical analysis. This research is part of the project "CLIMED" funded through the ANR grant 09-CEP-007.

Discussion générale et synthèse

Figure 37. Photo d'*Ommatoiulus sabulosus* enroulé sur lui-même, position qu'il adopte pour se protéger d'un danger ou de la dessiccation.

L'objectif principal de ma thèse était d'étudier l'effet des détritivores sur la décomposition des litières d'arbustes méditerranéens en fonction de la disponibilité en eau. Durant ces 3 années de thèse mon travail s'est articulé autour de deux aspects de l'effet des détritivores sur la décomposition (Figure 38). Dans une première partie, j'ai utilisé *Ommatoiulus* comme une espèce modèle pour étudier en détail les effets directs (consommation de litières) et indirects (dépôt de fèces, décomposition des fèces) des détritivores sur le processus de décomposition en fonction de la disponibilité en eau. La deuxième partie avait pour but d'intégrer l'effet de différentes espèces de détritivores à l'échelle de la communauté et de comprendre comment les différences fonctionnelles entre espèces peuvent influencer le processus de décomposition en fonction de la disponibilité en eau et de la diversité des litières.

Dans un premier temps, la discussion aborde les limites méthodologiques des approches utilisées puis s'articule en deux grandes parties ayant pour but d'intégrer les résultats obtenus par les différentes expériences et de proposer des pistes de recherches afin d'approfondir les sujets traités et de compléter mes travaux.

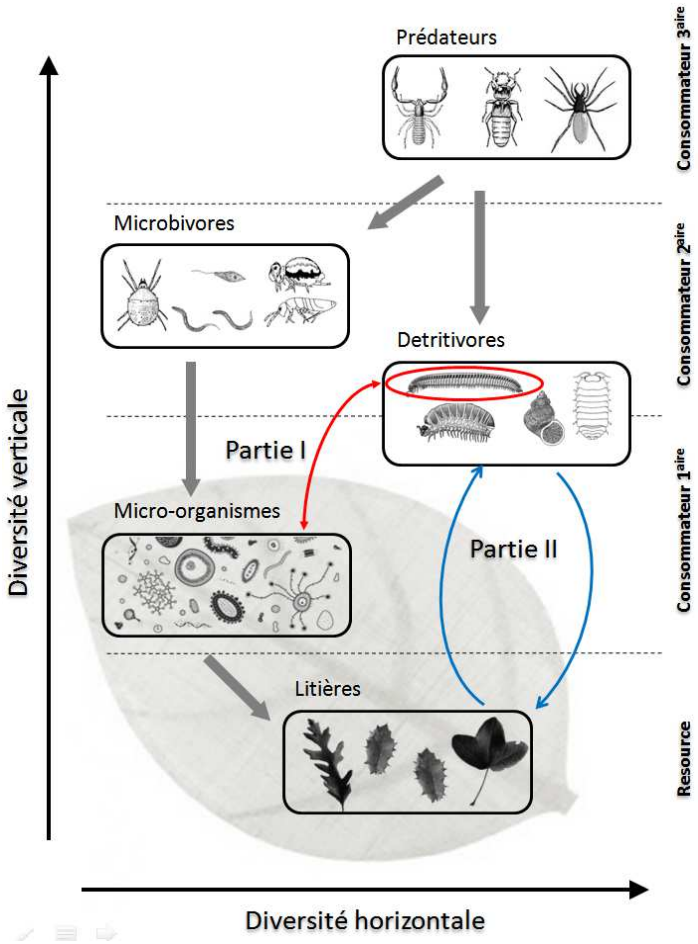

Figure 38. Schéma replaçant les interactions étudiées au cours de ma thèse dans un cadre trophique plus général. La flèche rouge indique les interactions entre détritivores et microorganismes et les flèches bleues font référence aux interactions entre la diversité des litières et la diversité des détritivores.

LIMITES METHODOLOGIQUES

De nombreux facteurs biotiques et abiotiques agissent directement mais également en interaction les uns avec les autres dans la régulation du processus de décomposition. Etudier un processus aussi complexe est donc un challenge d'un point de vue conceptuel et méthodologique. Le scientifique observe généralement le résultat du processus (par exemple la perte de masse) mais n'a pas toujours accès à la part relative de chaque mécanisme (lessivage, fragmentation, minéralisation,…). Comme la décomposition suit souvent une dynamique non linéaire, l'échelle de temps à laquelle le processus est étudié peut influencer le résultat. Au cours de ma thèse j'ai étudié « comment varie l'effet de la faune détritivore sur la décomposition en fonction de la sécheresse» via une approche expérimentale. Néanmoins j'ai réalisé 4 expériences à des niveaux d'organisation et de complexité contrastés allant d'une expérience de 7 jours en conditions contrôlées à une expérience *in situ* de 1 an (Tableau 15).

La comparaison des résultats obtenus dans les 3 principales expériences de ma thèse montre que les valeurs absolues des taux de perte de masse des mêmes litières, issues d'un lot identique constitué à partir de feuilles ramassées sur le terrain, varient selon les expériences (Figure 39) et que la différence relative entre les différentes espèces varie aussi. Ces différences peuvent être expliquées par les différences de conditions expérimentales (température, humidité,…), ainsi que par la durée variable de chaque expérience. Pour comprendre en détail certains mécanismes complexes tels que les interactions entre macrofaune et microorganismes, il a été nécessaire de faire des expérimentations dans des conditions contrôlées assez éloignées des conditions naturelles. Cette approche est puissante, car elle permet de comprendre de manière mécaniste certains aspects du processus de décomposition. Cependant les résultats obtenus peuvent-ils être transposés aux écosystèmes naturels ?

Il est très difficile de répondre de manière catégorique à cette question. Certains résultats semblent transposables de manière fiable, ainsi les préférences alimentaires d'*Ommatoiulus* étudiées dans le chapitre 1 sont confirmées par d'autres expérimentations (cf. chapitre 4 ainsi que d'autres tests non inclus dans le manuscrit). A l'inverse, d'autres résultats ne semblent pas transposables. Par exemple, les différences relatives de taux de perte de masse des 4 espèces de litières varient fortement selon les conditions expérimentales (Figure 39). Dans l'expérience B, en microcosmes sans sol, la litière de ciste se décompose beaucoup plus rapidement que celle de chêne, alors que sur le terrain (expérience D), les deux espèces ont une perte de masse identique.

Tableau 15. Caractéristiques des différentes expériences réalisées au cours de cette thèse.

		Hypothèses	Exp.	Chap.	Sol	Durée (jours)	Nb d'unités exp.	Nb d'ind. (faune)	Echelle spatiale	Niveau d'org.
(Mesure des traits fonctionnels sur les détritivores)			A	3 & 4	sans	7	25	1	12 x 9 cm	individu
H1	a	Les fèces stimulent la décomposition des litières sur lesquelles elles sont déposées	B	1	sans	30	40	8	40 x 33 cm	population
	b	*Ommatoiulus* consomme moins de litière dans les conditions sèches								
H3	a	La diversité fonctionnelle des litières et des détritivores interagit de manière synergique	C	3 & 4	avec	80	310	4	18 x 12 cm	communauté
	b	La relation diversité-fonction s'accentue dans les conditions de stress hydrique								
H4	a	Quels traits fonctionnels expliquent le mieux l'effet des détritivores sur la décomposition ?								
	b	L'effet de la diversité des détritivores sur la décomposition varie selon l'identité des litières								
H2	a	Les boulettes fécales se décomposent moins rapidement que les litières intactes	D	2	avec	370	180	NA	160 x 60 m	écosystème
	b	L'enfouissement des boulettes dans le sol accélère la décomposition								

Ce résultat peut être du à la dynamique de perte de masse qui est différente suivant les espèces. Mais on peut également envisager que les différentes conditions expérimentales n'ont pas affecté toutes les espèces de la même manière. Par exemple la présence de sol dans les expériences peut fortement influencer la décomposition car les microorganismes du sol (notamment les champignons) peuvent coloniser les litières et en exploiter les ressources tout en bénéficiant d'une humidité plus favorable dans le sol. Ainsi lorsqu'il est en présence de sol (dans l'expérience C), le romarin se décompose plus rapidement. Comme les litières de romarin sont très denses, elles forment une couche de litières en contact intime avec le sol, ce qui est propice aux interactions. A l'inverse, les autres litières sont plus volumineuses et ne sont que partiellement en contact avec le sol.

Ces interactions entre l'identité des espèces et les conditions expérimentales rendent donc difficile l'interprétation des résultats de perte de masse obtenus dans des microcosmes sans sol. Cette considération devrait être prise en compte lors de futures études sur la décomposition menées en

microcosmes. Une méthode intéressante est l'utilisation dans les microcosmes de sachets à maille fine contenant du sol – les «soilbags» – permettant des interactions entre sol et litières tout en étant adapté à des manipulations précises telles que la séparation et la quantification des litières restantes et des boulettes fécales de détritivores.

Plus largement, le dispositif expérimental du site du Massif de l'Etoile que j'ai contribué à mettre en place au cours de ma thèse permettra dans les années à venir d'aborder de manière plus réaliste l'influence des assemblages de litières et de détritivores et l'influence d'une diminution des précipitations sur la décomposition des litières, par exemple via des expériences de manipulation de la macrofaune *in situ*.

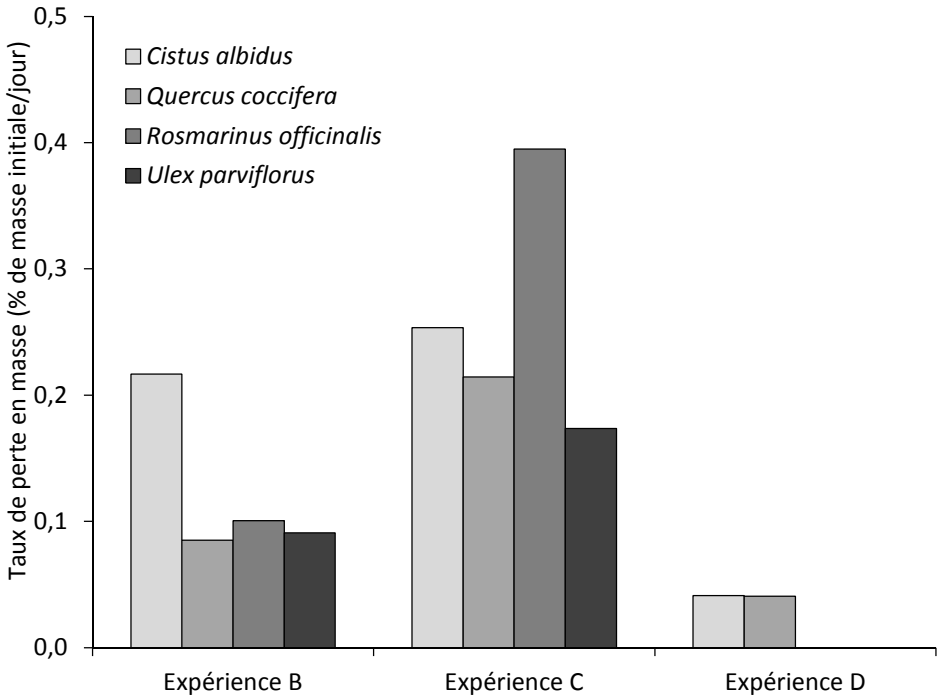

Figure 39. Comparaison des taux de perte de masse dans les 3 principales expériences de ma thèse.

LES LEÇONS DU IULE DES SABLES

Le rôle d'Ommatoiulus dans le fonctionnement de la garrigue

L'ensemble de mes résultats suggèrent qu'*Ommatoiulus sabulosus* a un effet important sur la décomposition des litières des 4 principaux arbustes de la garrigue du massif de l'Etoile.

Durant sa période d'activité, qui est concentrée pendant le printemps et l'automne, la population d'*Ommatoiulus* ingère d'importantes quantités de litières. Néanmoins certains individus peuvent être observés se nourrissant de fèces de lapins ou de pétales de fleurs de ciste tombés au sol, ce qui reflète le caractère opportuniste de ces animaux détritivores. La plupart des individus ont été observés dans la litière en train de se nourrir de feuilles mortes qui constituent la plus grande part du régime alimentaire de cette espèce. Nous avons mesuré un taux de consommation des litières de 84 ± 4 mg/g/jour (à une température et une photopériode proches des conditions naturelles pendant le pic d'activité de ces organismes). En extrapolant à partir de la biomasse d'*Ommatoiulus* sur le site du massif de l'Etoile (9.4 g/m²), on obtient une consommation d'environ 24 g de litière par mois. Sachant que les chutes annuelles de litières sur le site sont d'environ 230 g/m² (Santonja, données non publiées), en seulement quelques mois d'activité au cours de l'année, *Ommatoiulus* est susceptible d'ingérer une part très importante des chutes annuelles de litières.

Lorsqu'il a le choix entre les litières de plusieurs espèces, *Ommatoiulus* a une préférence alimentaire marquée pour les litières de ciste, ce qui suggère qu'à l'échelle de l'écosystème, ce sont principalement les litières de cette espèce qui sont consommées et fragmentées par la population d'*Ommatoiulus*. Or l'appétence des différentes espèces de litières peut changer au cours de la dynamique de décomposition (Lavelle & Spain 2001). Il est donc probable que les autres espèces de litières soient également consommées en grande quantité après qu'elles aient subi un conditionnement microbien les rendant plus appétantes, comme cela a déjà été observé en forêt tempérée par (Slade & Riutta 2012).

Contrairement à l'hypothèse H1a, dans l'expérience B, les boulettes fécales produites en grandes quantités par *Ommatoiulus* n'ont pas eu d'influence sur la décomposition des litières non consommées. D'autre part, la masse de boulettes produite est sensiblement identique à la masse de litière consommée durant l'expérience correspondante, ce qui suggère que malgré un effet important sur la fragmentation des litières, *Ommatoiulus* a un effet à court terme négligeable sur la minéralisation de la matière organique.

Cependant, à plus long terme, ces fèces tendent à se décomposer plus rapidement que les litières intactes (expérience D). Ce résultat va à l'encontre de nos attendus et montre qu'*Ommatoiulus* a la capacité de modifier la trajectoire de décomposition de la matière organique sur le long terme. A

l'instar de précédentes études, nous avons trouvé que la matière organique dans les boulettes fécales est plus récalcitrante que dans les litières intactes. Cependant plusieurs autres facteurs ont contribué à augmenter la décomposition des boulettes fécales :

1- L'enfouissement des boulettes fécales sur seulement quelques centimètres permet aux microorganismes de bénéficier de meilleures conditions d'humidité qu'à la surface (H2b).
2- L'ingestion et le passage des litières dans le tube digestif ont fragmenté les litières et considérablement augmenté la teneur en composés solubles dans les boulettes fécales, ce qui peut favoriser la perte en masse par lessivage.

La redistribution de la matière organique dans les horizons du sol par *Ommatoiulus* accélère donc potentiellement le recyclage du carbone et des nutriments contenus dans les litières et est susceptible de modifier la répartition dans le profil du sol de la matière organique et des nutriments disponibles pour les plantes.

Enfin, mon travail n'a pas pris en compte la consommation de fèces par d'autres organismes du sol (acariens, collemboles, vers de terre,…). Toutefois, les fèces d'*Ommatoiulus* peuvent également servir de source de nourriture pour la faune coprophage. En rendant les litières plus facilement accessibles pour ces organismes, les macroarthropodes pourraient donc faciliter leur activité. Plusieurs études ont ainsi montré que les vers de terre préfèrent se nourrir de fèces de macroarthropodes plutôt que de litières intactes (Scheu & Wolters 1991; Bonkowski *et al.* 1998). D'importantes quantités de turricules ont été observées à la surface du sol sur le site du massif de l'Etoile, notamment pendant l'hiver, ce qui suggère que la facilitation entre vers de terre et macroarthropodes est vraisemblablement un élément important du fonctionnement du sol de cet écosystème. Cependant l'étude des vers de terre du massif de l'Etoile est très difficile car se sont des espèces adaptées à l'aridité qui ont la capacité de s'enfouir très profondément. De plus, le sol très caillouteux rend problématique un échantillonnage efficace de ces organismes.

Effet de la sécheresse sur l'activité des détritivores

L'effet de la sécheresse sur l'activité de la faune du sol est très peu étudié. Plusieurs études menées en région tempérée ont montré qu'une réduction de la disponibilité en eau peut fortement diminuer la consommation de litière par la faune et réduire son effet sur la décomposition (Dias *et al.* 2012; Collison *et al.* 2013). Mes résultats contredisent ceux des précédentes études puisque lors de 2 expériences réalisées avec des espèces de détritivores différentes (expériences B et C), la consommation de litière n'a pas été modifiée par la réduction de la disponibilité en eau (H1a). Ce résultat suggère qu'en milieu méditerranéen, l'activité de la faune est moins sensible à la sécheresse que l'activité des décomposeurs microbiens. La macrofaune détritivore pourrait donc jouer un rôle important dans les écosystèmes méditerranéens, en continuant à être active et donc à influencer le

processus de décomposition pendant les périodes de sécheresse qui risquent d'être plus fréquentes et plus marquées à cause des changements climatiques.

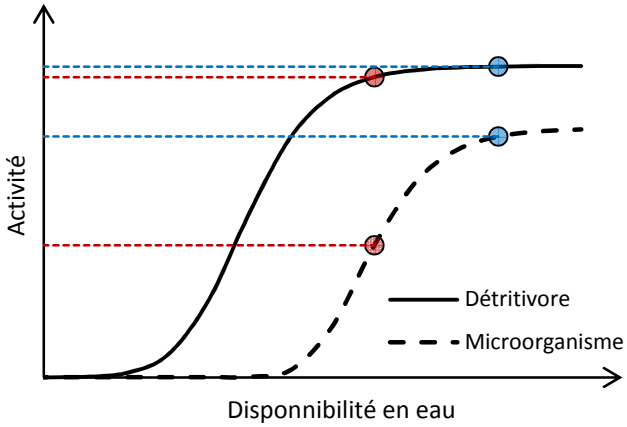

Figure 40. Courbe de réponse théorique de l'activité des détritivores et des microorganismes à la variation de la disponibilité en eau. Les points rouges et bleus font références à des conditions d'humidité respectivement sèches et humides.

Cependant il faut rester prudent avec l'interprétation de ces résultats. En effet, même si une attention particulière a été portée à la manipulation de la disponibilité en eau (cf. m&m des chapitres 1 et 3), seulement deux niveaux d'humidité ont été appliqués pour simuler la « sécheresse ». Mes résultats sont donc dépendants du choix des niveaux d'humidité. De plus, l'activité de la faune et des microorganismes ne répond probablement pas de manière linéaire à la variation de la disponibilité en eau. Par exemple Sardans & Peñuelas (2013) suggèrent qu'en dessous de 13 à 20 % d'humidité dans le sol, les microorganismes sont inactifs. De tels seuils n'ont pas été étudiés pour l'activité des microorganismes dans les litières, ni pour les détritivores. De plus, le seuil d'activité des détritivores est probablement inférieur à celui des microorganismes, ce qui expliquerait la résistance relative des détritivores face à la sécheresse (Figure 40). Pour aller plus loin, il serait souhaitable de faire des expériences incluant une gamme complète de niveaux d'humidité pour détecter ce seuil d'activité chez différentes organismes détritivores. Ces résultats permettraient une meilleure compréhension des relations entre l'activité de la faune du sol et la disponibilité en eau ainsi que d'anticiper de manière plus réaliste l'effet des changements climatique sur le fonctionnement du sol.

Enfin, même si nos résultats montrent que l'activité de certains détritivores est relativement persistante en conditions sèches, cela n'exclut pas que la croissance et la valeur sélective des individus soient diminuées à plus long terme. Une diminution de la densité des populations pourrait dans ce cas entrainer indirectement une baisse de l'effet de la faune sur la décomposition. Garcia-Pausas *et al.* (2004) ont montré en étudiant un gradient de précipitations en Espagne, que l'effet de la faune diminue avec les précipitations pour finalement être nul dans le site semi-désertique.

Les interactions entre detritivores et microorganismes

Il est généralement admis que la faune stimule l'activité microbienne en fragmentant les litières et en rendant la matière organique plus accessible aux microorganismes. Les boulettes fécales sont donc supposées avoir une activité microbienne plus importante que les litières correspondantes non ingérées. Cette conception du rôle de la faune dans le processus de décomposition est la plus répandue et figure dans de nombreux livres d'écologie et de biologie du sol (Cadisch & Giller 1997; Lavelle & Spain 2001; Chapin III & Matson 2002; Bardgett 2005; Bardgett & Wardle 2010).

Cependant, quelques études ont montré que l'activité microbienne pouvait être inchangée, voire même inférieure dans les boulettes fécales. Nos résultats du chapitre 1 vont également dans ce sens. Plusieurs éléments peuvent expliquer cet effet négatif. La première hypothèse (i) est que l'assimilation préférentielle par la faune des composés facilement métabolisables tend à augmenter la proportion relative des composés récalcitrants (lignine, cire cuticulaire, …) dans les boulettes fécales, ce qui n'est pas favorable au développement microbien. La seconde hypothèse (ii) consiste à envisager le passage dans le tube digestif et la fragmentation des litières comme une perturbation pour les microorganismes. En effet, la plupart des hyphes mycéliens sont tués et digérés tout comme une forte proportion des bactéries (Byzov *et al.* 1998). Malgré la reconstitution rapide des populations bactériennes dans le tube digestif, cette perturbation peut avoir un effet négatif sur les communautés microbiennes.

Bien que de nombreux résultats montrent qu'une « inhibition » des microorganismes durant l'ingestion des litières par la faune est possible, ils ne remettent pas en cause qu'une « stimulation » des microorganismes existe également. Alors comment expliquer l'existence de ces effets opposés ? Il faut considérer que l'effet de la macrofaune détritivore sur l'activité microbienne dans les fèces est modulé par plusieurs facteurs :

1-Identité des détritivores : L'effet des détritivores sur l'activité microbienne dans les fèces peut varier d'une espèce de détritivore à l'autre. Par exemple, en comparant la respiration des boulettes fécales de diptères (Bibionidae) à celle de litières non ingérées, Frouz & Simek (2009) ont observé une stimulation de la respiration pour une espèce alors que pour une autre espèce du même genre, il n'y a eu aucun effet détectable.

2-Identité des litières : L'effet des détritivores sur l'activité microbienne dans les fèces peut également varier suivant l'identité des litières et donc la qualité de la matière organique ingérée. Au cours de ma thèse, j'ai cherché à tester cette hypothèse. J'ai ainsi participé à la préparation du sujet et à l'encadrement d'un stage de master 1 (co-encadré avec François-Xavier Joly) ayant pour objectif de comparer l'activité microbienne d'une large gamme de litières intactes à celle des boulettes fécales issues de ces litières. Les résultats préliminaires de cette expérience montrent que l'effet des détritivores sur la respiration des fèces change fortement suivant l'espèce de litière ingérée (Encadré n°1).

<u>Encadré n°1 :</u> L'activité microbienne des fèces varie selon la qualité initiale des litières

Afin de tester l'hypothèse selon laquelle l'effet des détritivores sur l'activité des microorganismes dans les fèces dépend de la qualité initiale des litières, nous avons mis en place une expérience pour comparer la respiration en conditions standardisées (Substrate Induced Respiration) des litières d'une trentaine d'espèces d'arbres et la respiration de boulettes fécales de *Glomeris marginata* issues de ces litières.

Cette étude a permis de montrer que l'effet des détritivores sur l'activité potentielle des microorganismes dans les fèces dépend de l'identité des litières consommées. Comparée à l'activité microbienne dans les litières, celle des fèces peut-être stimulée, inchangée, ou inhibée (Figure 41). De plus, ce gradient de réponses est expliqué par la qualité initiale des litières. En effet, les cas d'inhibition ont été mis en évidence pour les litières dites de « bonne » qualité (riche en N, pH neutre, capacité de rétention en eau forte), alors que la respiration microbienne était stimulée pour les litières de moindre qualité.

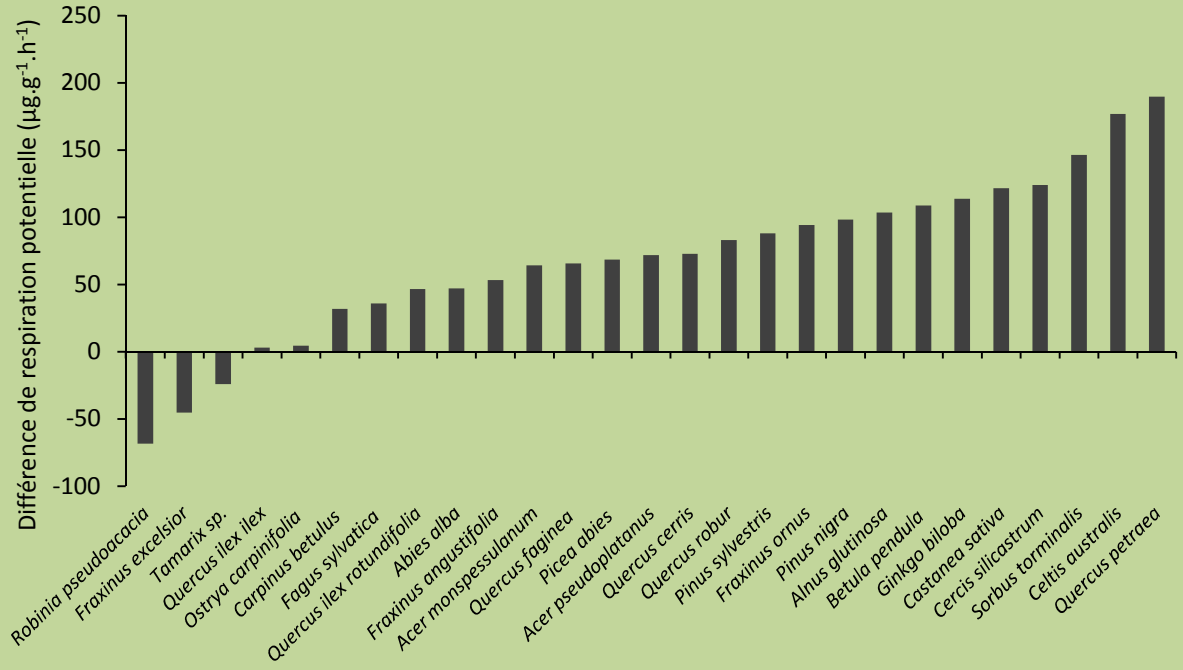

Figure 41. Différence absolue de respiration entre boulettes et litières intactes pour chaque espèce d'arbre.

Ces résultats permettent de supposer que le passage des litières dans le tube digestif améliore la qualité des fèces issues de litières de mauvaise qualité, en rendant la matière organique plus accessible, mais a un effet négatif sur la qualité des fèces issues des litières de bonne qualité, pour lesquelles les composés facilement métabolisables sont assimilés par le détritivore.

3-Conditions environnementales : Enfin, l'activité microbienne des boulettes peut être fortement modulée par les conditions environnementales. En effet, il est clair que si les boulettes se dessèchent immédiatement après avoir été émises, aucune activité microbienne n'est possible.

L'analyse des phospholipides membranaires dans l'expérience B (Chapitre 1) a montré que le dépôt de fèces sur les litières peut modifier la composition des communautés microbiennes des litières dans des conditions d'humidité favorables. Cependant la réduction de la disponibilité en eau a annulé cet effet. De plus les microorganismes des boulettes fécales ont été plus sensibles à la sécheresse que les microorganismes des litières, ce qui suggère que le cumul de la perturbation liée au passage dans le tube digestif et du stress hydrique est négatif pour les microorganismes des boulettes fécales et confirme le point 3.

Ces deux résultats montrent que la sécheresse conditionne les interactions à court terme entre les macroarthropodes du sol et les décomposeurs microbiens. Par conséquent, même si la faune semble pouvoir maintenir son activité de consommation et de fragmentation des litières en cas de stress hydrique modéré, son effet indirect (stimulation microbienne) peut être fortement modifié par une diminution de la disponibilité en eau.

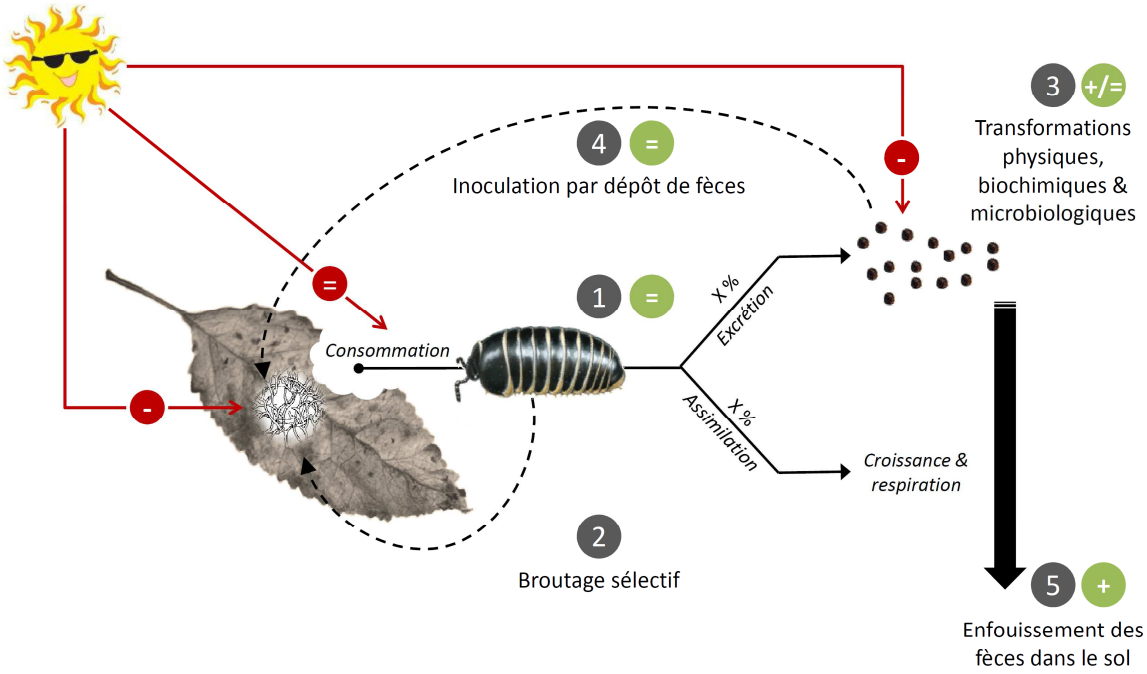

Figure 42. Schéma conceptuel regroupant les effets directs et indirects des détritivores sur la décomposition des litières. Les principaux résultats obtenus au cours de la thèse ont été replacés sur ce schéma présenté en introduction. Les symboles +, - ou = signifient respectivement une augmentation, une inhibition ou un effet nul sur la décomposition des litières ou des boulettes fécales. Les symboles rouges font référence aux effets de la disponibilité en eau et les symboles vert aux effets des détritivores (*Ommatoiulus*).

LES INTERACTIONS ENTRE DETRITIVORES

La communauté de détritivores du massif de l'Etoile est un cas particulier car une seule espèce de détritivore domine la communauté à 98%. Dans la plupart des écosystèmes du même type, plusieurs espèces de détritivores cohabitent au sein de communautés parfois assez diversifiées, par exemple dans le sud de la France, entre 9 et 15 espèces de détritivores peuvent cohabiter localement (David 1999). Les interactions entre les différentes espèces, et donc la diversité des détritivores, peuvent influencer le fonctionnement de l'écosystème. Or le rôle de la diversité des détritivores dans le fonctionnement de l'écosystème est encore peu connue.

Mes résultats de thèse ont permis de confirmer que la dissimilarité fonctionnelle des détritivores a un impact positif sur la décomposition des litières (Heemsbergen, *et al.* 2004; Hedde *et al.* 2010). De plus la dissimilarité fonctionnelle des détritivores peut influencer d'autres processus importants pour le fonctionnement du sol tels que le lessivage du carbone organique ou de l'azote. La diversité des détritivores apparait donc comme un élément important pour le fonctionnement du sol : la modification des flux d'azote influence la disponibilité de ce nutriment pour la végétation et la modification des flux de carbone organique dissout a des conséquences pour les microorganismes du sol et le stockage du carbone dans les horizons minéraux du sol (Kalbitz & Kaiser 2008). Nous avons d'ailleurs observé un effet significatif assez fort de l'identité des communautés de détritivores sur la respiration potentielle du sol (Figure 43), ce qui constitue un élément supplémentaire permettant d'affirmer que l'influence des détritivores ne se limite pas à la couche de litières superficielles mais s'étend au fonctionnement du sol dans son ensemble.

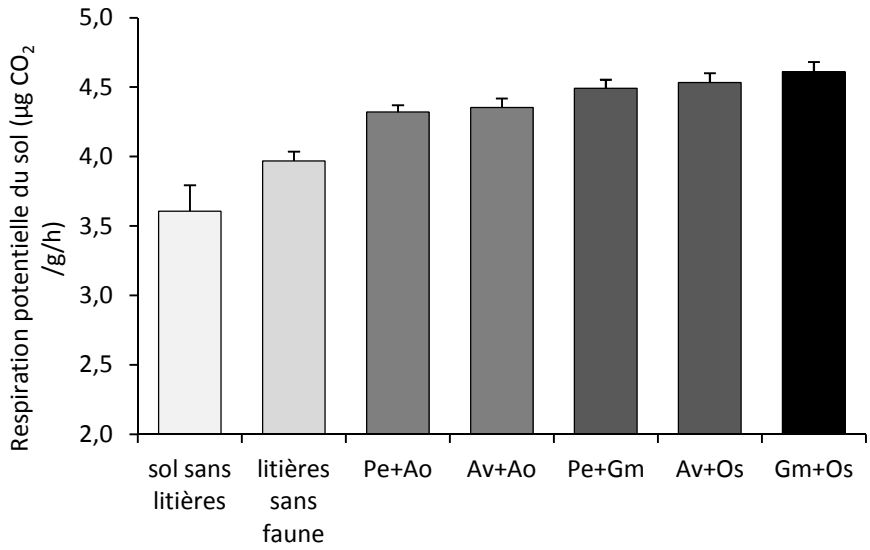

Figure 43. Effet des différentes communautés de détritivores sur la respiration potentielle (SIR) du sol. La barre noire indique les communautées incluant à la fois *Glomeris* (Gm) et *Ommatoiulus* (Os) (les deux espèces ayant été observées en train de remodeler le sol). Les barres gris foncé (Pe+Gm et Av+Os) indiquent les communautés contenant l'une de ces deux espèces et les deux barres gris clair indiquent les commuanutés de détritivores ne contenant aucune des deux espèces ayant un impact sur le sol (Pe+Ao et Av+Ao).

Les interactions trophiques

Parmi les 5 processus du sol étudiés, seule la décomposition des litières a été affectée par une interaction entre la dissimilarité des litières et la dissimilarité des détritivores. Cette interaction montre que la diversité a un effet au sein de chaque groupe trophique ainsi qu'entre les groupes trophiques. Cependant contrairement à l'hypothèse H3a, la diversité de ces deux niveaux trophiques n'a pas interagi de manière synergique, c'est-à-dire que la perte en masse n'était pas à son maximum dans les communautés combinant à la fois les mélanges de litières les plus dissimilaires et les communautés de faune les plus dissimilaires. Il semble donc difficile de pouvoir généraliser les effets positifs de la diversité sur le fonctionnement de l'écosystème.

L'effet de la diversité des litières et de la diversité des détritivores avait déjà été étudié, mais seulement séparément. En compilant les données de 28 études indépendantes dans une méta-analyse, Srivastava *et al.* (2009) ont montré que la diversité des litières n'a pas d'effet direct sur la perte de masse alors que la diversité des détritivores a un effet positif sur la perte de masse des litières. Cependant mes résultats sur l'effet de la diversité à plusieurs niveaux trophiques montrent qu'il est possible que la diversité des litières ait un effet indirect via son interaction avec la diversité des détritivores. Malgré un effet direct qui peut être faible, via cette interaction, la diversité des litières pourrait donc avoir un effet fort sur le processus de décomposition, tout particulièrement dans les conditions naturelles où les communautés d'organismes détritivores peuvent être très abondantes et contribuer fortement au processus de décomposition.

Zimmer *et al.* (2005) ont montré, via une expérience en microcosmes, que les interactions entre un isopode et un ver de terre peuvent être synergiques, antagonistes ou que leurs effets peuvent être simplement additifs, selon la qualité ou la diversité des litières dont ils se nourrissent. Les résultats présentés dans le chapitre 4 concordent avec cette étude puisque selon l'identité de l'espèce de litière considérée, la dissimilarité des détritivores a eu soit un effet nul (*Cistus*), soit un effet négatif (*Quercus*), soit un effet positif (*Rosmarinus* et *Pinus*). Cependant, contrairement à l'hypothèse suggérée par Zimmer *et al.* (2005), les effets de la dissimilarité des détritivores ne semblent pas liés à la qualité des litières puisque la litière peu décomposable (*Pinus*) a été positivement affectée alors que les litières plus décomposables (*Cistus* et *Rosmarinus*) ont été affectées de manières contrastées par la dissimilarité. Il est donc pour l'instant difficile de comprendre pourquoi certaines espèces de litières promeuvent des effets synergiques entre les détritivores et d'autres non. L'identification des traits fonctionnels des litières à l'origine des interactions positives entre les organismes détritivores est donc une piste de recherche prometteuse.

Pour aller plus loin dans la compréhension des interactions entre la diversité verticale et la diversité horizontale (Figure 38), il serait également intéressant d'étudier l'effet « top-down » des prédateurs sur l'activité des détritivores et les conséquences sur la décomposition des litières. Jabiol *et*

al. (2013) ont étudié l'effet d'un poisson prédateur (simulé par la diffusion d'odeur dans l'eau) sur l'activité des détritivores aquatiques. Leurs résultats montrent que certaines espèces de détritivores réduisent leur activité pour limiter leur vulnérabilité, alors que d'autres espèces ne sont pas sensibles car elles sont protégées par leur fourreau minéral (trichoptères). Cette étude montre donc que les prédateurs peuvent modifier les mécanismes de compétition ou de complémentarité à l'origine des effets de la diversité des détritivores sur le processus de décomposition, cependant cet effet n'a pas encore été étudié en milieu terrestre.

Importance relative de l'identité et de la dissimilarité fonctionnelle

La part relative de la dissimilarité fonctionnelle dans les modèles expliquant l'effet des détritivores sur la décomposition est en moyenne de 13 % alors que la part de l'identité fonctionnelle est en moyenne de 85 % (cf. Chapitre 4). Ce résultat montre que la dissimilarité fonctionnelle des détritivores a un rôle non négligeable dans le processus de décomposition, mais que l'identité (fonctionnelle) des espèces est l'élément de la communauté de détritivores ayant l'impact le plus important sur le processus de décomposition.

Ce résultat correspond aux conclusions de plusieurs études récentes (Vos *et al.* 2011; Treplin *et al.* 2013) qui insistent sur l'importance de l'identité des espèces de détritivores sur le processus de décomposition et amènent à se focaliser sur les traits moyens des détritivores qui sont importants pour prédire le processus de décomposition.

Quels traits sont importants pour prédire l'effet faune ?

Parmi les 5 traits fonctionnels que nous avons mesurés sur les détritivores, les traits liés aux stratégies alimentaires de la faune sont ceux qui expliquaient le mieux l'effet des détritivores sur la décomposition. Les moyennes pondérées (CWM) du taux de consommation ainsi que du rendement d'assimilation sont les deux traits expliquant le mieux l'effet de la faune sur la perte de masse des litières. Les communautés composées d'espèces ayant un fort taux de consommation ainsi qu'un faible rendement d'assimilation (conso+/assim-) avaient donc tendance à avoir un effet fort sur la perte de masse; à l'opposé les communautés composées d'espèces ayant un faible taux de consommation et un fort taux d'assimilation (conso-/assim+) avaient tendance à avoir un effet relativement plus faible. Ces observations suggèrent qu'il existe bien un compromis entre le taux de consommation et le rendement d'assimilation. Il y a en effet une relation négative entre ces deux variables pour les 5 espèces étudiées (R^2=0.13, p=0.04) mais qui n'est pas nette, probablement à cause du nombre restreint d'espèces étudiées. Il serait donc intéressant de tester l'existence d'un tel compromis sur un plus grand nombre d'espèces.

Ces deux composantes de la stratégie alimentaire des détritivores pourraient ensuite être mises à profit pour faire des prédictions de l'effet de la faune sur la perte de masse. Par exemple, des

communautés dominées par des espèces "conso+/assim-" devraient avoir un effet fort sur la perte de masse des litières alors que des communautés dominées par des espèces ayant une stratégie conso-/assim+ auront un effet faible sur la perte de masse. Ces « prédictions » peuvent sembler triviales, cependant elles sont un point de départ intéressant car elles peuvent servir d'hypothèse nulle pour tester en milieu naturel l'effet des traits des espèces de détritivore sur le processus de décomposition.

Cette approche basée sur les traits parait prometteuse, mais il reste une part importante de l'effet faune qui n'est pas expliqué par les traits des espèces. Cette part de variabilité non expliquée peut être due à la fiabilité des mesures de traits ou au manque de connaissances biologiques et écophysiologiques sur les espèces et donc à l'oubli d'un trait essentiel pour le processus.

Fiabilité et signification de la mesure des traits

Dans la définition du trait fonctionnel, il est explicitement dit qu'il n'y aucune référence aux conditions environnementales (Violle *et al.* 2007). Cependant certains traits sont très sensibles et peuvent varier énormément en fonction des conditions environnementales. Cela pose un problème lorsque l'on utilise (comme c'est le cas ici) les traits moyens de chaque espèce en tant que variable prédictive.

Par exemple le taux de consommation peut être surestimé s'il est mesuré en absence de sol. D'autre part, la consommation change suivant l'espèce de litière consommée, la température ou encore l'humidité. Si les valeurs absolues changent mais que les différences entre espèces et donc leur hiérarchie est conservée, il est alors possible d'utiliser les mesures de traits faites en conditions standardisées (comme dans nos études) pour prédire les processus en conditions plus naturelles. Cependant si les différences relatives entre les espèces changent, il n'est alors plus possible d'utiliser ces mesures de traits. Un moyen de prendre en compte ce biais est de mesurer également la variabilité intraspécifique des valeurs de trait, pour connaitre la réponse des espèces aux variations environnementales et permettre une extrapolation plus fiable des données aux conditions naturelles.

Le manque de connaissance sur la biologie des détritivores

La biologie et l'écologie des organismes du sol sont assez peu connues. Il est donc possible de passer à coté d'un élément important pour le processus étudié. Pour illustrer ce propos, je vais prendre l'exemple de l'impact des détritivore sur le sol. Habituellement, on considère que les détritivores consomment des litières et que leur activité est concentrée dans les horizons organiques du sol et par conséquent qu'ils ont peu d'impact sur le sol minéral. Cependant au cours de l'expérience C réalisée à l'Ecotron, plusieurs espèces de détritivores ont été observées en train de remodeler le sol. *Ommatoiulus* s'est enterré tout au fond (3 cm) du microcosme pour muer et a fréquemment été observé fouissant dans le sol (Figure 44). *Glomeris marginata* a également eu un impact sur le sol mais d'une toute autre manière, à savoir en ingérant du sol minéral pour construire une loge de mue ou

pour entourer ses œufs (Figure 44). A part ces deux espèces, aucune autre n'a été observée ayant une interaction avec le sol de manière systématique. Ces comportements ont probablement eu un impact important sur l'activité microbienne du sol comme le suggère les données de respiration potentielle (Figure 43). Cependant, aucun trait fonctionnel n'a permis de rendre compte de l'impact de ces espèces sur le remodelage et la bioturbation du sol.

Un des challenges pour mieux comprendre l'effet de la faune détritivore sera donc de définir de nouveaux traits fonctionnels prenant en compte non seulement l'effet des détritivores sur la perte de masse des litières mais aussi sur d'autres processus clefs du fonctionnement du sol.

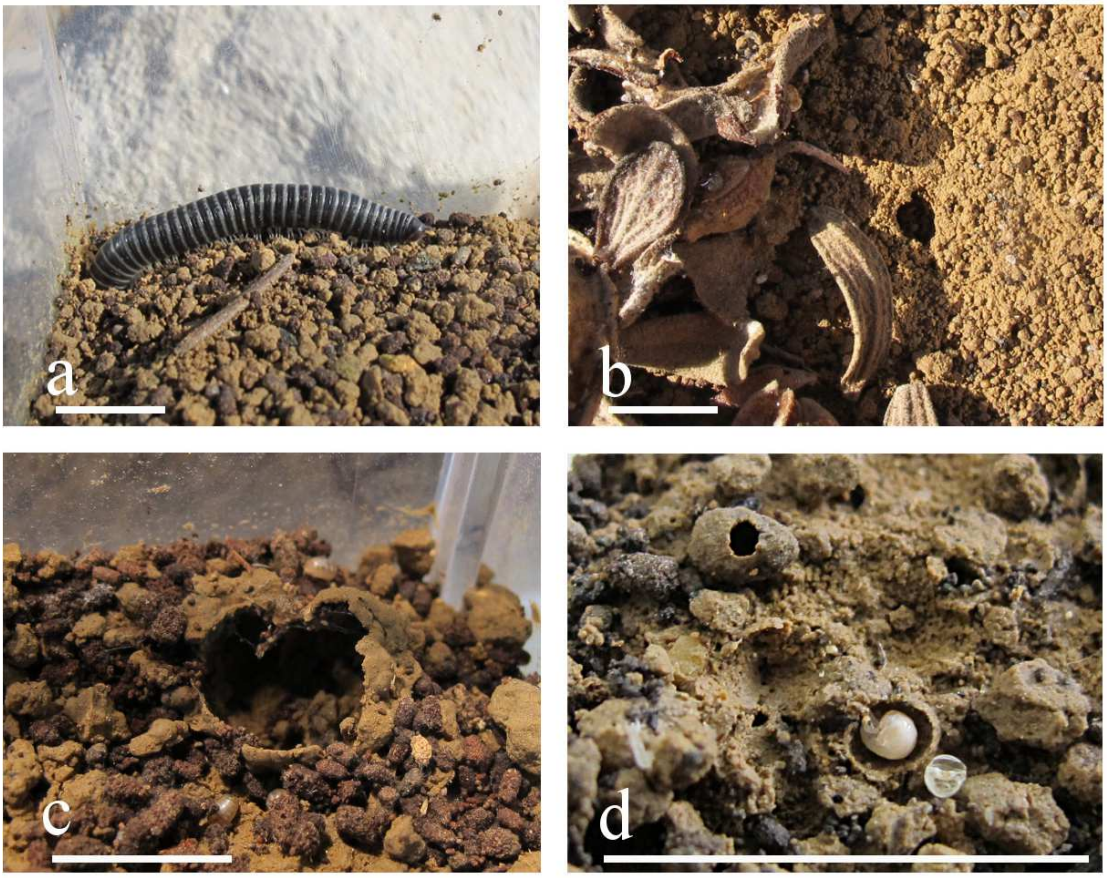

Figure 44. Photographies montrant les effets d'*Ommatoiulus* (a) et (b) et de *Glomeris* (c) et (d) sur le sol. La photo (a) montre un *Ommatoiulus* en train de s'enfouir et la photo (b) le trou résultant de l'enfouissement. La photo (c) montre une loge de mue utilisée par un *Glomeris* adulte et la photo (d) montre une capsule de sol protégeant un œuf de *Glomeris* éclos ainsi qu'un individu de stade I ou II en train de muer. La barre blanche représente 1cm.

CONCLUSION

Il existe différentes conception du rôle de la faune détritivore dans le processus de décomposition. De manière schématique, les détritivores sont vus soit comme catalyseurs[1] de la décomposition microbienne car ils fragmentent les litières et stimulent les microorganismes, soit comme stabilisateurs[2] car ils rendent la matière organique plus récalcitrante. Mes résultats de thèse confirment plutôt la première conception et suggèrent que la faune participe à accélérer le recyclage de la matière organique et à favoriser la libération des nutriments essentiels pour les plantes. Cependant deux éléments nuancent cette conclusion. D'une part l'effet de la faune dépend de l'espèce de litière, en effet *Ommatoiulus* tend à accélérer la décomposition du chêne kermès mais pas du ciste. L'effet des détritivores peut donc être modulé par la composition et la diversité des communautés végétales. Les interactions entre qualité des litières et effet de la faune sont complexes, cependant des travaux en cours semblent montrer que lorsque la faune se nourrit de litière de bonne qualité, son effet est négatif alors que lorsqu'elle se nourrit de litière de moins bonne qualité son effet est positif. D'autre part mes résultats sont difficilement conciliables avec une vision de la faune comme un catalyseur des activités microbiennes car il semble que la décomposition du chêne kermès a été accélérée grâce à une augmentation du lessivage et non à une augmentation de l'activité microbienne. Ce résultat est intéressant car il met en évidence un mécanisme indirect de stimulation de la décomposition par la faune qui a peu été étudié et participe avec l'ensemble de me résultats à dresser un tableau plus complet des nombreux effets directs et indirects par lesquels les détritivores influencent le processus de décomposition (Figure 42).

À l'échelle de la communauté, l'identité ainsi que la diversité fonctionnelle des détritivores ont une influence importante sur la décomposition des litières mais également sur plusieurs autres processus clef du fonctionnement des sols tels que l'activité potentielle et le lessivage de nutriments et de carbone à travers le sol. L'utilisation d'une approche basée sur les traits fonctionnels a permis à partir de mesures de traits fonctionnels effectuées sur les espèces de détritivores d'expliquer l'effet de différentes communautés de détritivore sur la décomposition. Cette approche a également permis d'identifier les traits reliés aux stratégies alimentaires des espèces (consommation et assimilation) comme essentiels pour expliquer l'effet de la faune sur la décomposition. De plus amples recherches sur ce sujet sont nécessaires pour mieux caractériser les stratégies alimentaire des détritivores et ainsi améliorer la classification fonctionnelle de ces organismes dans le but de mieux comprendre l'effet des détritivores à l'échelle de la communauté.

Enfin un des fils conducteurs de mon travail a été le rôle de la sécheresse ou plus précisément le rôle de la disponibilité en eau sur l'effet de la faune dans le processus de décomposition. Mes résultats

[1] par exemple Bardgett & Wardle (2010)
[2] par exemple Prescott (2010)

ont montré que les détritivores sont plus résistants que les microorganismes et peuvent donc maintenir leur activité dans des conditions plus sèches. Bien que la sécheresse affecte peu l'effet direct de la faune sur la décomposition (consommation), l'effet indirect de la faune sur la décomposition risque néanmoins d'être affecté négativement par la disponibilité en eau (cf. Figure 42), ce qui pourrait avoir des conséquences pour le fonctionnement de l'écosystème si les sécheresses s'accentuent dans les années à venir. De plus les communautés de détritivores les plus performantes ont été plus fortement affectées par la diminution de la disponibilité en eau, ce qui suggère qu'il existe un compromis entre les performances des organismes du sol (dans la décomposition) et leur résistance à une perturbation. Pour une meilleure interprétation de ce résultat il serait intéressant d'étudier la réponse des communautés de détritivores *in situ* à une modification de la disponibilité en eau. Le dispositif d'exclusion de pluie du projet Climed que j'ai participé à installer au cours de ma thèse permettra dans les années à venir d'apporter des éléments de réponse à cette question.

Figure 45. Photo des dispositifs d'exclusion de pluies du projet Climed.

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Annexes

ANNEXE 1 : LISTE DES ESPECES VEGETALES DU SITE DE L'ETOILE

Nom latin	Famille
Allium sphaerocephalon L. subsp. sphaerocephalon	Alliaceae
Alyssum alyssoides (L.) L.	Brassicaceae
Anthyllis vulneraria L. subsp. praepropera (A. Kern.) Bornm.	Fabaceae
Aphyllanthes monspeliensis L.	Aphyllanthaceae
Arenaria serpyllifolia L. subsp. leptoclados (Rchb.) Nyman	Caryophyllaceae
Argyrolobium zanonii (Turra) P.W. Ball subsp. zanonii	Fabaceae
Asterolinon linum-stellatum (L.) Duby	Primulaceae
Avenula bromoides (Gouan) H. Scholz subsp. bromoides	Poaceae
Bituminaria bituminosa (L.) C.H. Stirt.	Fabaceae
Bombycilaena erecta (L.) Smoljan.	Asteraceae
Brachypodium retusum (Pers.) P. Beauv.	Poaceae
Carex halleriana Asso subsp. halleriana	Cyperaceae
Cistus albidus L.	Cistaceae
Clypeola jonthlaspi L.	Brassicaceae
Dianthus sylvestris Wulfen subsp. longicaulis (Ten.) Greuter & Burdet	Caryophyllaceae
Dorycnium pentaphyllum Scop. subsp. pentaphyllum	Fabaceae
Erodium cicutarium (L.) L'Hér. subsp. cicutarium	Geraniaceae
Fumana ericoides (Cav.) Gand. subsp. montana (Pomel) Güemes & Muñoz Garm.	Cistaceae
Fumana thymifolia (L.) Spach ex Webb	Cistaceae
Galium corrudifolium Vill.	Rubiaceae
Globularia alypum L. subsp. alypum	Globulariaceae
Hornungia petraea (L.) Rchb.	Brassicaceae
Iris lutescens Lam. subsp. lutescens	Iridaceae
Juniperus oxycedrus L. subsp. oxycedrus	Cupressaceae
Leuzea conifera (L.) DC.	Asteraceae
Linaria simplex (Willd.) DC.	Scrophulariaceae
Phillyrea angustifolia L.	Oleaceae
Pinus halepensis Mill. subsp. halepensis	Pinaceae
Poa bulbosa L.	Poaceae
Quercus coccifera L.	Fagaceae
Quercus ilex L. subsp. ilex	Fagaceae
Reseda phyteuma L. subsp. phyteuma	Resedaceae
Rosmarinus officinalis L. subsp. officinalis	Lamiaceae
Rubia peregrina L. subsp. peregrina	Rubiaceae
Rumex intermedius DC.	Polygonaceae
Sanguisorba minor Scop.	Rosaceae
Scandix australis L.	Apiaceae
Scilla autumnalis L.	Hyacinthaceae
Teucrium chamaedrys L.	Lamiaceae
Teucrium flavum L. subsp. flavum	Lamiaceae
Teucrium polium L. subsp. polium	Lamiaceae
Thapsia villosa L.	Apiaceae
Thymus vulgaris L. subsp. vulgaris	Lamiaceae
Trifolium campestre Schreb. subsp. campestre	Fabaceae
Ulex parviflorus Pourr. subsp. parviflorus	Fabaceae
Valantia muralis L.	Rubiaceae

ANNEXE 2 : APPENDIX OF CHAPTER 3

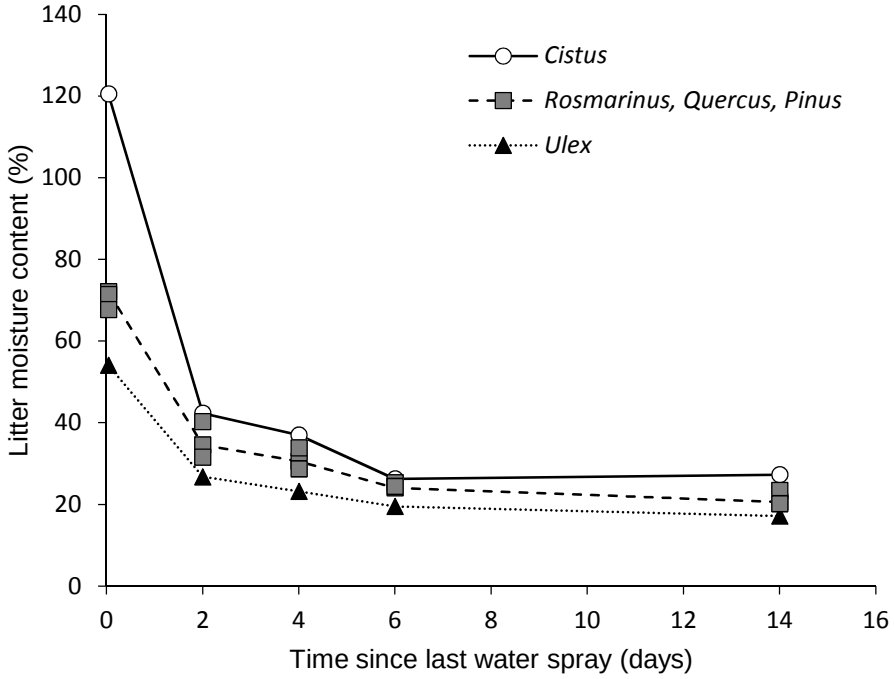

Figure A: Dynamics of litter moisture after rewetting. Since moisture of *Rosmarinus*, *Quercus* and *Pinus* litter was not significantly different at the beginning of desiccation dynamic, those three species are represented by the same symbol.

Table A: Litter mass loss (% of initial dry mass) of all treatment combinations (mean ±SE, n=5).

		Controls without litter	*Quercus/ Rosmarinus*	*Rosmarinus/ Ulex*	*Cistus/ Ulex*	*Cistus/ Pinus*	*Quercus/ Pinus*	Mean accross litter mixtures
Control without detritivore	humid	-	24.4±1.7	22.5±1.2	18.7±1.4	16.8±0.5	16.2±1.7	19.7±0.9
	dry	-	21.7±0.6	23.2±1.4	15.5±0.7	14.7±0.9	13.2±0.9	17.7±0.9
Armadillidium/Armadillo	humid	-	38.1±2.6	29.4±1.1	39.1±2.6	38.9±1.9	29±1.2	34.9±1.2
	dry	-	37.4±1.8	25.8±1.6	38.3±1.9	37.1±3.5	28.7±1	33.4±1.4
Armadillidium/Ommatoiulus	humid	-	43.6±1.4	39±2.6	48.5±1.4	44.5±3.4	30±2.3	41.1±1.6
	dry	-	47.2±2.3	33.5±2.5	41.4±2.3	43.1±2	30.2±2	39.1±1.6
Pomatias/Armadillo	humid	-	35.4±1.8	30±0.4	32.8±0.5	33.2±1.5	24.4±1.6	31.2±0.9
	dry	-	34.6±2.2	28.8±1.8	32.4±1	33.5±1	24.9±0.8	30.9±0.9
Glomeris/Ommatoiulus	humid	-	54.1±2.8	39.1±2.3	55.2±2.9	55.9±2	33.5±1.2	47.5±2.1
	dry	-	51.2±1.7	37.3±2.8	50.9±2.2	53.5±0.9	30.1±1.6	44.6±2
Pomatias/Glomeris	humid	-	47.5±0.9	34.8±2.8	54.7±1.6	49.3±2.1	29.4±1.2	43.1±2.1
	dry	-	41.7±2.2	34.4±1.7	46.1±2	45.5±1.2	29.2±1	39.4±1.5
Mean accross detritivore communities	humid	-	40.5±1.9	32.5±1.3	41.5±2.5	39.8±2.5	27.1±1.2	36.3±1.0
	dry	-	39±1.9	30.5±1.2	37.4±2.2	37.9±2.4	26.1±1.2	34.2±0.9

Table B: Leaching of dissolved organic carbon (mg of C per kg of soil dry mass) of all treatment combinations (means ±SE, n=5).

		Controls without litter	*Quercus/ Rosmarinus*	*Rosmarinus/ Ulex*	*Cistus/ Ulex*	*Cistus/ Pinus*	*Quercus/ Pinus*	Mean accross litter mixtures
control without detritivore	humid	0.3±0.06	3.6±0.18	3.1±0.20	1.7±0.16	2.4±0.24	2.6±0.28	2.3±0.21
	dry	0.6±0.18	3.3±0.30	3.3±0.44	2.0±0.14	2.4±0.21	2.4±0.18	2.3±0.19
Armadillidium/Armadillo	humid	-	3.5±0.12	3.3±0.22	1.6±0.12	2.1±0.15	2.7±0.32	2.6±0.17
	dry	-	4.1±0.19	3.4±0.14	2.1±0.15	2.5±0.16	3.0±0.20	3.0±0.16
Armadillidium/Ommatoiulus	humid	-	3.5±0.36	2.8±0.17	1.3±0.12	2.0±0.13	2.5±0.07	2.4±0.18
	dry	-	3.5±0.36	3.3±0.31	2.1±0.30	1.9±0.17	2.4±0.25	2.6±0.17
Pomatias/Armadillo	humid	-	3.6±0.11	2.7±0.26	1.8±0.14	1.8±0.13	2.3±0.25	2.4±0.15
	dry	-	3.5±0.18	2.8±0.28	1.9±0.08	2.1±0.25	2.4±0.22	2.5±0.15
Glomeris/Ommatoiulus	humid	-	3.3±0.20	3.0±0.23	1.4±0.12	1.4±0.08	1.9±0.19	2.2±0.18
	dry	-	3.1±0.29	3.4±0.26	2.0±0.31	1.9±0.21	2.4±0.15	2.6±0.16
Pomatias/Glomeris	humid	-	3.2±0.15	3.0±0.20	1.4±0.10	1.4±0.11	2.2±0.14	2.2±0.17
	dry	-	3.7±0.20	2.9±0.12	1.5±0.06	2.0±0.16	1.9±0.15	2.4±0.17
Mean accross detritivore communities	humid	-	3.5±0.08	3.0±0.09	1.5±0.06	1.9±0.09	2.4±0.10	2.4±0.07
	dry	-	3.5±0.11	3.2±0.11	1.9±0.08	2.1±0.08	2.4±0.09	2.6±0.07

Table C: Leachate aromaticity (l g^{-1}) of all treatment combinations (means ±SE, n=5).

		Controls without litter	*Quercus/ Rosmarinus*	*Rosmarinus/ Ulex*	*Cistus/ Ulex*	*Cistus/ Pinus*	*Quercus/ Pinus*	Mean accross litter mixtures
Control without detritivore	humid	16.4±2.1	13.3±0.7	10.4±0.4	14.0±0.4	11.7±1.0	14.8±0.6	13.0±0.4
	dry	14.2±0.6	12.3±1.0	10.9±0.9	15.2±0.8	10.0±0.4	14.3±0.7	12.5±0.6
Armadillidium/Armadillo	humid	-	13.6±0.5	11.8±0.9	13.6±0.7	11.4±0.6	14.9±0.9	13.9±0.6
	dry	-	12.5±0.3	10.4±0.4	13.9±2.0	10.6±0.7	14.9±0.8	12.7±0.6
Armadillidium/Ommatoiulus	humid	-	15.5±1.6	12.5±0.7	16.0±1.3	10.6±0.9	14.7±0.6	14.3±0.5
	dry	-	13.6±2.0	11.4±0.2	14.0±0.5	10.2±0.6	15.0±0.1	13.0±0.7
Pomatias/Armadillo	humid	-	13.8±0.4	13.7±1.1	13.8±0.9	12.1±1.2	16.1±0.6	13.9±0.5
	dry	-	13.0±0.4	11.3±0.5	14.0±0.2	10.9±0.8	16.1±0.7	13.1±0.5
Glomeris/Ommatoiulus	humid	-	15.2±0.7	12.7±0.5	15.8±1.1	11.5±0.9	16.2±1.1	13.4±0.5
	dry	-	14.8±1.3	12.5±0.3	12.1±3.4	10.7±0.8	14.5±0.5	13.0±0.5
Pomatias/Glomeris	humid	-	13.3±0.4	11.7±0.6	15.9±0.4	10.8±0.6	15.3±0.6	13.4±0.5
	dry	-	12.7±0.7	11.9±0.7	15.1±0.4	10.5±0.3	15.6±0.4	12.8±0.4
Mean accross detritivore communities	humid	16.4±2.1	14.1±0.3	12.0±0.3	14.9±0.4	11.3±0.4	15.3±0.3	13.7±0.21
	dry	14.2±0.6	13.1±0.5	11.4±0.2	14.1±0.6	10.5±0.2	15.0±0.3	12.9±0.21

TableD: Leaching of total dissolved nitrogen (mg of N per kg of soil dry mass) of all treatment combinations (means ±SE, n=5).

		Controls without litter	*Quercus/ Rosmarinus*	*Rosmarinus/ Ulex*	*Cistus/ Ulex*	*Cistus/ Pinus*	*Quercus/ Pinus*	Mean accross litter mixtures
Control without detritivore	humid	1.75±0.24	1.24±0.10	1.08±0.11	1.57±0.25	1.80±0.19	1.60±0.14	1.51±0.08
	dry	1.12±0.11	1.45±0.35	1.63±0.37	1.80±0.19	1.48±0.21	2.62±0.58	1.72±0.16
Armadillidium/Armadillo	humid	-	1.35±0.05	1.33±0.14	1.63±0.09	1.62±0.17	1.85±0.08	1.56±0.06
	dry	-	1.33±0.16	1.89±0.35	2.08±0.31	2.07±0.37	2.08±0.23	1.89±0.13
Armadillidium/Ommatoiulus	humid	-	1.38±0.21	1.24±0.12	1.78±0.26	1.34±0.18	1.88±0.20	1.53±0.10
	dry	-	1.28±0.11	1.64±0.35	1.62±0.14	1.25±0.25	2.00±0.46	1.56±0.13
Pomatias/Armadillo	humid	-	1.26±0.18	1.64±0.34	1.53±0.09	1.52±0.32	1.81±0.16	1.55±0.10
	dry	-	2.18±0.50	1.39±0.32	1.59±0.28	1.54±0.15	2.47±0.44	1.85±0.17
Glomeris/Ommatoiulus	humid	-	1.33±0.14	1.47±0.31	1.33±0.22	1.20±0.11	2.03±0.21	1.47±0.10
	dry	-	1.13±0.13	1.41±0.19	1.81±0.38	1.57±0.10	2.45±0.55	1.67±0.16
Pomatias/Glomeris	humid	-	1.16±0.11	1.24±0.10	1.18±0.07	1.19±0.09	2.13±0.18	1.38±0.09
	dry	-	1.01±0.12	1.28±0.17	1.64±0.21	1.55±0.24	1.85±0.24	1.47±0.10
Mean accross detritivore communities	humid	1.75±0.24	1.29±0.05	1.33±0.09	1.50±0.08	1.44±0.08	1.88±0.07	1.50±0.04
	dry	1.12±0.11	1.4±0.12	1.55±0.12	1.76±0.1	1.58±0.10	2.24±0.17	1.69±0.06

TableE: Substrate induced respiration of soil (µg of CO_2 per g of soil dry mass per hour) of all treatment combinations (means ±SE, n=5).

		Controls without litter	*Quercus/ Rosmarinus*	*Rosmarinus/ Ulex*	*Cistus/ Ulex*	*Cistus/ Pinus*	*Quercus/ Pinus*	Mean accross litter mixtures
Control without detritivore	humid	3.37±0.35	4.06±0.15	4.07±0.21	3.45±0.23	4.06±0.33	4.02±0.07	3.84±0.11
	dry	3.84±0.08	3.76±0.37	4.13±0.06	3.99±0.17	4.03±0.15	4.13±0.09	3.98±0.07
Armadillidium/Armadillo	humid	-	4.18±0.18	4.31±0.16	4.28±0.27	4.43±0.18	4.21±0.11	4.28±0.08
	dry	-	4.33±0.06	4.10±0.21	4.24±0.25	5.05±0.24	4.39±0.09	4.43±0.10
Armadillidium/Ommatoiulus	humid	-	4.37±0.21	4.37±0.20	4.61±0.14	4.27±0.32	4.24±0.06	4.37±0.09
	dry	-	4.87±0.14	4.62±0.27	4.64±0.23	5.01±0.17	4.44±0.15	4.70±0.09
Pomatias/Armadillo	humid	-	4.10±0.14	4.26±0.14	4.26±0.12	4.19±0.32	4.12±0.09	4.19±0.07
	dry	-	4.55±0.18	4.50±0.17	4.50±0.14	4.49±0.11	4.24±0.09	4.46±0.06
Glomeris/Ommatoiulus	humid	-	4.48±0.08	4.44±0.25	4.79±0.28	4.50±0.18	4.17±0.17	4.48±0.09
	dry	-	4.91±0.16	4.56±0.14	4.85±0.23	4.89±0.36	4.52±0.15	4.75±0.10
Pomatias/Glomeris	humid	-	4.51±0.39	4.50±0.13	4.60±0.14	4.49±0.17	4.20±0.23	4.46±0.10
	dry	-	4.39±0.12	4.63±0.15	4.61±0.14	4.77±0.11	4.22±0.23	4.52±0.08
Mean accross detritivore communities	humid	3.37±0.35	4.28±0.09	4.32±0.07	4.33±0.11	4.33±0.10	4.16±0.05	4.26±0.04
	dry	3.84±0.08	4.47±0.10	4.42±0.08	4.47±0.09	4.70±0.10	4.32±0.06	4.46±0.04

TableF: Potential cellulose decomposition (mass loss in % of initial dry mass DM) of all treatment combinations (means ±SE, n=5).

		Controls without litter	*Quercus/ Rosmarinus*	*Rosmarinus/ Ulex*	*Cistus/ Ulex*	*Cistus/ Pinus*	*Quercus/ Pinus*	Mean accross litter mixtures
Control without detritivore	humid	24.7±2.1	18.2±2.0	20.2±1.7	20.7±3.3	15.9±2.9	23.8±1.6	20.5±1.1
	dry	23.5±3.3	15.6±2.7	17.7±1.5	19.6±2.7	18.5±2.1	18.2±3.7	18.8±1.1
Armadillidium/Armadillo	humid	-	25.4±2.8	19.4±1.5	25.4±3.1	20.4±1.6	23.4±2.5	22.8±1.1
	dry	-	21.5±1.6	21.3±2.1	22.7±1.6	21.4±1.4	21.8±2.0	21.7±0.7
Armadillidium/Ommatoiulus	humid	-	23.8±2.5	24.4±2.6	25.8±2.8	17.9±3.2	22.0±1.3	22.6±1.2
	dry	-	19.5±1.8	19.6±2.3	24.8±3.5	18.2±1.8	17.2±1.5	19.9±1.1
Pomatias/Armadillo	humid	-	22.7±2.2	18.8±1.5	23.5±1.1	23.3±1.6	23.2±4.0	22.2±1.0
	dry	-	21.2±2.7	17.4±1.1	19.3±1.9	19.6±1.5	22.0±2.1	20.0±0.9
Glomeris/Ommatoiulus	humid	-	21.7±2.5	20.7±1.6	21.7±1.6	22.9±2.9	22.8±1.6	21.9±0.9
	dry	-	19.5±1.5	19.2±1.3	22.0±1.6	20.4±1.4	22.6±3.5	20.7±0.9
Pomatias/Glomeris	humid	-	21.0±2.7	18.8±2.1	20.7±2.1	20.5±1.7	27.7±2.8	21.7±1.1
	dry	-	17.6±2.7	19.7±2.2	24.0±3.0	22.3±2.6	22.3±3.6	21.2±1.3
Mean accross detritivore communities	humid	24.7±2.1	22.1±1.0	20.4±0.8	22.8±1.0	20.1±1.0	23.9±1.0	21.9±0.4
	dry	23.5±3.3	19.1±0.9	19.2±0.7	22.0±1.0	20.1±0.7	20.7±1.1	20.3±0.4

ANNEXE 3 : APPENDIX OF CHAPTER 4

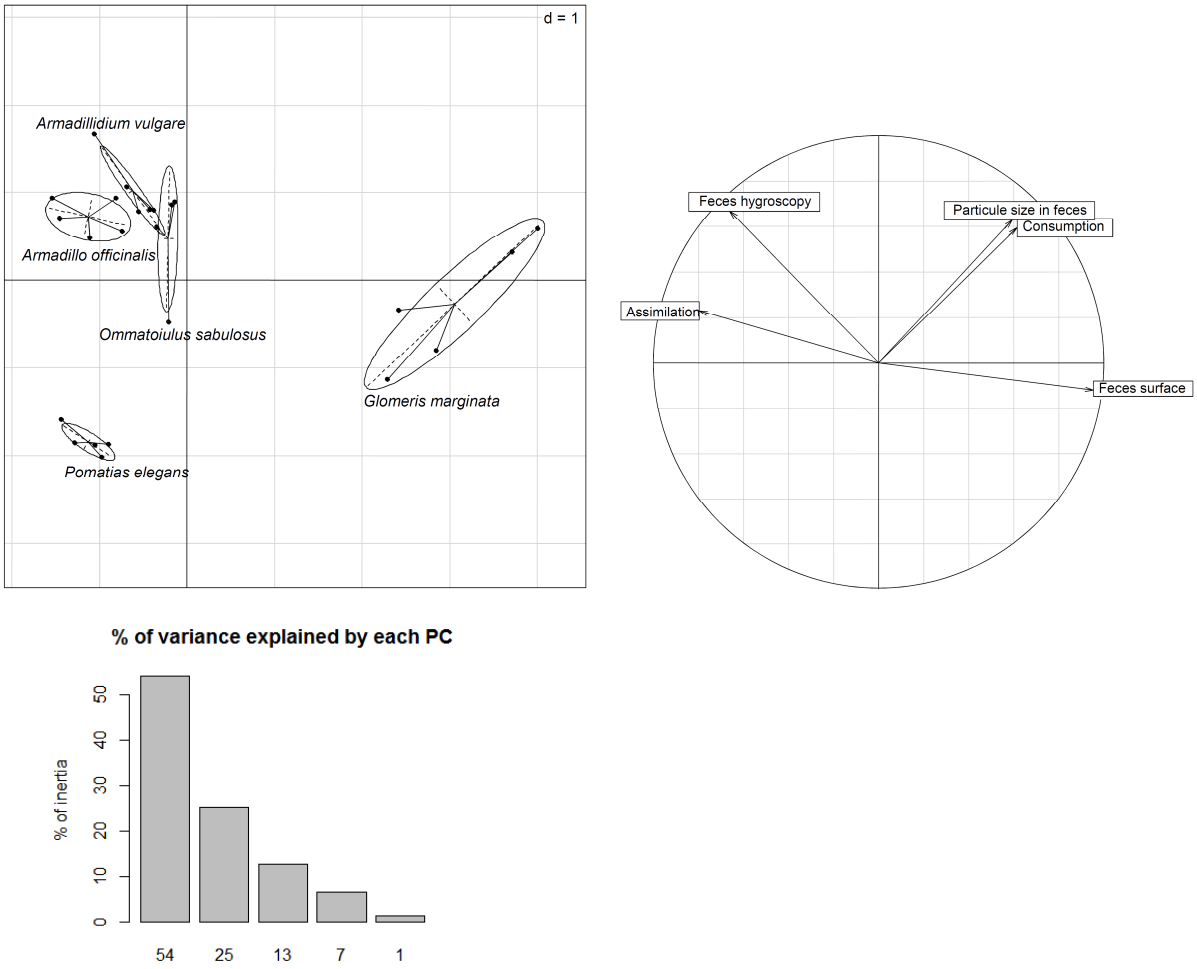

Figure A. Principal Component Analysis (PCA) for the five detritivore species used in the experiment. As detailed in the barplot, the first component account for 54 % of the variability and the second component for 25 %. Top left plot show the projection of detritivore species in functional trait space and plot on top right show the projection of variables, i.e. functional traits.