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# DYNAMIQUE D'ASSEMBLAGE D'UNE COMMUNAUTE DE MACROINVERTEBRES AQUATIQUES: IMPACTS DES INTERACTIONS, DE LA DERIVE, DE LA DISPERSION, DE LA PHENOLOGIE ET DES EFFETS DE PRIORITE

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PAR

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« *Notre Père qui êtes aux cieux*
*Restez y*
*Et nous nous resterons sur la terre*
*Qui est quelquefois si jolie* »
Jacques Prévert, Paroles, 1949

# AVANT-PROPOS

Ce mémoire contient un chapitre, présenté sous forme d'article scientifique, que j'aimerais soumettre sous peu. La contribution des auteurs est précisée par l'ordre d'apparition des auteurs dans la liste d'auteurs de l'article, sauf pour Christian Nozais qui apparaît en dernier en tant que directeur de recherche. Dominique Gravel a particulièrement apporté son aide pour ce qui est des analyses statistiques, en plus de ses commentaires sur l'ensemble du manuscrit. Christian Nozais et François Charles ont eu un rôle de supervision permettant une grande amélioration du mémoire.

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# RÉSUMÉ

L’assemblage des communautés est encore aujourd’hui un processus dont la structure n’est pas totalement comprise. Quelle est la part de déterminisme et de stochasticité, quels sont les processus impliqués, y en a-t-il qui prennent le dessus, sont autant de questions qui restent sans réponse. Dans cette étude, nous avons utilisé une approche expérimentale afin d’étudier l’assemblage des communautés. Nous nous sommes intéressés à la communauté de macroinvertébrés vivant en zone littorale d’un lac boréal. Cette communauté est en partie basée sur la litière de feuilles d’arbres de la zone riveraine. Les communautés vivant en lac et basées sur les détritus ont particulièrement été négligées dans les études précédentes. Cette étude avait deux objectifs. Dans un premier temps, le but était de confirmer la présence d’une certaine structure au sein de la communauté, et que l’assemblage n’était pas totalement aléatoire. Le second objectif était de déterminer si certains processus étaient dominants parmi les suivants lors de la dynamique d’assemblage des communautés : les interactions, la phénologie, la dérive, la dispersion, les effets de priorité. Notre première hypothèse était la suivante : les processus déterministes apportent une certaine structure à l’assemblage de la communauté. Notre seconde hypothèse était que les interactions seraient le processus dominant, et les réplicats auraient donc des compositions de plus en plus similaires au cours de l’expérience.

L’étude s’est déroulée au lac des Baies, dans l’Est du Canada. Pour répondre à nos objectifs, nous avons installés dans la zone littorale du lac des microcosmes renfermant de la litière. Deux dispositifs expérimentaux ont été utilisés. Le dispositif SR (Sequential Removal) a consisté à installer 24 microcosmes en zone littorale au mois de juin, puis les retirer par groupes de trois toutes les deux semaines jusqu’en octobre. Le dispositif SA (Sequential Addition) a consisté à installer trois microcosmes toutes les deux semaines durant l’été, puis tous les retirer en octobre. Le terme réplicat est utilisé ici pour désigner des microcosmes qui ont été installés et retirés aux mêmes dates. Les organismes ont été identifiés à la famille. Lorsque la durée d’immersion des microcosmes étaient inférieure à dix semaines, les dispositifs SR et SA ne se superposaient pas au niveau des dates. Par contre, à partir de dix semaines à jusqu’à 16 semaines, les dates d’immersion des deux dispositifs se superposaient de plus en plus.

L'influence des processus déterministes a été vérifiée. Un « *turnover* » dans la composition de la communauté était visible, et ce dans les deux dispositifs (Figures 4 et 5). Au sein du dispositif SR, la dissimilarité entre les réplicats était constante. Ainsi, les réplicats qui avaient passé deux semaines dans l'eau étaient autant similaires entre eux que les réplicats qui avaient passé plus de trois mois dans l'eau. Par contre, les microcosmes restés seulement deux semaines avaient des compositions vraiment différentes de ceux restés 16 semaines (figure 7a). Concernant le dispositif SA, les réplicats étaient de plus en plus similaires lorsque la durée d'immersion augmentait. Au sein des deux dispositifs, les réplicats étaient similaires à environ 60% après 4 mois d'expérimentation. Si les processus stochastiques avaient été les seuls à influencer l'assemblage des communautés, la disimilarité entre les réplicats aurait augmenté avec la durée de l'expérience, puisque la stochasticité et les effets de priorité amènent les communautés à se différencier, malgré un pool régional partagé. Or, dans aucun des deux dispositifs la dissimilarité n'a augmenté de manière significative avec le temps. De plus, les figures 4, 5, 7, ainsi que les abondances de certains groupes trophiques confirmaient la présence d'une succession au cours de l'expérience. La première hypothèse a donc été vérifiée. Au sein du dispositif SA néanmoins, la succession était moins évidente compte tenu du fait que ce dispositif ne suivait pas la saisonnalité. Cela influait donc sur le pool régional, et donc sur la capacité et la disponibilité des organismes à se disperser.

Concernant la prédominance d'un processus, les conclusions sont plutôt mitigées. Au sein du dispositif SR, la dissimilarité entre les réplicats était constance et en dessous de 0.5, (sauf pour deux valeurs). Ainsi dans ce dispositif, la durée d'immersion des réplicats ne modifiait pas leur similarité. Une plus grande durée d'immersion n'a pas amené les réplicats à se ressembler malgré le fait que les interactions avaient eu plus de temps pour se mettre en place. La phénologie semble donc avoir été le processus déterministe dominant durant l'assemblage de la communauté. Dans le dispositif SA, plus les réplicats étaient immergés longtemps, plus ils étaient similaires. Pour rappel, tous les microcosmes du dispositif SA ont été retirés à la même date en octobre, quelle que soit leur durée d'immersion. Si la phénologie était le processus dominant pour ce dispositif, la date de retrait (similaire pour tous les microcosmes) aurait amené les microcosmes à être tous similaires par leur composition. Or, malgré une même date de retrait, les microcosmes SA n'étaient pas généralement similaires (Figure 7b). Néanmoins, ceux qui avaient été immergés le plus longtemps étaient un peu plus similaires (Figure 6b). Cela fait ressortir le fait que la durée de l'expérience plutôt que les dates d'immersion a influencé l'assemblage de la communauté. Plus les interactions avaient le temps de se mettre en place dans le dispositif SA, plus les réplicats étaient similaires. Les microcosmes immergés plus de huit semaines avaient des périodes d'immersion en partie superposées entre les dispositifs SR et SA. Ces microcosmes ont donc subi partiellement les même événements phénologiques et facteurs environnementaux. Lorsque les microcosmes avaient passé moins de huit semaines dans l'eau, donc lorsque les dispositifs SR et SA avaient des dates d'immersion totalement différentes, les communautés SR et SA étaient plutôt dissimilaires (Annexe III). Une exception est à noter sur les microcosmes ayant été immergé deux semaines, puisqu'ils sont plutôt similaires. Une possibilité serait l'apport de litière qui aurait nécessité l'arrivée des premières espèces qui utilisent la litière. Lorsque les dispositifs avaient des dates d'immersion qui se superposaient (immersion supérieure à huit semaines), les communautés étaient davantage similaires. Pour une même durée d'immersion entre quatre et six semaines, les communautés du dispositif SR étaient vraiment différentes de celles du dispositif SA, ce qui confirme encore l'influence de la phénologie. La saisonnalité a donc eu un impact évident sur la dynamique d'assemblage de la communauté puisque les deux dispositifs n'ont pas subi les mêmes processus dans les mêmes mesures. Il ressort de cette étude que la phénologie et les interactions amènent les réplicats à se ressembler dans leur composition, sans jamais devenir similaires. Cela peut s'expliquer par les effets de priorité, la dérive et la dispersion qui peuvent avoir des impacts contradictoires avec les interactions et la phénologie dans le processus d'assemblage. Il semble y avoir un seuil de dissimilarité minimal, partagé par les deux dispositifs expérimentaux, qui appuie cette influence des processus stochastiques.

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# INTRODUCTION GÉNÉRALE

L’étude de la dynamique d’assemblage des communautés est un élément clef de l’écologie des communautés (Belyea et Lancaster 1999, Chase et Leibold 2003). Une communauté peut être définie comme des « organismes qui cohabitent et affectent leurs distribution et abondance respectives » (Connell et Slatyer 1977). L’assemblage des communautés est influencé par quatre processus fondamentaux : la dérive, la dispersion, la spéciation et la sélection (Vellend 2010). La spéciation et la dispersion amènent de nouvelles espèces aux communautés, tandis que la sélection et la dérive sont les processus qui influencent les abondances de ces espèces (Vellend 2010). La dérive représente les changements dans l’abondance des espèces, la spéciation est l’apparition d’une nouvelle espèce, et la dispersion définit le déplacement des individus dans l’espace (Vellend 2010). La spéciation ne sera pas développée dans cet article en raison de la durée trop courte de l’étude pour prendre un compte ce processus. Par sélection, Vellend (2010) résume les deux règles de la formation des communautés de Diamond (1975) : premièrement, le filtrage environnemental permet que seules les espèces adaptées aux conditions environnementales puissent s’installer. Ensuite, le principe d’exclusion compétitive fait en sorte que si deux espèces possèdent des niches trop similaires, elles ne pourront coexister, et une des deux espèces sera exclue (Gause 1934, MacArthur et Levins 1967). Les « *trade-off* » permettent la coexistence de certaines espèces, qui vont alors faire des compromis dans certaines dimensions de leur niche et éviter une trop grande ressemblance de celles-ci (Fargione et al. 2003, Kneitel et Chase 2004). Vellend utilise donc le terme de sélection pour résumer l’impact des interactions abiotiques et biotiques sur une espèce. Nous utiliserons dans cet article le terme d’interactions. HilleRisLambers et al. (2012) considèrent que les processus de dérive et dispersion agissent « en plus, et non à la place des facteurs environnementaux et des interactions biotiques qui influencent la composition et la structure des communautés locales », soit les deux règles de Diamond évoquées auparavant (1975). Il est aussi important d'inclure la notion de phénologie d'après Lieth (1974) : « la récurrence des événements biologiques, les causes de leur récurrence selon les forces biotiques et abiotiques, ainsi que les interrelations entre les phases de certaines espèces ». La phénologie influence la capacité de dispersion des organismes ainsi que les effets de priorité, par des phénomènes tels que l'émergence par exemple, ou les période de reproduction.

Le déterminisme et la stochasticité, à travers différents processus, influencent l'assemblage de la communauté, et le nouveau défi est de «  placer les communautés le long d'un continuum entre les deux extrêmes » (Gewin 2006, Vellend et al. 2014). En effet, plus notre compréhension des processus sera fine, plus les modèles des écosystèmes seront précis et efficaces. Dans un contexte de perte de biodiversité, il est important de pouvoir comprendre le fonctionnement actuel des communautés, et prévoir une probable modification de ce fonctionnement, et ses conséquences. Les interactions représentent l'adaptation déterministe des espèces (Vellend 2010). Tout comme la sélection, la phénologie est déterministe d'après sa définition par Lieth (1974). Il est plus délicat de classifier la dispersion et la dérive en tant que processus totalement stochastiques. Y a t-il vraiment un événement qui arrive seulement par hasard ? Ou bien manquons-nous d'informations pour expliquer cet événement ? Afin de clarifier notre utilisation du terme, nous préciserons la définition suivante : « une variable est stochastique par rapport à une autre » (Vellend et al. 2014). La dérive, d'après Vellend (2010), est stochastique. Lorsque l'on parle de dérive stochastique, il s'agit en fait de stochasticité démographique, soit «  un changement aléatoire dans les abondances relatives des espèces locales » (Hubbell 2001, Vellend et al. 2014). La dispersion est généralement reconnue comme un des principaux processus à l'échelle régionale influençant l'assemblage des communautés (Davis et al. 2005). Si la dispersion limitée signifie que certains facteurs déterminent l'échelle à laquelle les espèces interagissent,  la stochasticité rentre en jeu lorsque les espèces se déplacent d'un

« pool » à un autre. La dispersion dépend directement de la disponibilité des organismes et donc de la phénologie, ce qui ramène ici une part de déterminisme. La dispersion a donc une composante déterministe, et une composante aléatoire. Il est aussi intéressant de prendre en compte la notion d'histoire dans l'assemblage des communautés. En effet, en intégrant un nouvel habitat, les espèces modifient leur environnement, et le rendent plus ou moins optimal pour d'autres espèces déjà installées ou potentiellement colonisatrices. Les effets de priorité représentent le fait que l'ordre dans lequel les espèces arrivent influence la composition finale d'une communauté. Par exemple, un prédateur installé sera peut être en mesure de s'imposer face à un compétiteur nouvel arrivant, alors qu'il n'aurait pas pu coloniser durablement l'environnement si son compétiteur avait déjà été présent. En fonction de tous ces critères, la niche d'une espèce pourrait donc être disponible mais non utilisée.

Environ 90% de la production primaire globale terrestre est consommée sous forme de détritus (Gessner et al. 2010). Les détritus peuvent être autochtones (dans cette étude provenant du lac tels que les fèces, organismes morts), ou allochtones (provenant de la zone riveraine comme les feuilles d'arbres tombées suite à l'abscission) (Webster et Benfield 1986, Wetzel 2001). Les détritus allochtones sont une ressource trophique non négligeable pour les macroinvertébrés, et ce particulièrement dans les lacs oligotrophes où la production primaire est limitée (Gasith et Hasler 1976, France 1995). De plus, ils sont aussi un habitat important pour certaines espèces, et jouent un rôle dans la productivité de la communauté de macroinvertébrés (Anderson et Cummins 1979, Bohman et Hermann 2006, Cummins et Klug 2009, France 1995, Mancinelli et al. 2005, Pope et al. 1999). Les trois étapes de décomposition des apports allochtones sont les suivantes : perte des éléments solubles, colonisation par le monde microbien, et enfin colonisation par les macroinvertébrés (Varga 2003). En commençant à dégrader les feuilles, les bactéries et hyphomycètes rendent la feuille plus « digeste » pour les macroinvertébrés détritivores, et principalement les déchiqueteurs (« *shredders* ») (Cummins et al. 1989, Irons et al. 1994, Pope et al. 1999). Ces déchiqueteurs sont surtout représentés par les arthropodes en milieu lacustre, dont l'espèce d'amphipodes *Hyalella azteca*. Il a été montré que les déchiqueteurs ne colonisent pas ou peu les feuilles non colonisées par les micro-organismes (Petersen et Cummins 1974). Les déchiqueteurs effectuent ce qu'on appelle le processus de « facilitation » : en consommant la matière détritique de taille grossière, ils la fragmentent en particules inférieures à 1 mm, qui pourront alors être utilisées par les collecteurs (Bedford 2004, Bohman et Herrmann 2006, Cummins et Klug 1979, Cummins et al. 1989, Mancinelli et al. 2007, Pope et al. 1999). Finalement, les prédateurs présents en zone littorale lacustre sont principalement représentés par les larves d'odonates et de plécoptères (Cummins et Klug 1979, Peckarsky et al. 1990). L'assemblage de la communauté des macroinvertébrés ne dépend pas seulement du régime trophique des espèces présentes, et les données empiriques montrent des grandes variations dans les processus d'assemblage des communautés (Lawton 1999).

L'influence de la stochasticité et du déterminisme sur la composition d'une communauté a déjà été étudiée. Chase (2003, 2007, 2010) a montré lorsque les conditions dans un habitat sont rudes (petit « *pool* » régional, forte dispersion, faible productivité et fort taux de perturbation), l'influence de la sélection en raison de la niche des espèces est forte, les processus déterministes sont donc les plus influents et les communautés subiront les mêmes « *turnover* », amenant à une même composition finale. Au contraire, lorsque les conditions environnementales sont moins contraignantes (nombreuses espèces dans le « pool » régional, forte productivité, faible taux de perturbation), les compositions finales des sites seront plutôt divergentes. En effet, dans ce cas, la dérive et les effets de priorité seront les processus les plus influents, et la stochasticité aura plus d'impact que le déterminisme (Chase 2007). Pope et al. (1999) ont étudié la composition d'une communauté d'invertébrés basée sur les détritus dans la zone littorale d'un lac canadien. Les collecteurs étaient les plus nombreux, tandis que les déchiqueteurs étaient plutôt rares. Cela reflète la double utilisation des détritus, comme ressource et habitat. La colonisation, la productivité et la composition de la communauté sont particulièrement influencées par le type de détritus, leur morphologie et leur texture en tant que substrat, ou encore leur composition chimique qui reflète leurs propriétés nutritives (pourcentage de lignine, ratio C/N/P) (Frainer et al. 2015, Handa et al. 2014, Lecerf et al. 2007, Cummins et Klug 1979, Gessner et al. 2010, Petersen et Cummins 1974, Varga 2003). De plus, considérant que la litière allochtone est une ressource éphémère, son absence ou sa rareté représente une forte perturbation pour la communauté. Ainsi, la litière, si elle est limitante, peut amener des conditions environnementales difficiles et amener les processus déterministes à être les plus influents lors de l'assemblage de la communauté. Son abondance pourrait aussi amener des conditions environnementales favorables, et les processus stochastiques pourraient prendre le dessus sur la dynamique d'assemblage de la communauté.

La colonisation de la litière a souvent été étudiée en milieu lotique, mais « ignorée dans les lacs » (Pope et al. 1999). Chaque hiver, la zone littorale d'un lac boréal est touchée par le gel, ce qui représente une perturbation majeure pour les communautés résidentes, et particulièrement la communauté des macroinvertébrés (Connell et Slatyer 1977). Une communauté locale, comme celle des macroinvertébrés en zone littorale lacustre, est formée lorsque des espèces d'un « pool » régional colonisent un nouvel habitat et s'y installent assez longtemps pour que des interactions se mettent en place (HilleRisLambers et al. 2012). En raison des conditions abiotiques trop rudes, la communauté est amenée à quitter cette zone, et doit à chaque printemps se réapproprier le lieu. Chaque année, le phénomène d'assemblage des communautés se déroule de nouveau. Encore aujourd'hui, l'écologie des communautés reste un sujet compliqué, et beaucoup de questions demeurent sans réponse concernant l'assemblage des communautés. Dans un contexte de perte de biodiversité, il est primordial de mieux comprendre cet assemblage, et quels processus l'influencent. Quels sont les processus impliqués, quels sont les plus influents, comment agissent-ils sur la communauté sont autant de questions d'actualité (Chase 2007, Gewin 2006, HilleRisLambers et al. 2012, Pope et al. 1999, Vellend et al. 2014).

## Objectifs de l'étude

Le but général de cette étude est de décrire la dynamique d'assemblage d'une communauté de macroinvertébrés dans la zone littorale d'un lac boréal, et de distinguer les impacts respectifs des processus déterministes et stochastiques sur l'assemblage.

Le premier objectif est de vérifier si l'assemblage de la communauté est influencé par les processus déterministes. Nous prévoyons qu'il y a effectivement une structure dans le changement de communauté, et que l'assemblage n'est pas totalement aléatoire. Pour vérifier notre hypothèse, plusieurs microcosmes contenant des feuilles d'arbres et entourés de filets ont été immergés pour différentes périodes au long de l'été 2014. Deux dispositifs sont à distinguer, en fonction des dates d'immersion (Figure 1). Le dispositif SR (Sequential Removal) consiste à immerger les microcosmes en début de saison, et les retirer par groupes de trois toutes les deux semaines jusqu'en octobre. Le dispositif SA (Sequential Addition) consiste à immerger les microcosmes par groupes de trois toutes les deux semaines, puis tous les retirer en octobre. Les organismes présents ont été identifiés à la famille. Les changements de composition de la communauté ont été analysés dans les deux dispositifs à l'aide de RDA.

Notre deuxième objectif consiste à comprendre s'il y a un processus dominant lors de l'assemblage de la communauté. Nous prévoyons que les interactions seront le principal processus impactant l'assemblage de la communauté, et qu'ainsi les réplicats convergeront vers une même composition avec le temps. L'évolution de la composition entre différents microcosmes a été étudiée. Plus particulièrement, l'évolution de la dissimilarité entre les réplicats de microcosmes au long de l'expérience permettra de faire ressortir la dominance de la phénologie ou bien des interactions.

# ASSEMBLAGE DYNAMICS OF AN AQUATIC MACROINVERTEBRATE COMMUNITY: THE IMPACTS OF INTERACTIONS, DRIFT, DISPERSION, PHENOLOGY AND PRIORITY EFFECTS

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## 1.1 ABSTRACT

It is still unclear how community assembly dynamics are influenced by different processes such as drift, dispersal, priority effects, phenology, and interactions. Even though both deterministic and stochastic processes are important, their relative influence has not been "quantified". In this study, we assessed whether deterministic processes, especially biotic interactions and phenology, were the main drivers of the litter-based community of macroinvertebrates in the littoral zone of lakes. The study took place in a boreal lake in Eastern Canada. Two different sampling designs were used in order to highlight impacts of different processes. The first sampling design consisted in 24 microcosms deployed in the littoral zone at the beginning of summer (SR design). Then, every two weeks, three replicates microcosms were removed. This design follows the seasonality. The second design (SA) consisted in the opposite: every two weeks during summer, three microcosms were put in the littoral zone, and they were all removed in October. In both designs, a turnover occurred in the communities' compositions. Microcosms that spent two weeks in water had really different compositions from replicates that spent 16 weeks. In SR design, macroinvertebrates richness was slightly positively correlated to the time microcosms spent in water. Abundance did not vary with time, and dissimilarity between replicates was constant. In SA design, richness and abundance were increasing with the duration of the experiment, and replicates were getting more similar. If only stochastic processes were involved, dissimilarity would have increased between replicates, in both designs. That was not the case here. It is clear that some deterministic processes are involved in community assembly. It was not possible though to assess a dominant process in both designs. In SR design, the dissimilarity between replicates was constant among the experiment. The duration of experiment had no influence on similarity between replicates. In this design, interactions did not bring more similarity through time. In SA design, replicates were more similar through duration of experiment. Moreover, in SA design, all microcosms had been removed the same day, and were not all similar though. Then, the date of removal was not the main criteria for a shared community composition. In SA design, impact of interactions seemed to be more important than phenology. Our two designs sent opposites signals, and it is then impossible to have a general conclusion. Finally, we looked at similarity between microcosms of both designs. After 2 weeks of immersion, even though SR and SA microcosms did not share immersion dates, they were quite similar. This could be explained by the fact that in both designs, the first species to use the litter did colonize the new leaf litter, which was necessary to the rest of the community. For four and six weeks of immersion, SR and SA designs still did not share immersion dates, and communities were really dissimilar even though they shared their immersion duration. It seemed in this case that phenology was more influent than interactions. From ten to sixteen weeks of immersion, SR and SA design were more similar with duration. Their immersion dates did superimpose more and more though. It is then difficult to distinguish interactions and phenology influences. Our study has shown that the community assembly underwent a directional change driven by deterministic processes. In both designs, the replicates were around 60% similar at the end of experiment. It is concluded that interactions and phenology were the primary drivers for community assembly, but dispersal, drift and priority effects probably prevented the replicates from getting more similar.

Key words: Community ecology, biotic interactions, phenology, priority effects, community assembly, aquatic macroinvertebrates, lakes

## 1.2 INTRODUCTION

Almost twenty years ago, Lawton (1999) called community ecology “a mess”. Indeed, ecological communities are very complex to study, and it is still a challenge to understand how different processes are involved in community assembly, what are the main drivers, and how important is their influence (Chase 2007, Gewin 2006, HilleRisLambers et al. 2012, Pope et al. 1999, Vellend et al. 2014). A community is defined as “the set of organisms that occur together and that significantly affect each other’s distribution and abundance” (Connell and Slatyer 1977). Local communities are formed when species from a regional pool colonize and interact, a process also known as community assembly (HilleRisLambers et al. 2012). The first step in community assembly in a detritus-based community is the colonization of detritus by microbes, such as bacteria and fungi (Pope et al. 1999). By “conditioning” the leaves, microbes make them available for shredders, which in lakes are dominated by amphipods (Cummins et al. 1989, Irons et al. 1994, Pope et al. 1999). Shredders then facilitate other organisms as they reduce the litter in small fragments of leaves (smaller than 1 mm) on which collectors can feed (Bedford 2004, Bohman and Herrmann 2006, Cummins and Klug 1979, Cummins et al. 1989, Mancinelli et al. 2007, Pope et al. 1999). Finally, the main invertebrate predators found in the littoral zone in lakes are Odonata and Plecoptera larvae (Cummins and Klug 1979, Peckarsky et al. 1990). The detritus-based community is thus clearly influenced by a bottom-up, sequential food web assembly. Even if we do have a good knowledge of the main path of assembly, empirical data still show high variability in the community assembly dynamics (Lawton 1999).

Vellend (2010) proposed four fundamental processes driving community assembly: drift, dispersal, speciation and selection. Speciation and dispersal introduce new species to communities, while selection and drift set their abundance. Vellend (2010) interprets selection as “ deterministic interactions among species and their environments” and uses it as a synonym of the niche. We will then use “interactions” to talk about selection as defined by Vellend (2010). Interactions, such as predation, competition, facilitation, mutualism and so on, are deterministic processes and might reflect whether there is a bottom-up or a top-down control in the food web along the community assembly. Speciation will not be discussed here because the timescale of the study is too short to measure its impact. Drift is a stochastic process, as defined by Hubbell (2001): when birth and death events occur randomly with respect to species identity. Dispersal is stochastic but might be influenced by phenology and be partly predictable. HilleRisLambers et al. (2012) considered that drift and dispersal "operate in addition, not instead of, the environmental factors and biotic interactions that influence the composition and structure of communities at local scales". Deterministic processes are then the main drivers, and community assembly is mostly driven by two rules: the species that disperse and colonize a given location must be adapted to the abiotic conditions, and their niche must be available (Diamond 1975). Thus, community assembly will lead to a certain community composition (Drake 1990). Historical contingencies also have a strong impact on community assembly, mainly because of priority effects, which represent the fact that order in which species colonize a habitat influences the final community composition (Fukami 2010, Vellend et al. 2014). Finally, phenology as defined by Lieth (1974): "timing of recurring biological events, the causes of their timing with regards to biotic and abiotic forces, and the interrelation among the phases of same or different species", is the last constraint we will take into account in this study. Indeed, phenology directly influences community assembly by impacting dispersal and priority effects because colonisation depends on seasonality. In this paper, the primary events that we refer to by phenology are mainly emergence phenomenon and dispersal capacity.

Chase studied the influence of stochasticity and determinism on community assembly following the publication of the neutral theory (2003, 2007, 2010). He has shown that deterministic processes mostly influence the community composition when the ecological filters are strong (small species pool, high level of dispersal, low productivity and high rate of disturbance) and lead to a strong "niche-selection filtering out". Conversely, when ecological filters are almost absent (large species pool, high productivity, low rates of disturbance for example), ecological drift and priority effects would be the primary processes involved. Thus, if there are no strong competitors, community assembly would mostly be driven by stochasticity, and there would be a low similarity between final community compositions (Chase 2007). The importance of deterministic processes might reflect how strong are ecological filters (Gravel et al. 2011).

In boreal lakes, the littoral zone freezes every winter, which is a major disturbance for the detritus-based macroinvertebrates community living in this area and leads succession to stop and start over again each year (Connell and Slatyer 1977). This community partly relies on riparian vegetation for food, which is available at abscission during fall, and when the snow melts and brings leaves to the lake during spring. In this context, how do biotic interactions, the phenology of organisms, dispersion, drift and priority effects combine to influence community assembly? The colonization of leaf litter has been studied in streams and rivers, but “ignored in lake systems”. Pope et al. (1999) studied the leaf litter-based invertebrate community composition in the littoral zone of a Canadian lake. Collectors were the main functional-feeding group and shredders were scarce, which means that in the community, leaf litter was more used as a habitat and after facilitation, than as a direct food resource by shredders. When used as a food resource, leaf litter quality, quantity and composition directly influenced invertebrates’ productivity (Frainer et al. 2015, Handa et al. 2014, Lecerf et al. 2007). Knowing that leaf litter from riparian vegetation is an ephemeral resource/habitat, and considering ice at the surface of the lake during winter, communities in lakes never reach a certain community composition equilibrium, and undergo a constant assembly dynamics.

In this study, our objective was to describe the assembly dynamics of lake littoral macroinvertebrates communities. We asked whether there is any directional change in community composition through time, and which process is the main driver of community assembly? To answer these questions, microcosms were immerged at different dates and for different durations in the littoral zone of a lake. Two different sampling designs were established (Figure 1). Richness, abundance, and similarity between microcosms among the experiment were measured. To answer the first question, we compared the change in community composition of microcosms through time using Redundancy Analyses (RDA). We predicted that there would be a directional change in the community composition along the summer, reflecting the fact that deterministic processes drive community assembly. To answer the second question, we measured the changes in dissimilarity between microcosms through time. We predicted that interactions would lead to a similarity increasing in community composition as time goes on.

## 1.3 MATERIAL AND METHODS

### Study site and field sampling

The experiment took place in Lac des Baies, Eastern Québec, Canada (48° 10' 44.00" N, 68° 39' 44.00" O). The lake of 569.8 hectares is oligotrophic, and surrounded by boreal forest with deciduous and evergreen trees.

Fallen leaves of red maple (*Acer rubrum*) were collected on the ground at the same place, just after abscission during Fall 2013 and air-dried. 1 gram (± 0.001 g) of dry leaves (equivalent to 1 to 3 entire leaves) was put in microcosms (9 cm diameter, and 12.5 cm length, with a mesh size of 5 mm). The mesh size was chosen so all the invertebrates that inhabit the lake could colonize the leaves (except maybe some gasteropoda), and fish could not penetrate the microcosms. 1m$^2$ frames were built, and 3 microcosms were attached to the corners of each frame. All the frames were weighted and deployed on the substrate, parallel to the shoreline and at a 3 meters distance to each other's, at a depth of 2 meters. Microcosms were removed individually from the frame and put in a plastic bag directly underwater so no invertebrates could escape. Frames were deployed and removed at different dates depending on the designs.

The first sampling design, referred as the sequential removal SR (Figure 1), consists of 8 frames (24 microcosms in total) that were deployed in the littoral zone the 18th June 2014. One frame (made of three replicates microcosms) was randomly removed every two weeks, between July and October 2014. The last microcosm was taken out on October 8th. This design allows assessing whether community composition converge over time to a shared composition through replicates, as a result of deterministic processes, and especially interactions. The second design, referred as the sequential addition SA, consists of 8 frames (24 microcosms at first, but one replicate was lost from the frame set the 27th of August) added sequentially at a two weeks interval from June 18th until September 25th. All SA microcosms were removed on the 8th of October. The SA design allows assessing whether different microcosms have the same community composition if there are removed together with no regarding to the amount of time they spent in the water. SA design allows highlighting the influence of phenology. Combining SR and SA designs, there is a total of 44 microcosms since they share three replicates immerged the June 18th and removed the 8th of October. Looking at both designs also allows highlighting the influence of interactions and phenology. Some microcosms did share they immersion duration, some did share their removal dates, some did share their immersion dates… Our two designs allowed us to build different combinations.

## Laboratory analyses

Back in the laboratory, the content of the plastic bag was put on a 250µm mesh. Leaves were rinsed to collect organisms possibly hidden in it. All organisms were stored in alcohol 95% for later identification.

All organisms have been identified to family except *Ostracoda* and *Oligochaetes* because of the difficulty to identify morphological traits at the family level (Brousseau et al. 2016, McCafferty 1983, Merritt et Cummins 1996, Peckarsky 1990, Thorp et Covich 2009). Similarly, *Hydrachnidia* were not identified at the family level because the classification of families is still unclear (Thorp et Covich 2009). To measure abundance, all the organisms found in the microcosms were taken into account even if they were identified only to the order level. Young instars of *Ephemeroptera* and *Trichoptera* difficult to identify were not taken into account for the data analysis as they could have biaised the results. Different stages of a same family have been taken into account as long as they do not share the same niche (Brousseau et al. 2016). For example, *Copepoda nauplii* and different pupas were taken into account separately (Appendix I). Pupas do not feed and are less active though (Merrit et Cummins 1996): wings, legs, antennae and eyes are for some species not functional yet. The cocoons of *Glossiphonidae* have also been considered, as they might be a prey, even though no evidence was found in the literature.

## **Data analysis**

### *Change in community composition and influence of processes*

Redundancy analyses (RDA) were used to assess whether there is a directional change in composition over the duration of the experiment. The dependent variable was the number of weeks spent by microcosms in the water. All abundance data was Hellinger-transformed (Legendre and Legendre 2012) using the *vegan* package in R (Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., et Suggests, M. A. S. S., 2007).

Dissimilarity was measured with Hellinger distance to assess whether the replicates get more similar through time and show the influence of deterministic processes. Hellinger distance was chosen because it prevents double-zero to appear as similarity in compositions. Dissimilarity was measured independently for the two datasets. Dissimilarity was first measured on the microcosms that were set at the same date (SR dataset), and then on the microcosms that had the same withdrawal date (SA dataset). For each dataset, dissimilarity was measured in between two replicates, so microcosms that were in the same frame. This way, we could compare the dissimilarity for microcosms that spent the same amount of time in water under the same abiotic variables, at the same time of the year. Then, once again for each dataset, dissimilarity was measured between microcosms that have spent a different number of weeks in water. The functions *decostand*, *dist,* and *stack* from package vegan (Oksanen et al., 2007) were used to measure the distance between the composition of microcosms and time intervals. A linear regression was done on dissimilarity values between replicates to assess whether dissimilarity significantly change through duration of experiment. Finally, a PCoA was done on the 44 microcosms composition (SA and SR designs combined) with a Bray-Curtis distance to assess whether the two data set compositions were getting more similar through time.

All statistical analyses were performed using the R software, version 3.2.2 (The R Foundation for Statistical Analyses 2015).

## 1.4 RESULTS

### Richness and abundance

In the 24 microcosms of the SR design, 5576 invertebrates belonging to 35 different taxa and stages were found. Abundance increased during the first four weeks of the experiment. The microcosms containing the largest densities were taken out of water after four and six weeks of experimentation (removed the 16th and 30th of July) with 418 and 479 individuals respectively. Between six and sixteen weeks of experiment, abundance decreased and reached between 111 and 146 individuals per microcosm after 16 weeks in water (removed the 8th of October). Taxonomic richness reached maximums after six, twelve and sixteen weeks of immersion (Figure 2). A low peak occurred after eight weeks (removed the 13th of August), but for only two of the three replicates. All the microcosms contained between 10 and 20 different taxa, except one microcosm removed the 8th of October that contained 23 taxa and was dominated by *Ephemeroptera* and *Trichoptera*. The correlation between richness and the date of removal was weak ($R^2_{adj}$=0.13) but significant (p=0.045, $F_{1,22}$ = 4.518) (Figure 2). There was no significant correlation between total invertebrate abundance in the microcosms and the time spent in water ($R^2_{adj}$=0.06).

In the 23 microcosms of the SA design, 2505 invertebrates belonging to 28 different taxa and stages were found. The microcosms with largest densities were taken out after eight and fourteen weeks (respectively added the 13th of August and the 2nd of July). All the microcosms contained in between nine and 17 different taxa, except one microcosm containing 22 different taxa, mostly with more *Ephemeroptera* taxa. Abundance and specific richness increased linearly during all the experiment. The correlation between richness and setting date was strong ($R^2_{adj}$=0.57) and significant ($p<0.001^{-5}$, $F_{1,21}$ =28.31) (Figure 3). Similarly, total abundance and time spent in water were also strongly correlated ($R^2_{adj}$=0.47, $F_{1,18}$=18.04, p<0.001).

*Chironomidae* was the most abundant family. They were present in all the microcosms and represented more than 30% of the total abundance in 23 out of the 44 microcosms (dataset SR and SA combined). *Cladocera, Ephemeroptera,* and *Copepoda* were the most abundant orders. The combined abundances of *Cladocera*, *Ostracoda*, *Chironomidae* and *Ephemeroptera* ranged from 43 to 79% of the total abundance in the SR design, while it ranged from 70 to 91% of the total abundance in the SA, except for one microcosm where it summed to 52%.

In the SR dataset, the abundance of shredders (*Hyalellidae, Leptoceridae, Phryganeidae*) was the highest in the microcosms that spent less than six weeks in water (between 5 and 12% of the total abundance). Their relative abundance was always under 5% in microcosms that spent six weeks or more in water but slightly increased in the last weeks of the experiment. The abundance of collectors increased for the first six weeks of the experiment and decreased for the next ten weeks. Their relative abundance in microcosms was always higher than 73% though. Predators were always present. Their relative abundance was always under 5% except in microcosms that spent 16 weeks in water (between 5% and 8%). In the SA dataset, only two families were found as shredders: *Hyalellidae* and *Leptoceridae.* They were absent in six out of the 23 microcosms. Their highest relative abundance was in the microcosms that spent 8 weeks in water, and reached 6%. The relative abundance of collectors was always above 76%, and their abundance always increased through the experiment. Predators never represented more than 8% of the total abundance and were absent in two microcosms (after two and six weeks in water).

## Change in community composition and influence of processes

Both RDA with SR and SA dataset showed a systematic turnover of composition over the course of the experiments (SR dataset: $R^2_{adj}$ = 0.10, p=0.001, $F_{(1,22)}$= 3,594, figure 4 ; dataset SA :$R^2_{adj}$ = 0.099, p=0.001 $F_{(1,21)}$= 3,439, figure 5). The first axis of the RDAs represented the only environmental variable, the duration of the experiment (figures 3 and 4). The dissimilarity among replicates was low (between 0.2 and 0.5) and quite constant over time for the SR design (Figure 6a). Only two pairs of replicates had dissimilarity values over 0.5: one pair of microcosms that spent two weeks in water, and one pair of microcosms that spent 16 weeks in water. In the SA dataset, the dissimilarity between replicates was negatively correlated to the time replicates spent in water ($R^2_{adj}$= 0.19, p=0.023, $F_{1,20}$ = 6.04). The highest dissimilarity occurred between replicates installed the 10th of September (so after four weeks spent in water as all SA microcosms were removed the 8th of October), and the lowest one between replicates put on the 2nd of July (14 weeks of experiment, Figure 6b). In both designs, the dissimilarity between pairs of microcosms increased with the removal time interval in the pair of microcosms (Figure 7). All the pairs of microcosms with the maximum removal time interval (14 weeks) had a dissimilarity higher than 0.6.

SR and SA microcosms immerged for two weeks were quite similar, even though they had different immersion dates (Appendix II). SR and SA microcosms immerged for four and six weeks were really dissimilar. They did not share their immersion dates. For SR and SA microcosms that spent eight weeks and more immerged, they were more similar through duration of experiment. The more they were immerged, the more they shared their immersion dates.

## 1.5 DISCUSSION

The objectives of the study were to assess whether there was a directional change in community composition through time, and to identify which process was the primary driver, if there was one. We hypothesized that whatever the design (SR and SA), there would be a directional change through time reflecting the fact that deterministic process were the primary drivers. We also hypothesized that interactions would be the primary driver. Indeed, HilleRisLambers et al. (2012) considered that drift and dispersal "operate in addition, not instead of, the environmental factors and biotic interactions that influence the composition and structure of communities at local scales".

To understand the conclusions of this study, we first have to explain how to interpret the different results we could have had. Interactions are a process that lead replicates to be more similar through time, and sometimes can even lead to a certain final state. In a design, if replicates' compositions get more similar through time, it would mean that the more replicates had spent time in water, the more the communities were similar. In this case, the duration of the experiment would be the criteria for similarity increasing, and through time, the same interactions would have settled in the replicates, which would have driven the community assembly to be more similar. On the opposite, if replicates would get less similar through time, it would mean that stochastic processes and priority effects had driven the community assembly.

Second, if two microcosms spent the same amount of time in water, at different times of the year, and their compositions are similar, it would mean that interactions were the primary driver of the community assembly. Indeed, compositions would not depend on phenology events, and seasonality would not influence compositions. If these same microcosms had different compositions, it would mean that interactions were not the primary driver, because the same duration in water did not led to a shared composition.

If microcosms that had spent different durations in water, but were removed at the same time, had the same composition at the remove date, then phenology would have been the primary driver because removal date (and not the duration) would have been the primary driver. Finally, if these same microcosms had different compositions, it would mean that phenology was not the primary driver, because the same remove date did not lead to a shared composition.

Our study has shown that through the 16 weeks of the experiment, the two sampling designs (SR and SA) underwent directional changes mainly driven by deterministic processes. It is interesting to notice that our design allowed comparing compositions of microcosms that spent the same amount of time in the water but not at the same time of the year. The influence of interactions was more evident in the SA design. Indeed, replicates went more and more similar through duration of experiment. Moreover, though all SA microcosms were removed the same day, they did not all share a similar composition (Figure 7b). It seems thus that interactions were the primary driver for community assembly in SA design, and priority effects, drift and dispersal could explain that replicates were not perfectly similar. In this case, our data support the statement by HilleRisLambers et al. (2012): “ the environmental factors and biotic interactions influence the composition and structure of communities at local scales”.  On the contrary, SR replicates had the same dissimilarity among the experiment. It means that interactions did not drive the assembly process, which would have led to replicates more similar through time. Also, stochastic processes were not the primary driver, or else dissimilarity would have been higher through time. In the SR design, we cannot highlight the influence of phenology because all microcosms were not removed at the same date. In this design, it is quite difficult to assess which process was the primary driver.

For 2, 4, 6 and 8 weeks of experiment, communities from SR and SA design did not share the immersion dates. Communities' compositions were really different after 4 and 6 weeks of immersion, which highlight the impact of phenology. Indeed, for a same duration of immersion but at different dates, communities were really different. After 8 weeks of experiment and until 14 weeks, communities of the two designs were more similar. In this case, it is quite difficult to distinguish impacts of interactions and phenology because the immersion dates of the two designs did superimpose.

## Richness and abundance

After two weeks of experiment, abundances were higher in SR design. A SR replicate had a particularly high abundance value, because of *sididae* abundance that was around ten times higher than it the two other SR replicates. After four and six weeks, abundance values were still higher for the SR design. After eight weeks and until the end of experiment, abundances between SR and SA designs got closer and closer. It is here quite difficult to distinguish influences of phenology and interactions. Indeed, SR and SA replicates that spent eight weeks or less in water had immersion dates that did not superimpose. For the first eight weeks, we can then say that phenology events were different between SR and SA communities. Concerning replicates that spent ten weeks or more in the water, the more time the experiment lasted, the more SR and SA designs did superimpose, and thus microcosms underwent the same environmental factors and phenology events. It is then more difficult to disentangle interactions and phenology impacts on the two designs. Interactions could have led to a certain regulation that led to closer abundances, but emigration or emergence phenomenon could also have influenced abundances values.

There was a clear succession in the community assembly for the SR design. Indeed, replicates that spent two weeks in water were really different from replicates that spent 14 weeks in water (Figure 7a). Shredders exhibited their highest relative abundances in the first four weeks. After four weeks, there was a high peak of collectors, and predators' abundance increased after eight weeks. This succession might reflect the use of the leaf litter by shredders and how they facilitate collectors (Bedford 2004, Bohman et Herrmann 2006, Cummins et Klug 1979, Mancinelli et al. 2007, Pope et al. 1999). Finally, predators colonized leaf litter once their prey was present, supporting a bottom-up influence in the food web assembly (Gravel et al. 2011b).

In the SA design, the succession was also present (Figure 5 and Figure 7b). Predators were present even in microcosms that spent only two weeks in water, between the 25th of September and the 8th of October. That could be explained by the fact that the regional pool of predators was already present, or microcosms could have been colonized by predators that emigrated from other microcosms around, immerged weeks before. Predator's abundance increased with the number of weeks microcosms spent in the water, showing the influence of interactions and the necessity of having their preys available in the microcosm.

The total abundance in the SR dataset was more than twice the total abundance in the SA dataset. Moreover, for the same amount of time spent in water, abundance was always higher in microcosms from SR, except for microcosms that spent 14 weeks in the water. For the same amount of time spent in the water, the only difference between microcosms of the two designs was the dates of immersion. For example, microcosms that spent two weeks in the water in the SR design were set at the end of June and taken out at the beginning of July, whereas microcosms that spent two weeks the water in the SA design were set at the end of September and taken out in October. This difference of dates directly impacted phenology and dispersal that would lead to different priority effects and availability of organisms in the regional pool. Phenology and its impact on dispersal could explain these differences of abundance between the two designs because it could have led to fewer organisms available in the regional pool to disperse in September. Nonetheless, through time, the abundances for microcosms of SR and SA that spent the same time in water were closer and closer. This could be explained by the fact that the more microcosms spent time in the water, the more they shared their immersion dates between SR and SA designs. For example, microcosms that spent two weeks in the water from SR design and those that spent two weeks in the water from SA design were more than two months away ones from each other. However, if we consider microcosms that spent 12 weeks in water, for SR they were set in water the 18th of June and taken out the 10 of September, and for SA they were set on the 16th of July and taken out the 8th of October. Thus, they share eight weeks out of the 12. Environmental factors, similarity of regional pool and phenology, in addition to interactions, might have led to closer abundances values with more time spent in water.

### Change in community composition and relative influence of assembly processes

Community compositions of SR and SA designs did not follow the same assembly pattern neither they had the exactly same composition at the end of the experiment. Moreover, for four and six weeks of immersion, SR and SA communities were really dissimilar even if they spent the same amount of time in water, but at different dates (Appendix II). It is thus clear that interactions were not the only process influencing community assembly. Historical contingencies and priority effects could have led to those different assembly patterns and final states (Cole 1983, Drake 1985, 1991, Gilpin et al. 1986). Indeed, even communities based on the same regional pool can have different initial community compositions and follow alternative assembly trajectories (Drake 1991).

The litter loss was always below 20% of original leaf litter mass (data not shown). Most of the time, all the ligneous material was still present within the microcosms, showing that non-ligneous material has been consumed preferentially. The resource's use could have been influenced by different factors. First, it is well known that shredders preferentially consume the leaves that are "conditioned" by the microbial community (Petersen et Cummins 1974, Cummins et Klug 1979). Maybe the lack or the quality of the microbial community could explain the fact that there was still some resource at the end. Moreover, only ligneous material was often left and shredders might have been unable to use it. Finally, it could also be leaf litter that did not reached the threshold quantity in order for the shredders to colonize it, and they might have abandoned the resource in a “giving-up behaviour” (Mancinelli et al. 2005, Brown 1988, Basset 1995, Basset et al. 1997, WallisDeVries et al. 1999). If the litter’s quantity was limiting, it could have brought harsh conditions to the community, which can lead deterministic processes to be dominant over stochastic processes (Chase 2007). On the opposite, if litter led to higher community productivity and easy conditions, it could have brought stochastic processes to be more influent (Chase 2007). In both case, litter quantity played a role in processes’ influences.

In contrast with SR, dissimilarity between SA replicates was significantly decreasing through time. It is interesting to notice that the dissimilarity between replicates in SR was constantly between 0.2 and 0.6, and that in SA, the dissimilarity decreased from approximately 0.7 after 4 weeks of experiment to 0.4 (two replicates) and 0.6 (one replicate) after 14 weeks of experiment. So after two weeks of experiment, replicates in SR were more similar between themselves than replicates of SA between themselves. But after 14 weeks (if we do not consider the last replicates in week 16 that SA and SR share), replicates of SR had approximately the same dissimilarity as SA replicates. It seems that the dissimilarity value of approximately 0.4 could be a threshold linked to stochastic processes in priority effects in community assembly. We then could consider that replicates were 60% similar because of the phenology and interactions, and also because of the fact that they share a regional pool. It is interesting to notice that SA replicates that spent two weeks in water in September are really more similar between themselves than SR replicates that spent two weeks in June. This might have been biased by the dispersion and colonization of organisms that were present in the other microcosms already set around.

Our study has shown that through the 16 weeks of the experiment, communities in the two sampling designs (SR and SA) underwent composition changes mainly driven by deterministic processes. Indeed, if stochastic processes were the primary drivers, dissimilarities would always be increasing between replicates of SA and SR designs. Moreover, we have shown that there is not only one deterministic process that drives community assembly. If phenology were the only driver, it would mean that only the dates of immersion would influence the community composition. Then, replicates, which share dates of immersion, would be similar. It was not the case in SA design. If interactions were the primary driver, microcosms would be more and more similar through time because interactions would have had more time to influence community. However, when we look at dissimilarity between microcosms in SR design, communities do not become more similar through time. It seems that community assembly is primary driven by a combination of interactions and phenology, and partly influenced by priority effects and some stochastic processes.

## 1.6 CONCLUSIONS AND PERSPECTIVES

In this study, we assessed whether there was a structure among the community assembly process. We looked at abundance and richness in microcosms, and dissimilarity in between microcosms through time. After four months in the water, replicate microcosms in SA and SR designs were both around 60% similar. Communities from SR and SA designs did not follow the same sequence of community assembly though. Interactions' influence in SA design was more evident, whereas phenology's impact was the most evident in SR design. Nonetheless, in both cases, the community assembly was primary driven by a combination of deterministic processes such as interactions and phenology. Priority effects, dispersal capacity and drift could explain why replicates were never really similar (the dissimilarity value was around 0.4 at the end of experiment).

It would be interesting to identify the organisms to the species level. Indeed, it could reveal more precise turnovers in community composition and understand in a better way the interactions between organisms. It would also allow us to analyse functional traits in a more precise way. In this study, we tried to analyse communities' compositions regarding to functional traits such as body size, feeding group and feeding mode (data not shown). Nothing was significant though, maybe because the family identification is too large. Another problem was the fact that though leaf litter mass at the end of experiment was never null, the type and quantity of leaf litter may have influenced to experiment, especially the fact that only ligneous materiel was left. In a next experiment, it could be interesting to put more than 1 gram of leaf litter in microcosms, to make sure that non ligneous leaf litter is not limiting. Finally, we had some difficulties to disentangle impacts of phenology and interactions because some microcosms in SA and SR designs shared some dates of immersion. In another experiment, it would be important to make sure that the two designs do not share immersion dates. The experiment took place in the littoral zone of a lake but results could be extrapolated at other aquatics habitats such as streams, rivers, and coastal marine habitats that undergo such conditions and where community rely on ephemeral resources such as terrestrial detritus.

# CONCLUSION GÉNÉRALE

Dans un contexte de perte de biodiversité, il est important de comprendre comment les communautés s'assemblent, et quels processus influencent ces assemblages. De nos jours, certaines interrogations persistent concernant l'impact des processus déterministes et stochastiques sur l'assemblage des communautés. De plus, la colonisation de la matière détritique reste peu étudiée en lac. Dans cette étude, ces deux problématiques ont été combinées. Le but général était de tester si la mise en place des assemblages d'espèces autour de la litière de feuilles d'arbres dans la zone littorale des lacs est un processus déterministe ou stochastique. Pour ce faire, un suivi de la composition d'une communauté de macroinvertébrés vivant dans la zone littorale du lac des Baies (Québec) et basée sur la matière détritique a été réalisé durant l'été 2014.

Les deux objectifs de l'étude étaient les suivants : 1- vérifier la présence d'un changement directionnel au cours de l'assemblage de la communauté qui témoignerait de l'impact de processus déterministes, 2- déterminer quel processus contribuait le plus fortement à cet assemblage, parmi les interactions, la phénologie, la dérive, la dispersion. Nos hypothèses étaient les suivantes : 1- un changement directionnel était effectivement présent et témoignait de la présence des processus déterministes, 2- les interactions se révélaient être les processus les plus influents sur la dynamique d'assemblage de la communauté. Pour répondre à ces objectifs, des microcosmes contenant de la matière détritique ont été installés dans la zone littorale d'un lac. Un premier design (SR) correspondait à une série de microcosmes posés en juin, puis retirés aux deux semaines par groupes de trois. Ainsi, les premiers microcosmes retirés (début juillet) n'avaient passé que deux semaines dans l'eau, tandis que les derniers (retirés en octobre) avaient passé plus de quatre mois dans l'eau. Un second design (SA) correspondait à des microcosmes posés par groupe de trois aux deux semaines durant l'été, puis tous retirés au mois d'octobre. Ainsi, les microcosmes posés en juillet avaient donc passé plus de quatre mois dans l'eau lorsqu'ils étaient retirés en octobre, et ceux qui avaient été posés fin septembre n'avaient passé que deux semaines dans l'eau lorsqu'ils étaient retirés en octobre. Il est important de remarquer que les deux dispositifs expérimentaux permettent de comparer la composition de microcosmes qui ont passé la même durée dans l'eau mais pas au même moment de l'année. Les organismes retrouvés dans les microcosmes étaient ensuite identifiés à la famille.

Concernant le premier objectif, l'hypothèse a été vérifiée. Les analyses ont confirmé l'impact des processus déterministes, c'est-à-dire les interactions et la phénologie. En effet, si seuls des processus stochastiques avaient été influents, la dissimilarité entre les réplicats aurait augmenté avec le temps, et ce dans les deux dispositifs. Or, ce n'est pas le cas. De plus, les RDA confirmaient la présence d'un *turnover* dans les compositions des communautés dans les deux dispositifs. Finalement, la succession était évidente dans le dispositif SR, au regard des abondances des différents groupes trophiques. Dans le design SA, la succession était moins évidente compte tenu du fait que ce dispositif ne suivait pas la saisonnalité, ce qui influait donc sur le pool régional, et donc sur la capacité et la disponibilité des organismes à se disperser.

Concernant le second objectif, différents éléments sont ressortis pour les deux dispositifs. Au sein du dispositif SR, la dissimilarité entre les réplicats est restée relativement constante au long de l'expérience (valeur de dissimilarité autour de 0.4). Cela laisse supposer que la phénologie était probablement plus influente que les interactions au cours de la dynamique d'assemblage de la communauté. Son impact était plus visible, tout du moins. Concernant le design SA, la dissimilarité diminuait au cours de l'expérience, avant d'osciller autour de 0.4 à la fin de l'expérience. Cela permettait de faire ressortir que la phénologie n'était pas le processus dominant, autrement tous les microcosmes auraient été similaires puisque retirés le même jour. Les interactions semblent avoir été particulièrement influentes au sein du dispositif SA. La dynamique d'assemblage des communautés différait en fonction du design concerné, bien que d'après la PCoA, les réplicats des deux dispositifs étaient de plus en plus similaires après 8 semaines d'expérience, et ce jusqu'à 16 semaines d'expérience. Il ressort de cette étude que la phénologie et les interactions sont des processus qui conduisent les réplicats de communautés à se ressembler dans leur composition, sans jamais devenir similaires. Cela peut s'expliquer par les effets de priorité, la dérive et la dispersion qui peuvent avoir des impacts contradictoires avec les interactions et la phénologie dans le processus d'assemblage. Il semble y avoir un seuil de dissimilarité minimal, partagé par les deux dispositifs expérimentaux. Cela confirme une forte contribution des processus stochastiques.

Les deux dispositifs ont faire ressortir les deux processus déterministes de manières différentes. Le design SR suivait la saisonnalité, ce qui n'était pas le cas pour le design SA. La saisonnalité a eu un impact clair puisque les deux dispositifs n'ont pas subi les mêmes processus dans les mêmes mesures. Une communauté locale étant fortement dépendante du pool régional, la capacité de dispersion, elle même influencée par la composition du pool régional et la phénologie pourrait être, à certaines périodes non favorables, le processus le plus influent.

Il serait intéressant d'identifier les organismes à l'espèce. En effet, il n'est pas rare de retrouver au sein d'une famille ou même d'un genre différents groupes trophiques, ce qui rend difficile l'identification des interactions trophiques au sein de la communauté. Cela peut donc nuire à la compréhension de la dynamique d'assemblage. Dans notre cas, une approche par traits fonctionnels avec des identifications à la famille n'a rien fait ressortir de significatif, probablement en raison de l'identification pas assez précise. Une identification à l'espèce, couplée à une approche par traits fonctionnels pourrait apporter de nouvelles informations.

# FIGURES

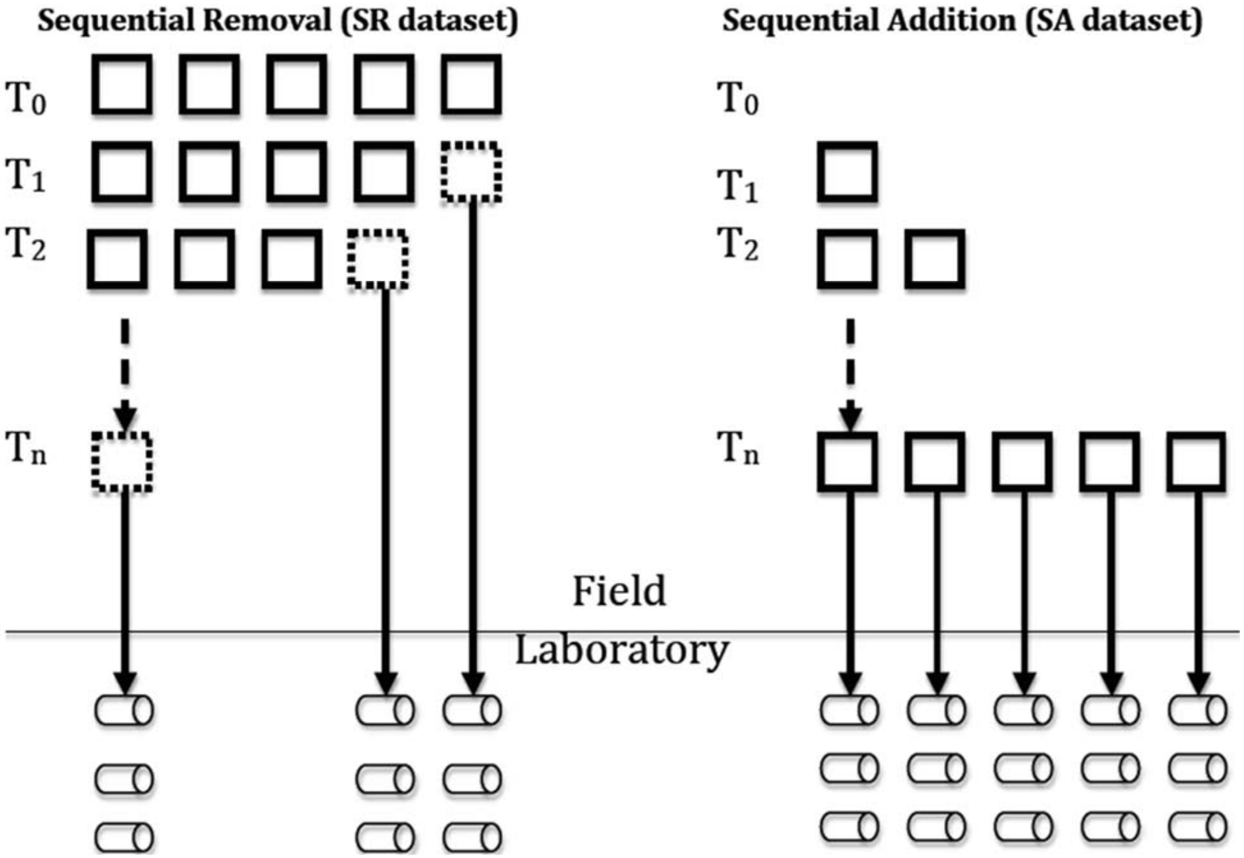


**Figure 1**.- Diagram of the SR and SA designs. A square represents a frame with three microcosms (cylinders) replicates set and removed at the same moment.

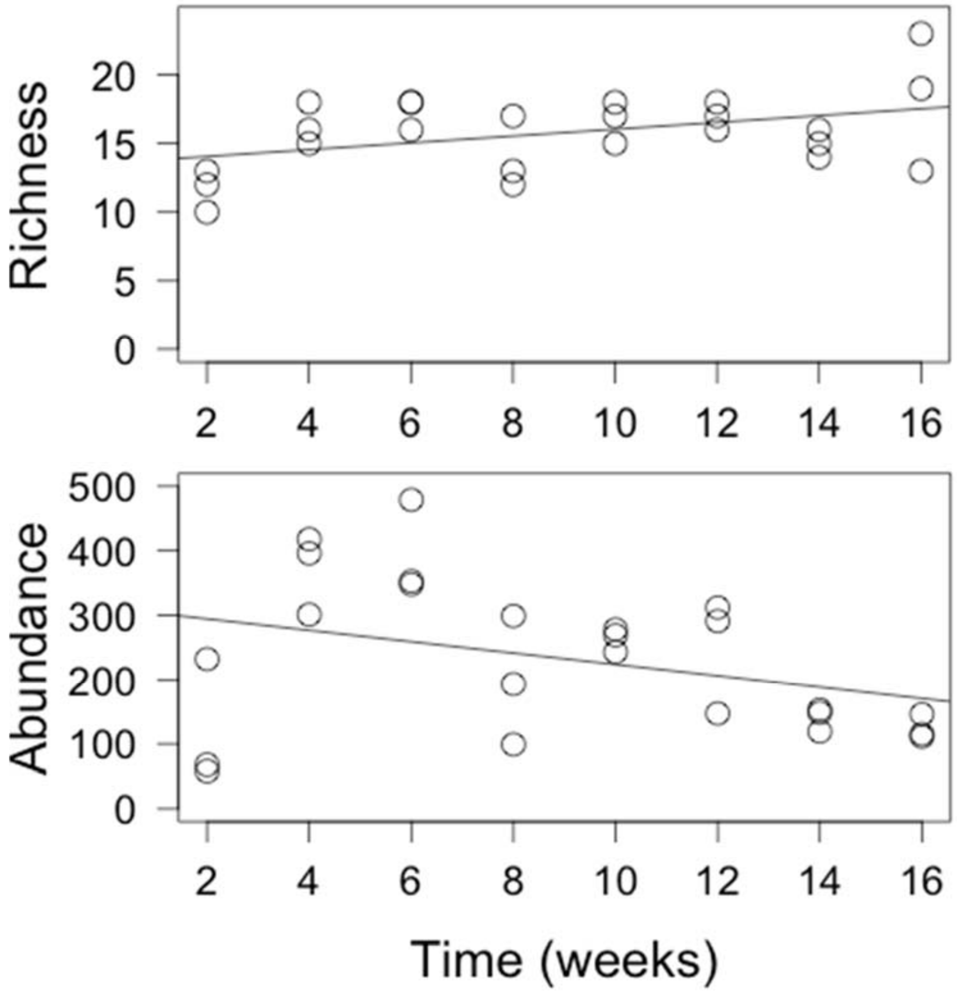


**Figure 2.-** Taxonomic richness ($R^2_{adj}$=0.13) and abundance ($R^2_{adj}$=0.06) in the microcosms of the dataset SR with sequential removal (n=24). All the microcosms were set on the 18th of June. Removal dates are on the x-axis.

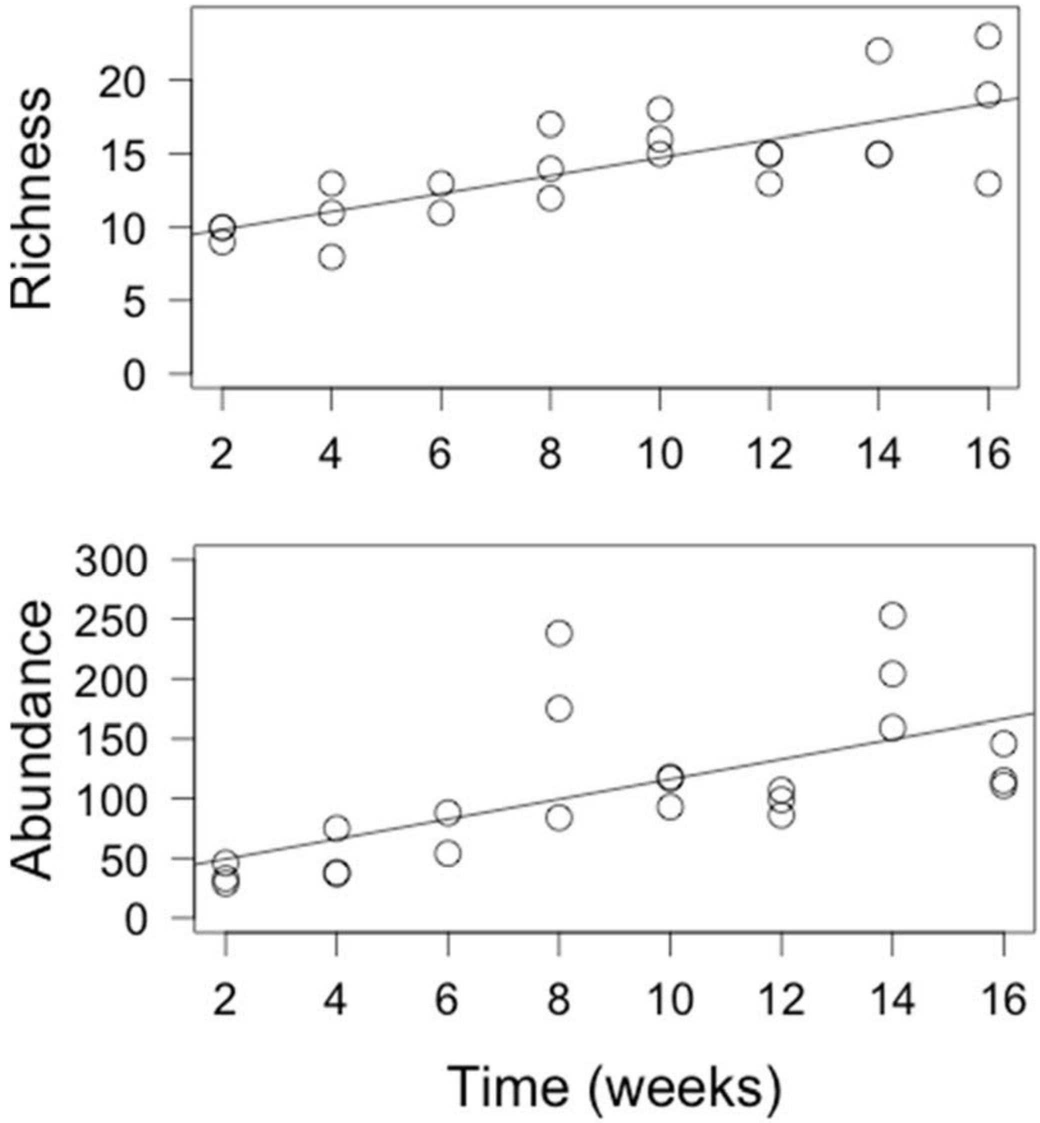


**Figure 3.-** Taxonomic richness ($R^2_{adj}$=0.57) and abundance ($R^2_{adj}$=0.47) in the microcosms of the dataset SA with sequential addition (n=23). All the microcosms were taken out in October. Thus, the replicates that spent only two weeks in water were set at the end of September, and those that spent 16 weeks were set in June.

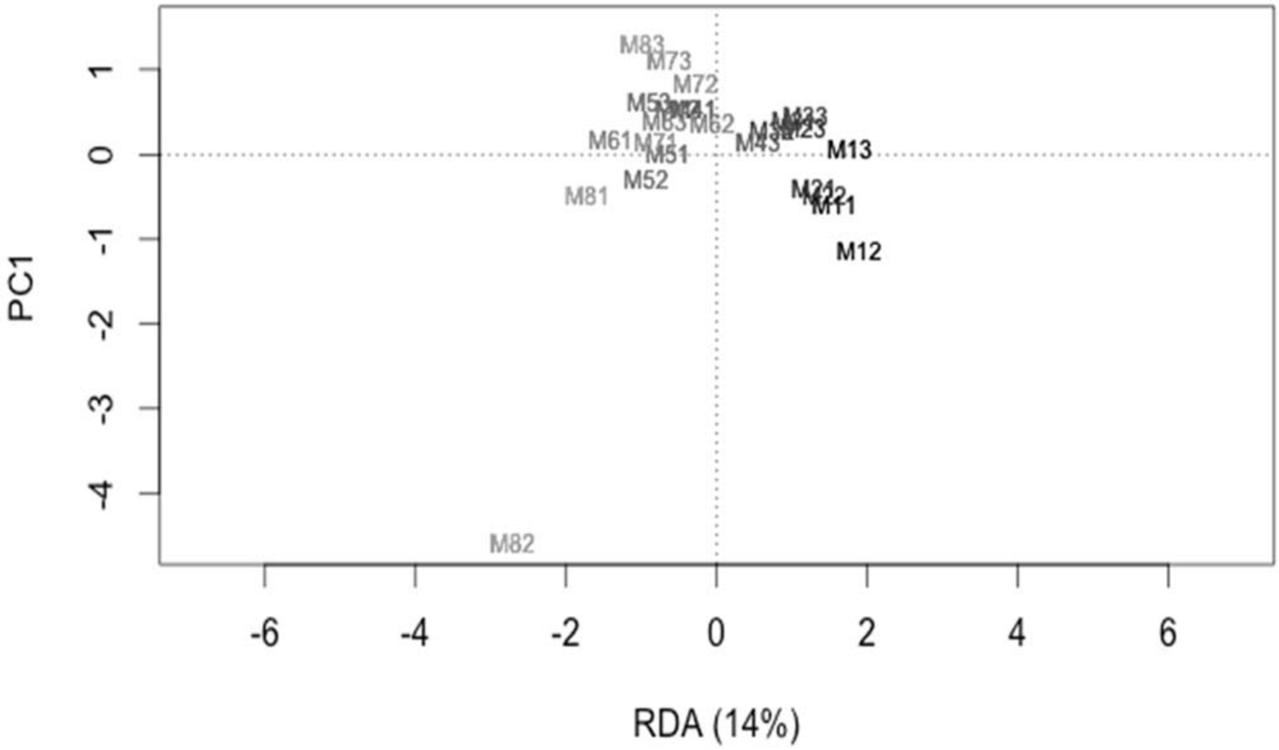


**Figure 4.-** Redundancy Analysis (RDA) showing the position of the microcosms of the dataset SR with regard to the first axis (n=24). Labels account for microcosm units (M), a first digit, numbered from to 1 to 8 and accounting for the order of microcosms collection and a second digit numbered from 1 to 3, accounting for replicated observation. For example, the microcosms M12 has been set in water on the 18th of June such as all the microcosms represented on this RDA. It also is the second replicate of the three first microcosms taken out (after 2 weeks of experiment, the 2nd of July).

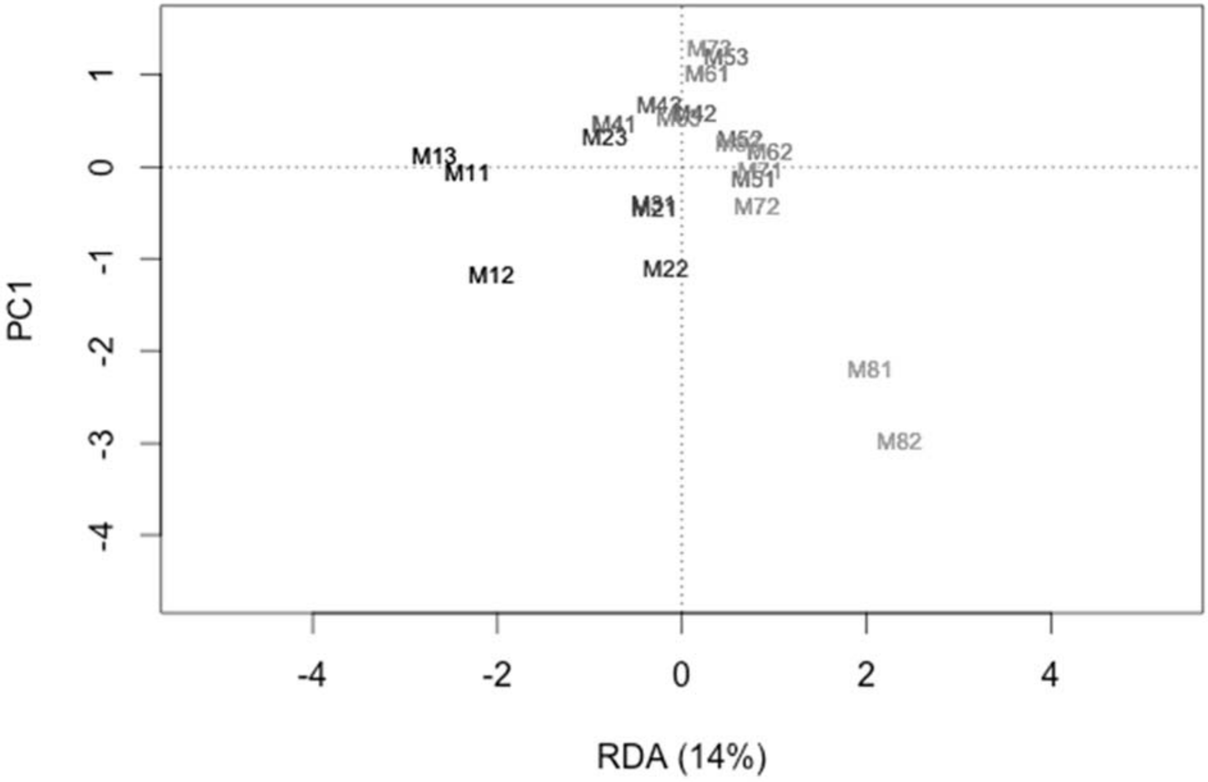


**Figure 5**.- Redundancy Analysis (RDA) showing the position of the microcosms of the SA dataset with regard to the first axis (n=23). Labels account for microcosm units (M), a first digit, numbered from to 1to 8 and accounting for the order of microcosms collection and a second digit numbered from 1 to 3, accounting for replicated observation.

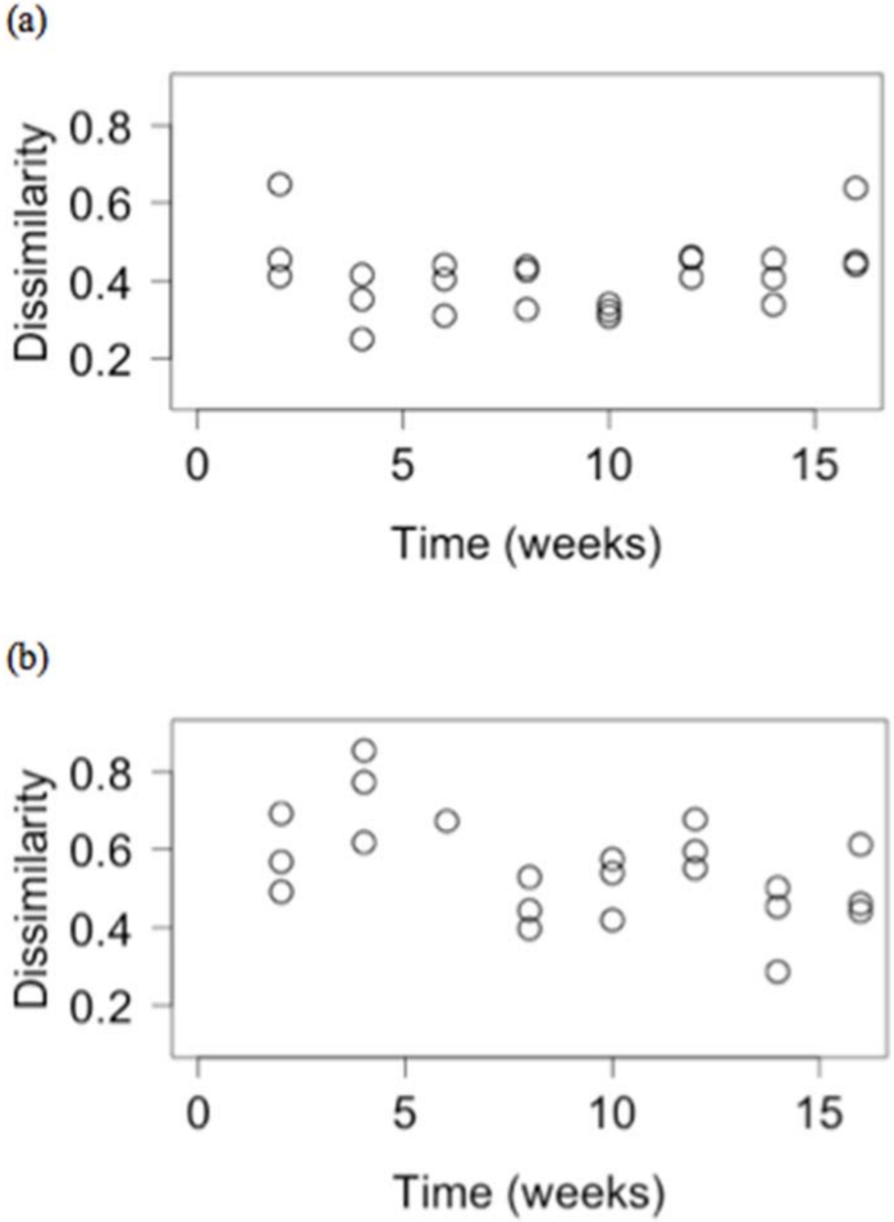


**Figure 6**.- Dissimilarity in between replicates (microcosms that have spent the same amount of time in water) of the dataset SR (a) and SA (b). Dissimilarity is measured in between microcosms that have been set and taken out of water at the same dates. As there is three replicates on each date, there is three dissimilarity values on each date. A dissimilarity of 0 would mean that the replicates have the same community composition in terms of taxa and abundance.

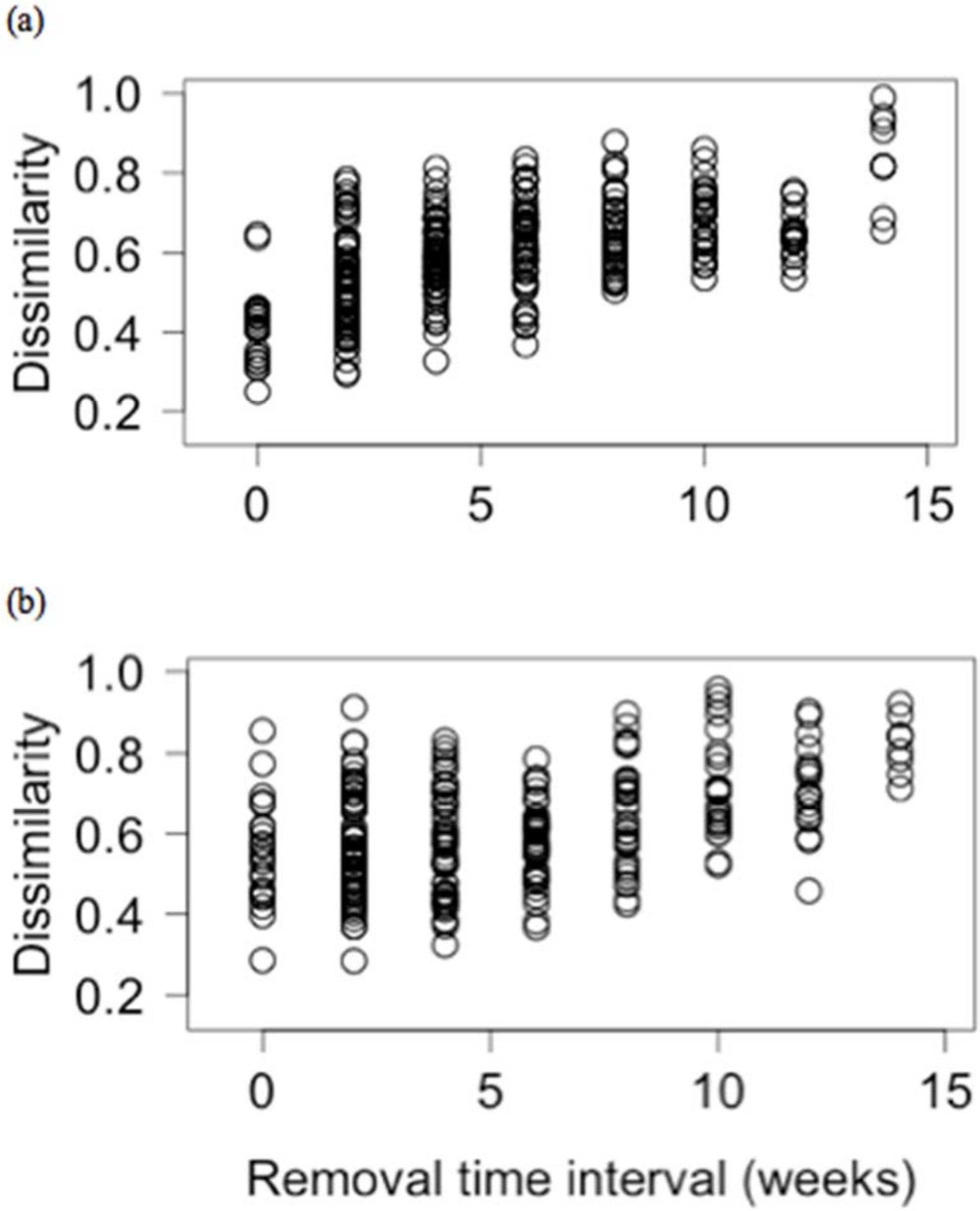


**Figure 7.-** Dissimilarity for the dataset SR (a) and SA (b) between pairs of microcosms that have spent different number of weeks in water. For example, if we measure the dissimilarity between a microcosm that spent two weeks in water, and another one that spent eight weeks in water, the dot for this dissimilarity will have an abscissa of six, representing six weeks of difference between their durations.

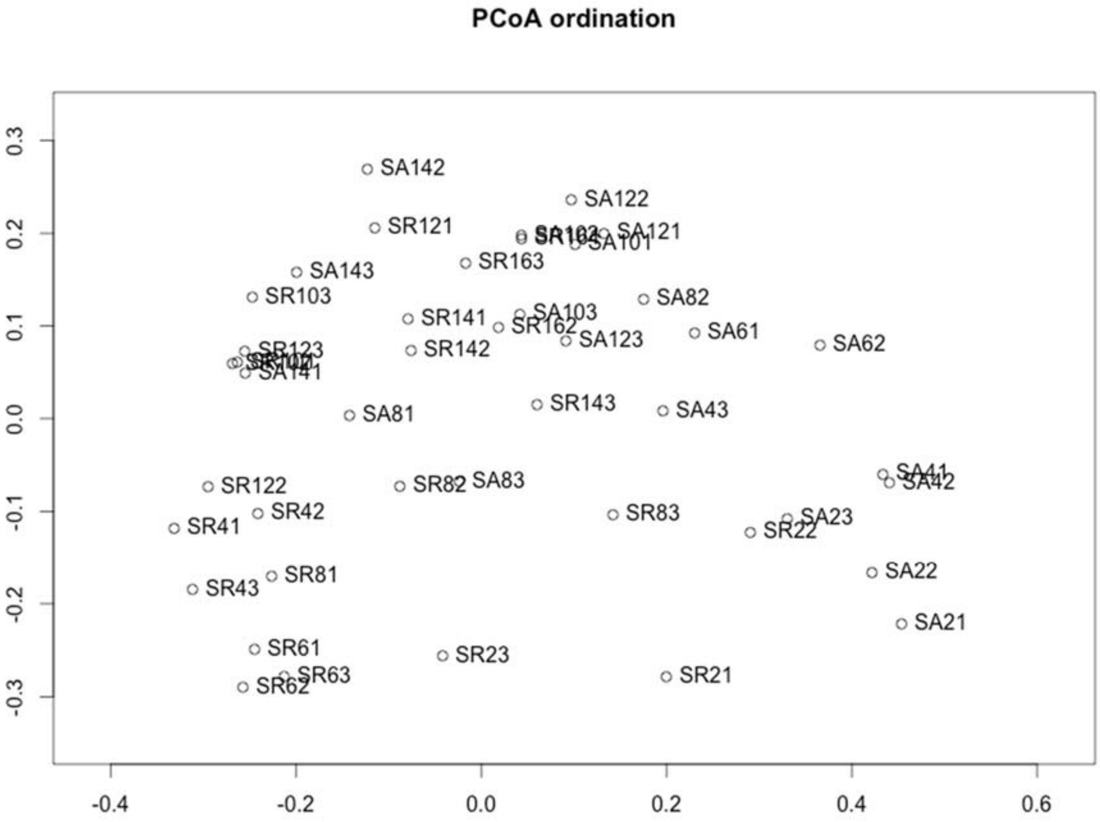
# APPENDIX

**Appendix I**. List of organisms found in microcosms and the respective functional feeding group they belong to. It explains whether they were taken into account to measure richness and abundance. We use the classification of Merritt and Cummins to classify taxa into functional feeding groups (2007).

| | Richness | Abundance | Functional feeding group |
|---|---|---|---|
| Daphniidae | Yes | Yes | Scrapers, collectors |
| Sididae | Yes | Yes | Scrapers, collectors |
| Chydoridae | Yes | Yes | Scrapers, collectors |
| Calanoida | Yes | Yes | Collectors |
| Cyclopoida | Yes | Yes | Collectors |
| Harpacticoida | Yes | Yes | Collectors |
| Hyalellidae | Yes | Yes | Shredder |
| Caenidae | Yes | Yes | Collector |
| Heptageniidae | Yes | Yes | Collector |
| Leptophlebiidae | Yes | Yes | Collector |
| Siphlonuridae | Yes | Yes | Scraper, collector |
| Baetidae | Yes | Yes | Collector |

| | | | |
|---|---|---|---|
| Neoephemeridae | Yes | Yes | Collector |
| Ephemerellidae | Yes | Yes | Collector |
| Chironomidae | Yes | Yes | Collector/predator |
| Hydrachnidia | Yes | Yes | Predator/parasite |
| Elmidae (adult) | Yes | Yes | Collector |
| Phryganeidae | Yes | Yes | Shredder |
| Polycentropodidae | Yes | Yes | Predator/collector |
| Libellulidae | Yes | Yes | Predator |
| Helicopsychidae | Yes | Yes | Scraper |
| Leptoceridae | Yes | Yes | Shredder, collector |
| Brachycentridae | Yes | Yes | collector |
| Trichoptera pupa | Yes | Yes | Considered not feeding |
| Perlidae | Yes | Yes | Predator |
| Ceratopogonidae | Yes | Yes | Predator |
| Hydridae | Yes | Yes | Predator |
| Physidae | Yes | Yes | Scraper |
| Lymnaeidae | Yes | Yes | Scraper |
| Glossiphonidae | Yes | Yes | Parasite |
| Aeshnidae | Yes | Yes | Predator |

| | | | |
|---|---|---|---|
| Ostracoda | Yes | Yes | Collectors |
| Oligochaeta | Yes | Yes | Collectors |
| Coenagrionidae | Yes | Yes | Predator |
| Elmidae (larvae) | Yes | Yes | Collector |
| Athericidae | Yes | Yes | Predator |
| Copepoda nauplii | Yes | Yes | Collector |
| Chironomidae pupa | Yes | Yes | Considered not feeding |
| Glossiphonidae cocoon | Yes | Yes | Considered not feeding |
| Trichoptera (NI) | No | Yes | |
| Ephemereoptera (NI) | No | Yes | |
| Chironomidae pre pupa | No | Yes | Collector/predator |



**Appendix II**. Dissimilarity among the 44 microcosms' compositions. The notation is the following: SR21 stands for microcosm from SR design, that spent 2 weeks in water, and is the first out of the three replicates.

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