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INTÉGRATION THÉORIQUE DE LA BIOGÉOGRAPHIE ET DU FONCTIONNEMENT DES ÉCOSYSTÈMES

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Composition du jury :

Béatrix Beisner, examinatrice, Université du Québec à Montréal

Ulrich Brose, rapporteur, iDiv Leipzig et Friedrich-Schiller-University Jena

Dominique Gravel, co-directeur de recherche, Université de Sherbrooke

David Mouillot, co-directeur de recherche, UMR MARBEC, Université de Montpellier

Jose M. Montoya, rapporteur, CNRS Moulis

Nicolas Mouquet, examinateur, UMR MARBEC, Université de Montpellier

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À mes parents

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et
l'Université de Montpellier (UM)
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Département de Biologie, Université du Québec à Rimouski
300, allée des Ursulines – Rimouski G5L3A1 – Québec – Canada

En France : **UMR MARBEC, Biodiversité Marine, Exploitation et Conservation**
Université de Montpellier – Place Eugène Bataillon - bât 24 - CC093
34 095 Montpellier cedex 05 – France

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RÉSUMÉ

Cette thèse a pour objectif de combiner plusieurs théories opérant à différentes échelles spatiales afin de mieux prédire l'effet des changements globaux, tels que la modification du climat, l'exploitation intensive des ressources ou la disparition des espaces naturels, sur la structure et le fonctionnement des écosystèmes. L'originalité de ce travail est l'utilisation de la masse corporelle des espèces pour caractériser à la fois leur dynamique spatiale, leurs interactions trophiques ainsi que les flux de biomasse au sein de l'écosystème. Cette approche offre l'avantage de relier les propriétés des écosystèmes à un trait fonctionnel mesurable à l'échelle de l'espèce, voire même de l'individu.

J'étudie dans un premier temps le lien entre la diversité des écosystèmes et leur stabilité, qui est une question centrale dans le domaine de l'écologie. Il a été démontré que les écosystèmes très diversifiés en espèces ne devraient pas perdurer du fait de leur trop grande sensibilité aux perturbations, ce qui soulève un paradoxe puisque les écosystèmes riches en espèces abondent dans la nature. Grâce à la compilation et à l'analyse d'un important jeu de données d'écosystèmes empiriques, je montre qu'il n'existe pas de relation entre la stabilité, la diversité et la complexité des écosystèmes. Une analyse détaillée des données démontre que la structure très organisée des flux de biomasse observés entre les prédateurs et leurs proies est l'un des principaux fondements de la stabilité des écosystèmes. Je relie ensuite ces propriétés stabilisantes à des caractéristiques mesurables à l'échelle de l'espèce. À partir de la masse corporelle des espèces, je détermine les interactions trophiques, les besoins énergétiques ainsi que les biomasses à l'équilibre des espèces d'un écosystème afin de modéliser des réseaux trophiques réalistes. Je trouve que les écosystèmes composés d'espèces de masses corporelles très différentes sont caractérisés par un nombre important d'interactions proie-prédateur de faible intensité et sont plus stables que ceux possédant des espèces de masse corporelle similaires.

J'étudie enfin l'effet de la taille et de l'isolement d'un habitat sur la moyenne et la variance de la masse corporelle des espèces qui y coexistent à partir de modèles intégrant les différences interspécifiques de dispersion, de vulnérabilité aux extinctions et la position trophique des espèces. Je compare les prédictions des modèles aux distributions de masse corporelle observées dans les assemblages de poissons récifaux tropicaux en me basant sur une base de données globale. L'analyse de ces données démontre que les assemblages locaux de poissons ne correspondent pas à un sous-ensemble aléatoire du pool régional et valident les prédictions de la théorie allométrique et trophique de la biogéographie des îles. L'intégration de l'écologie fonctionnelle, de la biogéographie et de la théorie sur la stabilité des systèmes dynamiques ouvre de nouvelles perspectives pour la conservation des écosystèmes puisqu'elle met en évidence l'effet de la fragmentation des espaces naturels sur la diversité fonctionnelle, et par extension sur la structure et le fonctionnement des écosystèmes.

Mots clés : réseau trophique, interactions, masse corporelle, relations allométriques, dynamique spatiale, macroécologie, diversité fonctionnelle, stabilité

Theoretical integration of biogeography and ecosystem functioning

ABSTRACT

The general objective of this thesis is to combine theories acting at different spatial scales in order to better predict the effect of global changes, such as such as resource overexploitation, climate change or habitat fragmentation, on ecosystem functioning. The unique feature of this work is the use of species body mass to describe both spatial dynamics, trophic interactions and biomass flows between the species of an ecosystem. An advantage to this approach is that it links ecosystem properties to a functional trait, measured at the species or even the individual level.

First, I study the relationship between the diversity and the stability of ecosystems. It has been demonstrated that species-rich, complex ecosystems should be too sensitive to perturbations to persist through time, which raises a paradox as many species-rich ecosystems are observed in nature. With the compilation and the analysis of a large dataset of empirically measured ecosystems, I show that there is no relationship between stability and diversity or complexity in real ecosystems. A further analysis demonstrates that the non-random organization of energy flows between predators and prey allows complex ecosystem to be stable.

A second step is to link this stabilizing structure to species functional traits. I derive food web topology, species energetic needs and equilibrium densities from body mass to build quantitative realistic food webs. I find that food webs composed of species with very different body masses are characterized by a high number of weak trophic interactions and are more stable than food webs with more similar species.

Finally, I study the effect of habitat area and isolation of the mean and variance of species body mass distribution, using models integrating the interspecific variability of dispersal ability, vulnerability to extinctions and trophic position. I compare model predictions to observed body mass distributions of fish assemblages found on tropical reefs with a global database. I find that body mass distribution in local fish assemblages does not correspond to a random sample of the regional species pool, which confirms the predictions of the allometric and trophic theory of island biogeography.

The integration of functional ecology, island biogeography and theory on the stability of complex systems open new perspectives in the fields of macroecology and ecosystem management since it highlights the potential impact of habitat destruction and fragmentation on the functional reorganization of species assemblages and therefore on the structure and functioning of ecosystems.

Keywords : food web, interaction network, body mass, allometric relationships, spatial dynamic, macroecology, functional diversity, stability

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INTRODUCTION GÉNÉRALE

Au cours de cette thèse, je me suis intéressé aux mécanismes responsables de la structure et de la stabilité des écosystèmes opérant à différentes échelles spatiales. Pour cela, j'ai développé un cadre théorique basé sur la masse corporelle des espèces, qui permet de caractériser à la fois leur dynamique spatiale, leurs interactions trophiques ainsi que les flux de biomasse circulant entre les espèces de l'écosystème. La réunion de domaines de l'écologie jusqu'alors déconnectés dans un cadre théorique commun me permet d'étudier l'influence de variables environnementales, telles que la taille ou l'isolement de l'habitat, sur le fonctionnement des écosystèmes. Dans cette introduction, je présente dans un premier temps le contexte général dans lequel s'inscrit cette thèse, ainsi que les concepts fondamentaux sur lesquels mon travail de recherche est basé. Ces éléments permettent de mettre en lumière la nécessité de développer une approche qui intègre l'écologie fonctionnelle et la biogéographie pour étudier l'effet de la taille et de l'isolement d'un fragment d'habitat sur la structure et la stabilité des écosystèmes. Je conclus cette introduction par la présentation de mes différents chapitres de thèse. Je détaille comment ceux-ci s'articulent autour de la masse corporelle des espèces, qui est la pierre angulaire de ce travail de recherche.

CONTEXTE

La modification du climat et des cycles biogéochimiques, l'exploitation intensive des ressources naturelles et la prolifération d'espèces invasives sont autant de changements globaux pouvant affecter de manière significative les biens et les services que nous fournissent les écosystèmes (Chapin et al., 2000; Petchey et al., 2015). Actuellement, notre compréhension de la vulnérabilité des écosystèmes face aux impacts des changements globaux est relativement faible (Scheffer et al., 2009; Barnosky et al., 2012), alors que la gestion efficace de ces changements dépendra de notre capacité à les anticiper (Evans et al., 2012). Ce contexte induit une forte demande de la part des législateurs, des gestionnaires et des gouvernements pour une science écologique prédictive, capable de production de scénarios explicites permettant de comprendre comment les systèmes écologiques vont se comporter dans des conditions futures, résultant de l'évolution du climat, de l'utilisation des terres, de la densité de population humaine ou des activités économiques (Clark et al., 2001; Mouquet et al., 2015; Petchey et al., 2015).

Le développement de modèles écologiques prédictifs a pour objectif de fournir une expertise globale, à l'image des modèles climatiques globaux, et d'aider à la prise de décision des gouvernements concernant la gestion des écosystèmes. La réalisation de ce type de prédictions est un défi, car les systèmes écologiques sont complexes à tous les niveaux d'organisation : ils sont caractérisés par un grand nombre de composants très hétérogènes, qui interagissent entre eux de façon non linéaire, à différentes échelles temporelles et spatiales (Wu and David, 2002; Dunne, 2006). Les processus évolutifs ont conduit à cette variété de formes et d'interactions et influencent continuellement la dynamique des systèmes biologiques (Godfray and May, 2014). La modélisation des écosystèmes doit donc prendre en compte une plus grande incertitude que celle issue des modèles de scénarios climatiques, qui reposent sur des équations physiques bien connues. D'autre part, il est probable que les réponses des espèces face aux changements globaux soient très variables en fonction de leurs caractéristiques (Rall et al., 2009). Le défi est donc d'identifier les traits biologiques qui déterminent la sensibilité des espèces aux changements globaux (Brose et al., 2012; Dillon et al., 2010; Cheung et al., 2012), afin de répondre aux questions suivantes : comment la biodiversité ainsi que les interactions entre les espèces vont-elles être affectées par les changements globaux ? Leur impact sera-t-il suffisamment fort pour mettre en péril la dynamique et la stabilité des écosystèmes ?

LES ÉCOSYSTÈMES SONT DES SYSTÈMES DYNAMIQUES COMPLEXES

L'écologie des communautés étudie les mécanismes de coexistence des espèces permettant d'expliquer l'incroyable diversité d'organismes vivant sur notre planète (Hutchinson, 1959). Les écosystèmes sont en effet composés d'une multitude d'espèces qui interagissent entre elles. Ces interactions créent des boucles de rétroactions, qui peuvent soit amplifier soit amortir un changement de la densité des populations. Le fonctionnement des écosystèmes englobe l'ensemble des processus liés aux flux d'énergie et de matière à travers les compartiments d'un écosystème. Ces flux peuvent être caractérisés par leur intensité ainsi que par leur variabilité au cours du temps.

Dans cette thèse, l'étude du fonctionnement des écosystèmes se concentrera principalement sur les mécanismes qui influencent la stabilité des réseaux trophiques. Les réseaux trophiques décrivent comment l'énergie et la ressource circulent entre les organismes, de la base au sommet de la chaine alimentaire (Figure 1). Ils représentent uniquement les interactions proie-prédateurs entre les espèces d'un écosystème et négligent les autres types d'interactions, tels que la compétition ou le mutualisme. L'environnement abiotique est intégré de façon implicite dans les modèles de réseaux trophiques : les processus démographiques sont généralement densité-dépendants, traduisant une quantité limitée de ressources exploitables par les espèces (Loreau, 2010).

Il est à noter que la notion d'unité quand on parle d'écosystèmes est subjective. Considérer les écosystèmes uniquement à une échelle locale, comme des systèmes fermés et déconnectés les uns des autres, peut donner lieu à des interprétations biaisées, telles que l'observation de pyramide des biomasses inversée. En effet, les espèces ne perçoivent pas l'espace avec la même résolution, certaines espèces ont des capacités de mouvement bien plus élevées que d'autres et répartissent leurs interactions à une très large échelle spatiale (McCann et al., 2005; Massol et al., 2011). Que ce soit par leur important domaine vital ou par leur caractère migratoire, certaines espèces agissent comme connecteur entre des écosystèmes correspondant à des entités séparées pour la plupart des espèces qui les composent. Comme nous le verrons dans la section suivante, des modèles théoriques ont été développés afin d'étudier l'effet des flux de migration sur la richesse spécifique d'une zone d'habitat.

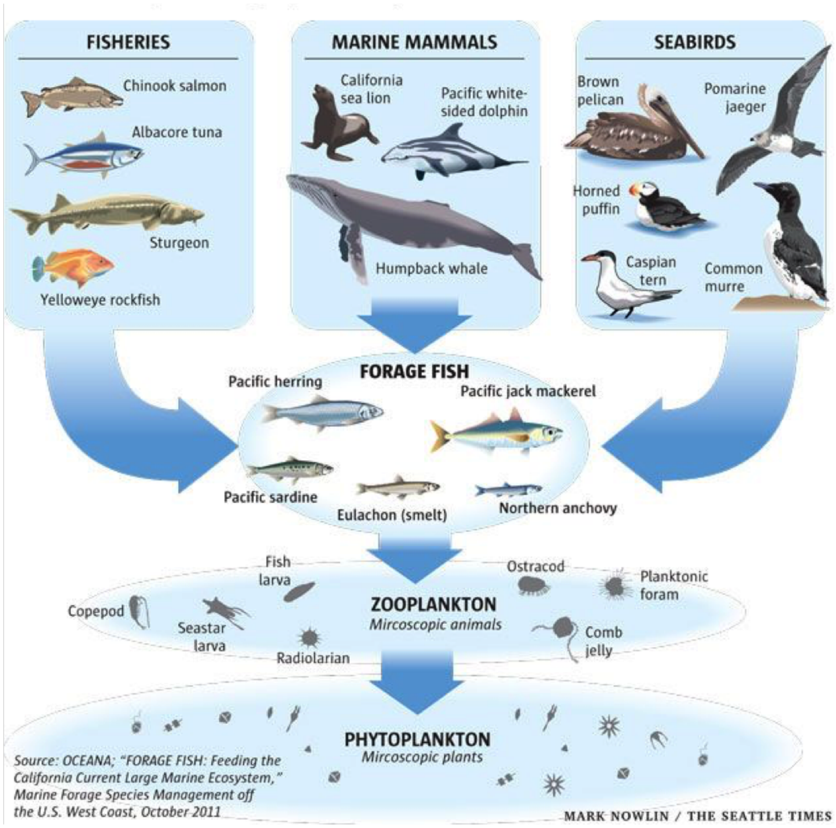

Figure 1: Représentation schématique d'un réseau trophique marin. Les flux d'énergie passent du phytoplancton au zooplancton qui est consommé par de petits poissons tels que les sardines ou les anchois, qui sont eux-mêmes consommés par différents types de prédateurs.

DIFFÉRENTES THÉORIES POUR DIFFÉRENTES ÉCHELLES SPATIALES

La théorie de la biogéographie des îles

La théorie de la biogéographie des îles (MacArthur and Wilson, 1967) est un symbole de la révolution qui est survenue il y a quatre décennies dans le domaine de l'écologie et de la biogéographie, faisant évoluer une approche principalement descriptive vers une approche analytique, qui tente de déterminer les mécanismes à l'origine des patrons observés dans la nature (Losos and Ricklefs, 2009). Cette théorie a initialement été développée dans le but d'expliquer pourquoi les îles de grande taille possèdent en général une richesse spécifique plus importante que celles de petite taille (figure 2). Le modèle ne tient pas compte de l'identité des espèces et suppose que les dynamiques de colonisation et d'extinction de ces dernières sont les facteurs essentiels pour prédire les différences de richesse spécifique entre les îles. Cette théorie, provocante pour l'époque, remit en perspective l'ensemble des travaux uniquement basés sur les différences interspécifiques à l'échelle locale pour expliquer la biodiversité. L'importance des mécanismes spatiaux dans la dynamique des populations a également été mise en évidence par Richard Levins, pionnier de la théorie des métapopulations, qui résume le concept central de ces deux théories de cette façon :

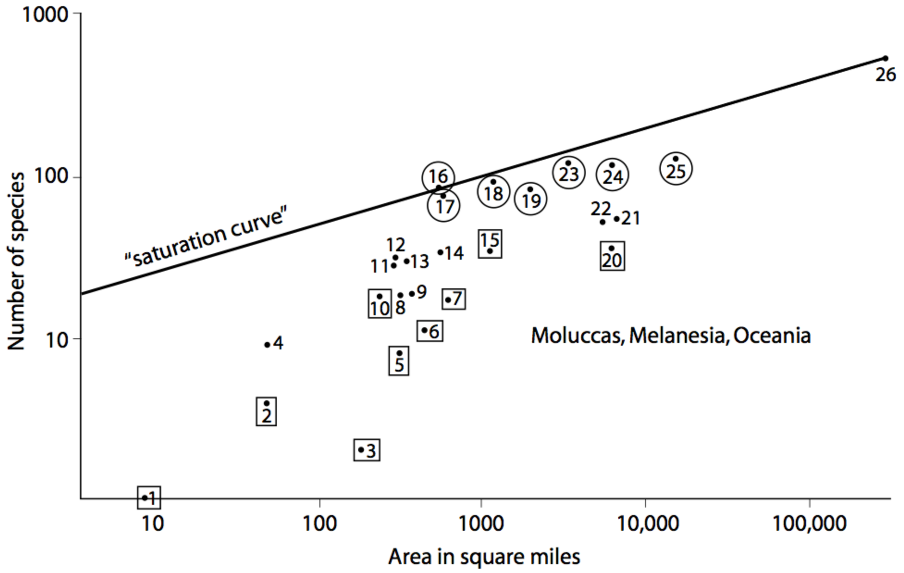

Figure 2: Courbe aire-espèce, montrant les effets de la taille et de la distance d'une île par rapport au continent sur la richesse spécifique insulaire (MacArthur and Wilson, 1967). Cette courbe correspond à une fonction de puissance entre le nombre d'espèces S et l'aire A d'une île : $S = cA^z$. Le paramètre c tient compte des variations entre les taxons et les régions biogéographiques, z est un paramètre qui demeure relativement constant à travers les taxons et est généralement compris entre 0.20 et 0.35.

« *Any real species is a population of local populations which are established by colonists, survive for a while, send out migrants and eventually disappear. The persistence of the species in a region depends on the rate of colonization successfullly balancing the local extinction rate.* » (Levins, 1968).

Depuis notre perspective actuelle, il semble surprenant que ces deux théories aient des origines indépendantes. On peut considérer que chacune d'elle explore un cas particulier d'un modèle plus général de métacommunautés (Losos and Ricklefs, 2009). Le modèle de Levins est adapté à l'étude d'un paysage très fragmenté, composé de petits fragments d'habitat. Ce modèle fait l'hypothèse que tous les fragments sont de la même taille et que la migration est également probable entre toutes les paires de fragments. Il ne contient aucune description de la structure du paysage et est centré sur la dynamique d'une espèce. Le modèle de MacArthur et Wilson correspond quant à lui à une extension de la théorie des métapopulations, où plusieurs espèces cohabitent, mais possèdent des dynamiques indépendantes les unes des autres. Ce modèle décrit une dynamique que l'on caractériserait à présent de source-puits (Pulliam, 1988) : le flux de migrants est unidirectionnel, du continent vers l'île, et la migration entre les îles est ignorée. Le continent est défini ici au sens large, il correspond à une grande zone d'habitat abritant un pool d'espèces avec des populations stables. Les îles sont l'équivalent de fragments d'habitat de taille et d'isolement variables. L'objectif est de déterminer comment le nombre d'espèces varie en fonction de la taille et de l'isolement d'une l'île par rapport au continent. Le modèle de biogéographie des îles est décrit par l'équation suivante :

$$\frac{dS}{dt} = I(P - S) - ES \tag{1}$$

Elle exprime l'évolution du nombre d'espèces présentes sur l'île en fonction du nombre d'espèces du pool continental P, du nombre d'espèces déjà présentes sur l'île S, du taux de colonisation I et d'extinction E des espèces. Ces deux derniers facteurs s'équilibrent pour fixer le nombre d'espèces capables d'occuper l'île :

$$\hat{S} = \frac{IP}{(I + E)} \tag{2}$$

Ce modèle démontre que la richesse spécifique peut être prédite par la distance géographique d'une île par rapport au continent (influençant le taux de colonisation) et par sa taille (influençant

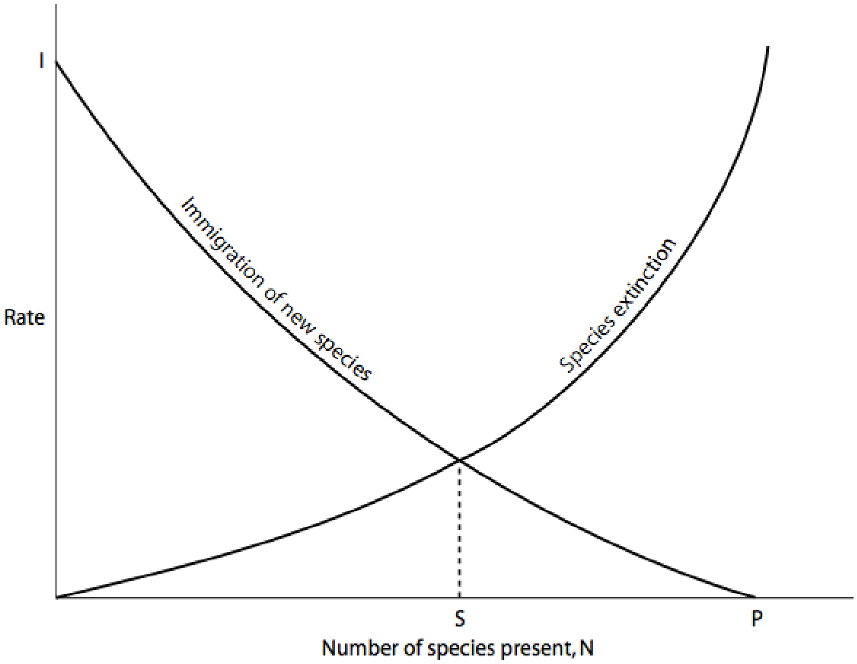

Figure 3: Illustration des conditions d'équilibre du modèle de biogéographie insulaire. Le taux d'immigration est maximal lorsqu'il n'y a pas d'espèces sur l'île et diminue à mesure que les espèces colonisent l'île. Le taux d'extinction augmente avec la richesse spécifique de l'île : plus il y a d'espèces, plus la probabilité que certaines d'entre elles disparaissent est forte. Le nombre d'espèces à l'équilibre $\hat{S}$ correspond au point d'intersection entre la courbe du taux d'immigration et celle du taux d'extinction (MacArthur and Wilson, 1967).

le taux d'extinction) (figure 3). La théorie de la biogéographie des îles propose une base théorique qui s'applique bien au-delà de l'étude des îles au sens propre. En effet, de nombreux paysages (sommets de montagnes, bosquets dans une zone agricole, réseau de lacs, récifs coralliens) peuvent être considérés de façon similaire, comportant des « îles » d'habitat dans une « mer » de non-habitat. Cette théorie a entrainé une profonde réflexion dans le domaine de la biologie de la conservation, la connectivité et la taille entre différentes zones de réserve sont à présent étudiées pour maximiser le maintien de la richesse spécifique générale (Diamond, 1975) (figure 4).

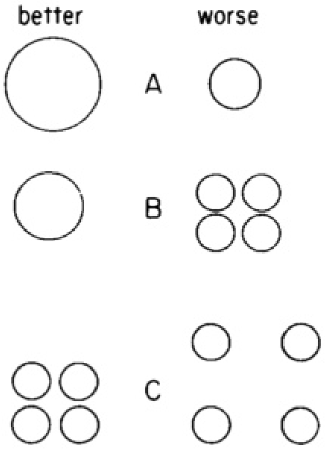

Figure 4: Illustration de quelques principes géométriques suggérés pour la création de réserves écologiques, dérivés de la théorie de la biogéographie des îles. Dans chacun des exemples A à C, le taux d'extinction des espèces sera plus faible pour les réserves présentées à gauche que celle présentée à droite. Une réserve de grande taille est préférable à une réserve de petite taille (A et B) : une réserve de grande taille peut supporter plus d'espèces à l'équilibre et aura un taux d'extinction plus faible. Si l'espace disponible est divisé en plusieurs réserves séparées, ces dernières devront être le plus proche possible les unes des autres (C). La proximité va augmenter le taux d'immigration entre les réserves et donc la probabilité que les immigrants d'une réserve recolonisent une réserve où la population s'est éteinte (Diamond, 1975).

La théorie trophique de la biogéographie des îles

Dans la théorie de la biogéographie des îles, les espèces sont supposées équivalentes au niveau de leur capacité de dispersion et de survie. Elles coexistent sur l'île, mais leurs dynamiques de colonisation et d'extinction respectives sont indépendantes les unes des autres. Or les interactions entre les espèces sont connues pour influencer leurs distributions à large échelle (Gotelli et al., 2010). Gravel et al. (2011) ont récemment développé une théorie trophique de la biogéographie des îles, qui étend la théorie classique afin de prendre en compte le rôle des interactions trophiques dans les processus de colonisation et d'extinction des espèces. Dans le modèle de MacArthur et Wilson, chaque espèce possède la même probabilité p d'occupation d'une zone d'habitat, indépendamment de la structure de l'écosystème régional ou local. La richesse spécifique à l'équilibre sur une île peut s'écrire de la façon suivante : $\hat{S} = P \times p^*$ avec P la richesse spécifique du pool régional et p^* la probabilité d'occupation des espèces à l'équilibre. La théorie trophique de la biogéographie des îles fournit quant à elle des probabilités d'occupation variables en fonction de la position trophique des espèces dans le pool régional d'espèce. Pour cela, le modèle formule deux hypothèses qui traduisent le concept de dépendance séquentielle des espèces le long des niveaux trophiques (Holt, 1997, 2009). Premièrement, pour qu'un prédateur puisse coloniser une île, au moins une de ses proies doit déjà être présente. Deuxièmement, un prédateur s'éteint lorsque sa dernière proie disparait de l'île.

Le modèle considère un réseau trophique régional avec P espèces, au sein duquel il y a P_C prédateurs. Le nombre potentiel de proies pour un prédateur donné est noté g (soit la taille de son régime alimentaire). Soit p_g la probabilité de présence d'un prédateur avec un régime alimentaire composé de g proies, on définit q_g la probabilité que ce prédateur possède au moins une de ses proies présente sur l'île et ϵ_g le taux d'extinction de ses proies. La dynamique d'occupation de l'île est donnée par l'équation suivante :

$$\frac{dp_g}{dt} = c(1 - p_g)q_g - (e + \epsilon_g)p_g \tag{3}$$

Le taux de colonisation $c(1 - p_g)q_g$ augmente avec la probabilité de trouver une proie dans la communauté locale (q_g) tandis que le taux d'extinction $(e + \epsilon_g)p_g$ augmente avec la probabilité de ne pas en trouver. On obtient la probabilité d'occupation à l'équilibre :

$$p_g^* = \frac{cq_g}{cq_g + e + \epsilon_g} \tag{4}$$

La richesse spécifique attendue sur l'île à l'équilibre $\hat{S}$ est alors obtenue en faisant la somme des probabilités de présence à l'équilibre p_g^* de chaque espèce du pool régional en fonction de la taille de son régime alimentaire g : $\hat{S} = \sum_{g=1} P_g \times p_g^*$.

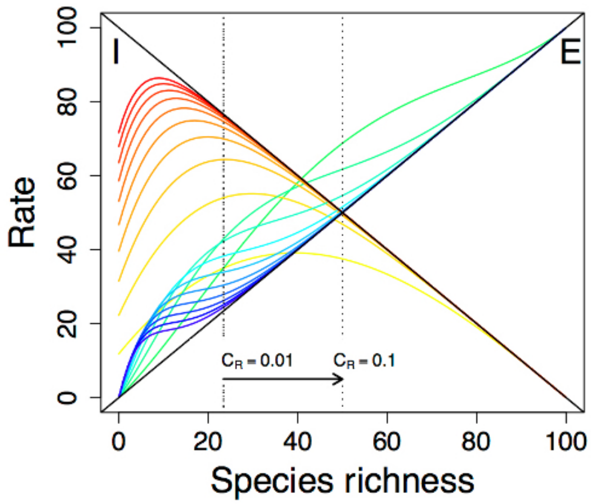

Figure 5: Prédictions de la théorie trophique de la biogéographie des îles. L'addition de contraintes trophiques aux taux de colonisation I et d'extinction E des prédateurs influence la richesse spécifique à l'équilibre sur l'île. Plus la connectance C_R du réseau trophique régional est élevée, plus la richesse spécifique à l'équilibre sur l'île est élevée.

En ajoutant seulement deux paramètres supplémentaires au modèle de MacArthur et Wilson, ce modèle trophique permet d'inclure des informations sur la structure des réseaux trophiques à l'échelle macroscopique (Figure 5). Les espèces sont différenciées en fonction de leur rang trophique. Avec une connaissance *a priori* de la structure d'un réseau trophique régional, on peut étudier l'effet de la taille et de l'isolement d'une zone d'habitat sur la structure de l'écosystème qu'elle contient (Gravel et al., 2011). Cette théorie ne prend toutefois pas en compte les différences de capacité de dispersion et de probabilité d'extinction entre les espèces, qui pourraient influencer la composition des écosystèmes insulaires.

Dans la section suivante, je montre que la masse corporelle est un trait fonctionnel déterminant à toutes les échelles du vivant. Son fort potentiel intégrateur dans le domaine de l'écologie permettrait de relier les propriétés macroécologiques des écosystèmes à des caractéristiques mesurables à l'échelle de l'espèce.

La masse corporelle à travers les échelles d'organisation du vivant

En se basant sur des principes de la chimie, de la physique et de la biologie, la théorie métabolique de l'écologie a pour ambition de relier la biologie des organismes à l'écologie des populations, des communautés et des écosystèmes (Brown et al., 2004). Cette théorie part du principe que tous les organismes subissent les mêmes contraintes énergétiques : pour se maintenir en vie, chacun d'eux possède un réseau par lequel il achemine, assimile, transforme et redistribue l'énergie et les nutriments de son environnement. L'observation d'importantes similarités dans la structure des systèmes biologiques suggère que les organismes, par le mécanisme de sélection naturelle, ont évolué pour fonctionner de la manière la plus efficace possible, ce qui se traduit par une acquisition, un transport et une utilisation optimale de l'énergie et des nutriments. Un organisme capable de maximiser l'utilisation de sa ressource pour la production de descendants capables eux-mêmes de se reproduire possède donc une forte valeur sélective (Brown et al., 1993). Ce principe est résumé en quelques mots par Alfred Lotka : '*in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favorable to the preservation of the species"* (Lotka, 1922).

Relation entre masse et taux biologiques des organismes

Le taux métabolique individuel correspond à la vitesse à laquelle un organisme prélève et transforme l'énergie et les nutriments de son environnement et les alloue aux processus permettant sa survie, sa croissance et sa reproduction (West and Brown, 1997). Les interactions entre les organismes et leur environnement (incluant les autres organismes) sont donc contraintes par le taux métabolique des espèces. Trois variables sont connues pour influencer le taux métabolique des organismes : la masse corporelle, la température et la disponibilité en ressource (Gillooly et al., 2001). La théorie métabolique de l'écologie fournit un cadre quantitatif qui permet d'étudier comment ces trois variables influencent le taux métabolique, et comment le taux métabolique influence en retour la dynamique des populations, des communautés et des écosystèmes (Allen and Gillooly, 2007). Gillooly et al.(2001) ont développé un modèle qui combine l'effet de la masse M et de la température T (en K) pour définir le taux métabolique individuel I (Gillooly et al., 2001). Le modèle peut être résumé par l'équation suivante :

$$I = i_0 M^{3/4} e^{-E/kT} \tag{5}$$

Où i_0 est une constante de normalisation indépendante de la masse et de la température de l'individu, E correspond à l'énergie d'activation (eV) et k est la constante de Boltzman.

Relation entre masse et abondance des populations

La relation entre la masse moyenne M des individus d'une espèce et la densité N de sa population, ainsi que les mécanismes liés à cette relation ont été l'objet de nombreuses études et revues de littérature (Damuth, 1981; Peters and Wassenberg, 1983; Blackburn and Gaston, 1997, 1998; Brown, 1995). Les études à l'échelle des réseaux trophiques trouvent des relations approximativement linéaires entre log(N) et log(M) avec une pente d'environ -3/4 (Cohen et al., 2003; Marquet et al., 1990; Jonsson et al., 2005; Woodward et al., 2005) (figure 6).

Une explication est proposée par l'hypothèse d'équivalence énergétique (Damuth, 1981) qui a été complétée par la théorie métabolique de l'écologie (Brown and Gillooly, 2003; Brown et al., 2004). La théorie prédit que si tous les individus d'une communauté partagent la même ressource, l'énergie métabolique totale E utilisée par chaque espèce est indépendante de la masse M : $E \propto M^0$. Comme l'énergie métabolique totale correspond au produit du taux métabolique individuel $I \propto M^{3/4}$ (équation 5) et de l'abondance N, il s'en suit $N \propto M^{-3/4}$. La relation entre la biomasse B d'une espèce et la masse moyenne M de ses individus est donc

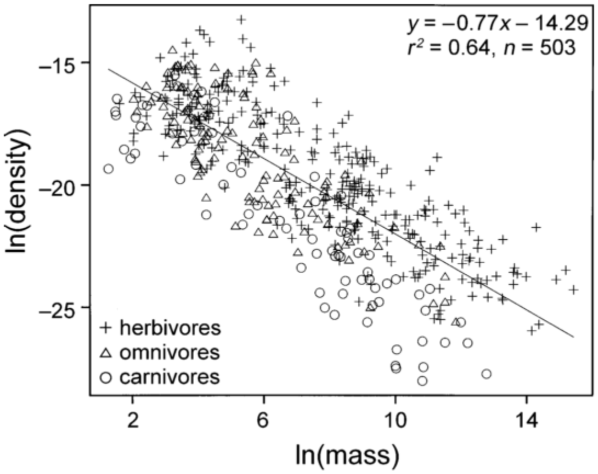

Figure 6: Corrélation entre la masse (*grammes*) et la densité de population des mammifères terrestres, (ind/km^2). La pente de cette relation donne un exposant allométrique proche de la valeur $-3/4$ prédite par la théorie métabolique (Brown et al., 2004; Damuth, 1987).

la suivante : $B \propto M \times N = M^{1/4}$.

L'hypothèse d'équivalence énergétique n'est toutefois pas respectée dans les réseaux trophiques. En effet, les consommateurs obtiennent l'énergie provenant de la ressource basale de façon indirecte, par la prédation d'espèces situées à des niveaux trophiques inférieurs. La seconde loi de la thermodynamique impose qu'il y ait moins d'énergie disponible à mesure que le niveau trophique augmente, d'une part à cause de la perte d'énergie survenant à l'intérieur d'un niveau trophique (par respiration et production de chaleur) et d'autre part à cause de la perte d'énergie survenant entre les niveaux trophiques, liée à l'inefficacité dans le transfert de la biomasse produite à un niveau trophique vers le niveau trophique supérieur (Lindeman, 1942). La perte d'énergie entre deux niveaux trophiques successifs est caractérisée par l'efficacité trophique ϵ (aussi appelée efficacité de transfert ou efficacité de Lindeman), qui correspond au ratio de l'énergie métabolique totale E du niveau trophique $n+1$ sur celle niveau inférieur n (Lindeman, 1942; Brown and Gillooly, 2003; Brown et al., 2004). D'après l'équation 5 et si l'on suppose que la température et les constantes de normalisation sont semblables entre les niveaux trophiques, on obtient :

$$\epsilon = \frac{E_{n+1}}{E_n} = \frac{N_{n+1}M_{n+1}^{3/4}}{N_n M_n^{3/4}} \tag{6}$$

Le taux auquel l'énergie diminue entre les niveaux trophiques dépend alors de l'efficacité trophique ϵ, mais également du ratio entre la masse moyenne d'un consommateur et celle de sa ressource, noté $\rho = M_{n+1}/M_n$ (Cyr, 2000; Brown and Gillooly, 2003; Brown et al., 2004). Ces deux paramètres peuvent être utilisés pour estimer la relation entre la biomasse et l'abondance des espèces à travers les niveaux trophiques. Les relations attendues entre l'énergie métabolique totale E, l'abondance N, la biomasse B et la masse M des espèces sont les suivantes (Jennings and Mackinson, 2003; Trebilco et al., 2013) :

$$E = x_E \times M^{log(\epsilon)/log(\rho)} \tag{7}$$

$$N = x_N \times M^{-3/4+log(\epsilon)/log(\rho)} \tag{8}$$

$$B = x_B \times M^{1/4+log(\epsilon)/log(\rho)} \tag{9}$$

où x_E, x_N et x_B sont des constantes de normalisation indépendantes de la masse des espèces.

Pour modéliser la distribution de la biomasse en fonction de la masse des espèces d'un réseau trophique, l'efficacité trophique et le ratio moyen de la masse entre prédateurs et proies doivent donc être estimés. Le ratio moyen de masse entre prédateur et proie est typiquement de 10^2 à 10^3 (Cushing, 1975; Jennings et al., 2002) (figure 7). Dans les écosystèmes marins, l'efficacité trophique est plus élevée aux niveaux trophiques faibles, avec une moyenne de

0.13 entre le phytoplancton et le zooplancton et de 0.10 entre le zooplancton et les poissons (Ware, 2000). Ces valeurs relativement faibles (de l'ordre de 10%) sont similaires dans les écosystèmes terrestres et lacustres (Jennings et al., 2002). Les processus liés à la dissipation d'énergie entre les niveaux trophiques incluent la respiration, la croissance et la reproduction. La qualité nutritionnelle des ressources consommées influence également le degré d'efficacité du transfert d'énergie. En effet les consommateurs convertissent plus efficacement les sources alimentaires qui fournissent des apports nutritionnels optimaux.

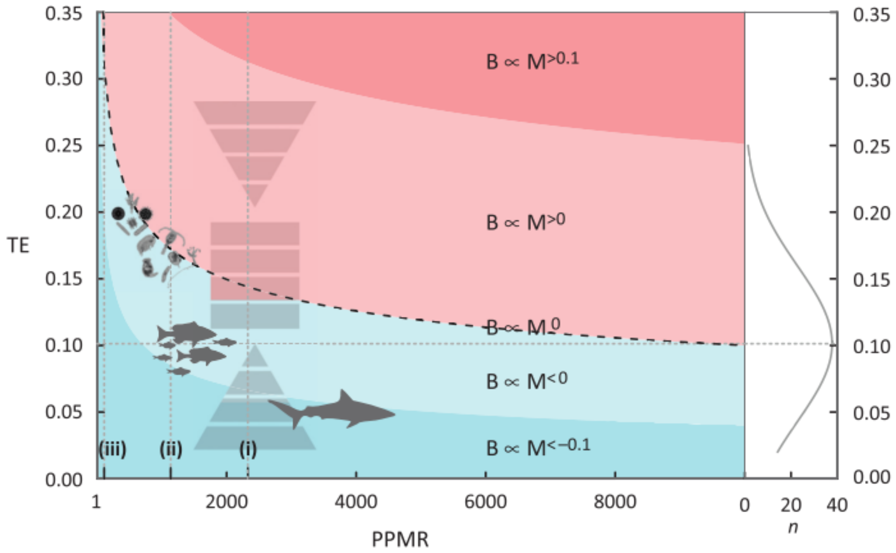

Figure 7: La forme des pyramides écologiques dépend de l'efficacité trophique ϵ (ici TE) et du ratio de masse entre prédateurs et proies ρ (ici PPMR). Les pyramides de biomasse ont une forme classique lorsque $B \propto M^{<0}$ (en bleu) et inversée quand $B \propto M^{>0}$ (en rose). La biomasse est invariante suivant la masse lorsque $B \propto M^0$. L'axe vertical de droite montre la distribution de l'efficacité trophique de réseaux trophiques marins (moyenne = 0.101, s.d. = 0.058) (Pauly and Christensen, 1995) la ligne en pointillé indique la moyenne (Trebilco et al., 2013).

Relation entre masse et structure des réseaux trophiques

Les interactions trophiques entre les espèces, le processus par lequel l'énergie et la ressource passent à travers les organismes, jouent un rôle fondamental dans le fonctionnement des écosystèmes (Lotka, 1925; Lindeman, 1942). Les réseaux trophiques décrivent la topologie de ces interactions, ce qui en fait un outil central en écologie pour étudier la diversité et la structure complexe des écosystèmes (Dunne, 2006). Le modèle de niche a été proposé par Williams and Martinez (2000) dans le but de générer et de prédire la structure de réseaux trophiques empiriques en utilisant un minimum d'hypothèses. Bien que ce modèle théorique donne une représentation simplifiée des réseaux trophiques, dans laquelle les interactions entre les espèces ne sont pas quantifiées, mais uniquement représentées de façon binaire (présence/absence), il capture la structure topologique liée au processus de transfert d'énergie survenant dans un écosystème (Williams and Martinez, 2000). Ce modèle se base sur deux paramètres d'entrée quantifiables empiriquement : la richesse spécifique S et la connectance $C = L/S^2$ où L correspond au nombre de liens observés dans un réseau trophique et S^2 à l'ensemble des liens potentiellement réalisables. La connectance C traduit donc la proportion de liens potentiels entre les espèces qui sont réalisés dans le réseau trophique (Dunne, 2006). Cette approche a été initialement proposée dans le modèle de cascade, qui suggère que les réseaux trophiques observés dans les données empiriques ne sont pas aléatoires, mais gouvernés par des règles simples (Cohen and Newman, 1985). Un seul axe et quelques hypothèses, traduisant la hiérarchie trophique entre les espèces, suffisent à générer des topologies de réseaux trophiques réalistes.

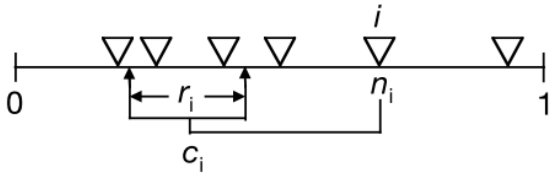

Figure 8: Schéma explicatif des règles du modèle de niche, représentant pour l'espèce i la position de sa niche n_i, le centre c_i et la gamme de ses proies potentielles r_i. Dans cet exemple où six espèces sont représentées (triangles inversés), deux espèces tombent dans la gamme de proies de l'espèce i.

Le modèle de niche diffère néanmoins par les règles qu'il utilise pour distribuer les liens entre les espèces. Une valeur aléatoire de niche n_i, issue d'une distribution uniforme dans l'intervalle [0,1], est assignée à chaque espèce i (figure 8). L'espèce i consomme toutes les espèces qui se trouvent dans sa gamme de proies potentielles r_i (c'est-à-dire la taille de son régime alimentaire). La taille de r_i est assignée aléatoirement à partir d'une fonction β, dont la valeur attendue $2C$ est multipliée par n_i afin d'obtenir une connectance C proche de celle définie initialement. Le centre de la gamme de proies potentielles c_i est issu d'une distribution uniforme dans l'intervalle $[r_i/2, 1 - r_i/2]$. Cela permet de conserver toutes les gammes de proies potentielles dans l'intervalle [0,1] et de placer le centre de la gamme de proies d'une espèce c_i toujours plus bas que sa propre valeur de niche n_i. Cette méthode autorise l'existence de cannibalisme puisque la moitié supérieure du r_i d'une espèce peut contenir sa propre valeur de niche n_i. Les espèces avec la valeur de niche n_i la plus faible ne possèdent pas de proies, par conséquent chaque réseau trophique possède au moins une espèce basale (Williams and Martinez, 2000). En résumé, chaque espèce possède trois traits : la position de sa niche n_i, la position c_i et la taille r_i de son régime alimentaire.

Le modèle de niche a été largement utilisé pour modéliser la structure de réseaux trophiques complexes, sans que le sens écologique de la niche à une dimension soit clairement défini. L'hypothèse de hiérarchie trophique du modèle pourrait refléter des processus naturels tels que les contraintes de taille sur l'acquisition des ressources des espèces (Dunne, 2006; Cohen et al., 1993; Arim et al., 2010; Trebilco et al., 2013). En ce sens, des études récentes proposent d'utiliser la masse corporelle comme dimension de la niche (Williams et al., 2010; Riede et al., 2011; Gravel et al., 2013).

Plus particulièrement, dans le modèle allométrique de niche développé par Gravel et al. (2013), un réseau trophique réaliste peut être reconstruit à partir de la distribution de masse des espèces et de la relation linéaire entre le logarithme de la masse des prédateurs en fonction de celle de leurs proies (figure 9) (Gravel et al., 2013). Les trois traits du modèle de niche sont dérivés de la façon suivante. Pour un prédateur i, la position de sa niche n_i correspond à la valeur standardisée entre 0 et 1 du logarithme de sa masse $log_{10}(M_i)$ (le minimum et le maximum de l'axe de la niche correspondent à la masse minimale et maximale des espèces de

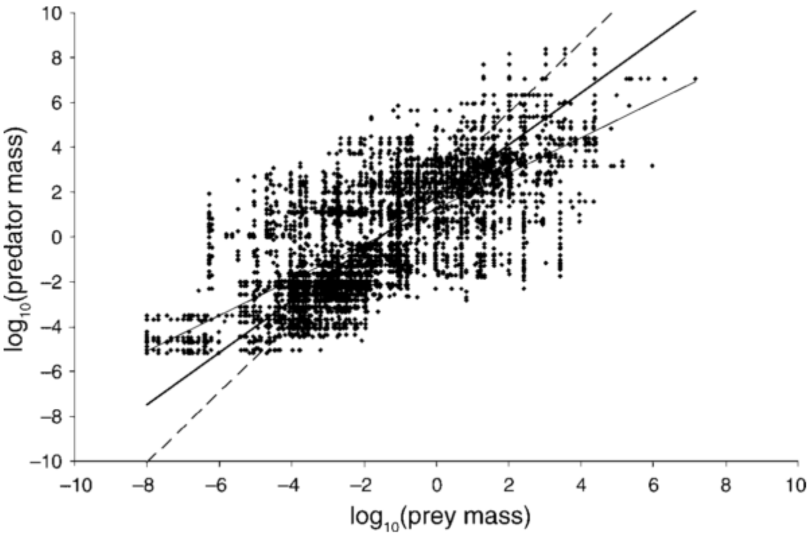

Figure 9: Masse des prédateurs en fonction de la masse des proies. La droite de régression principale (ligne continue) explique 86% de la variance du log_{10} de la masse des proies (n = 5103). La ligne en pointillé correspond à la régression inverse (log_{10} de la masse des proies vs log_{10} de la masse des prédateurs) dessinée en échangeant les axes (Brose et al., 2005b, 2006a).

l'écosystème). La position de sa gamme de proies c_i correspond à la masse moyenne de ses proies. Elle est estimée à partir de la droite de régression de la masse des proies $log_{10}(M_{prey})$ en fonction de la masse des prédateurs $log_{10}(M_{pred})$ (figure 9).

$$log_{10}(M_{prey}) = a \times log_{10}(M_{pred}) + b \tag{10}$$

La pente a et l'origine b de la droite vont donc déterminer la position de c_i en fonction de n_i tandis que la taille du régime alimentaire r_i du prédateur est bornée par les régressions quantiles à 5% et 95%. Le modèle de niche allométrique permet donc de générer des réseaux trophiques possédant une structure trophique réaliste à partir de la relation statistique entre la masse corporelle des prédateurs et celle de leurs proies. Ce modèle s'applique particulièrement bien aux réseaux trophiques où la relation entre la masse des prédateurs et des proies est forte, tel que les réseaux trophiques pélagiques des écosystèmes marins (Gravel et al., 2013).

Échelle macroécologique : relation entre masse et dynamique spatiale des espèces

Les modèles de biogéographie des îles vus précédement partent du principe que les dynamiques de colonisation et d'extinction des espèces sont les facteurs essentiels pour prédire les différences de richesse spécifique entre les îles. Or les probabilités de dispersion et d'extinction des espèces sont corrélées à leur masse corporelle. D'une part, la probabilité d'extinction est supposée augmenter avec la masse corporelle en conséquence de la relation négative entre l'abondance et la masse corporelle des populations (Damuth, 1981; Nee et al., 1991; Blackburn, 1999; White et al., 2007). Cette relation demeure néanmoins peu documentée et d'autres facteurs liés à la masse pourraient modifier cette relation, tels que la plus forte dépendance des espèces de petite taille à la complexité de l'habitat (Gaston and Blackburn, 2000; Graham et al., 2011; Marquet and Taper, 1998; Okie and Brown, 2009). D'autre part, l'effet positif de la masse corporelle sur la probabilité de colonisation est relativement bien documenté, notamment pour les organismes aquatiques (Peters and Wassenberg, 1983; Wieters et al., 2008). Dans les écosystèmes marins, tous les traits d'histoire de vie favorisant la dispersion, tels que la fécondité, la mobilité ou la généralité du régime alimentaire, sont positivement corrélés à la masse des espèces (Mora et al., 2003; Luiz et al., 2013; Nash et al., 2015; Kulbicki et al., 2013; Stier et al., 2014).

VERS UNE THÉORIE MULTI-ÉCHELLES POUR ÉTUDIER LA STABILITÉ DES ÉCOSYSTÈMES

Identifier les mécanismes liés la stabilité des écosystèmes

Comme nous l'avons vu en début d'introduction, comprendre comment les nombreux écosystèmes existant dans la nature sont capables de persister est un défi central en écologie

(McCann, 2000; Dunne, 2006). La stabilité des écosystèmes est en effet essentielle pour garantir le maintien de services écosystémiques, mais cette compréhension est également un défi scientifique. Il a été démontré que des écosystèmes aléatoires aussi complexes que ceux observés dans la nature possèdent des probabilités de persistance proche de zéro (May, 1972, 2001). La complexité d'un écosystème est définie ici comme le produit de la richesse spécifique, de la connectance et de la variance de la force des interactions entre les espèces. Les recherches pionnières suggéraient que la complexité stabilisait les écosystèmes en réduisant la dépendance des prédateurs sur chacune de leurs proies (MacArthur, 1955; Paine, 1966). Dans les années 70, Robert May démontra que cette explication est mathématiquement improbable en étudiant la stabilité locale d'écosystèmes théoriques :

> « *In short, there is no comfortable theorem assuring that increasing diversity and complexity beget enhanced community stability ; rather, as a mathematical generality the opposite is true. The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems.* » (May, 2001).

Un système est défini comme localement stable s'il retourne à son équilibre initial après une petite perturbation. Dans le cas des écosystèmes, la stabilité locale mesure les variations démographiques des espèces. Un écosystème est considéré comme stable si les abondances des espèces qui la composent retournent à leur équilibre initial après une perturbation. Au contraire, un écosystème dans laquelle on observe des explosions démographiques est considéré comme instable.

De nombreuses études se sont intéressées aux « stratégies » permettant aux écosystèmes complexes de persister (voir McCann (2000) pour une revue de littérature) et ont montré comment l'interdépendance de la masse corporelle (Yodzis and Innes, 1992), de la force des interactions (Paine, 1980; De Ruiter et al., 1995; McCann and Hastings, 1998; Neutel et al., 2002; Berlow et al., 2004; Brose et al., 2005a) et de la structure des réseaux trophiques (Dunne, 2006; McCann and Hastings, 1997; Vandermeer, 2006) pourrait expliquer la stabilité et la persistance des écosystèmes complexes. Les prédictions du modèle de R. May n'ont cependant jamais été testées à partir de données d'écosystèmes réels et nous ignorons toujours s'il existe une relation entre la stabilité et la complexité des écosystèmes.

Comprendre les mécanismes permettant l'émergence d'écosystèmes stables

D'autre part, la mise en évidence des propriétés stabilisantes des écosystèmes ne fournit qu'une réponse partielle au paradoxe de la stabilité des écosystèmes complexes. L'étape suivante consiste à identifier les mécanismes à l'origine de ces propriétés et de réussir à les modéliser en conservant un équilibre entre simplicité et pouvoir explicatif. En ce sens, l'utilisation de la masse corporelle pour déterminer la structure des écosystèmes et la force des interactions trophiques semble être une voie prometteuse, permettant de relier *in fine* les propriétés non aléatoires des écosystèmes à des caractéristiques mesurables à l'échelle de l'espèce.

Effet de la dynamique spatiale des espèces sur le fonctionnement des écosystèmes

La théorie de la biogéographie des îles (TBI) démontre que les caractéristiques géographiques de l'habitat influencent la richesse spécifique d'un assemblage local. Dans le contexte actuel de fragmentation et de destruction des habitats naturels par les activités humaines, on est alors en droit de s'interroger sur les effets potentiels de la structure de l'habitat sur d'autres variables, telle que la diversité fonctionnelle, qui influencent la structure et le fonctionnement des écosystèmes. Toutes les espèces ne possèdent pas la même sensibilité face à la modification de leur zone d'habitat. On s'attend par exemple à ce que les populations d'espèces très abondantes soient moins sensibles à une forte réduction de leur habitat naturel que les populations composées de quelques individus. On s'attend aussi à ce que les espèces possédant des capacités de dispersion importantes soient moins touchées par la fragmentation de leur habitat. Bien qu'élégante par sa simplicité, la TBI ne permet pas de telles prédictions, car elle ne prend pas en compte les différences interspécifiques influençant les probabilités de présence des espèces sur une île. Le développement de modèles biogéographiques prédisant des probabilités de présence dépendantes des traits fonctionnels des espèces permettrait de relier les mécanismes de structuration des écosystèmes agissant à l'échelle locale et biogéographique.

ARTICULATION DES CHAPITRES DE LA THÈSE

L'objectif général de cette thèse est l'intégration dans un cadre commun des mécanismes d'assemblage des espèces opérant à différentes échelles d'organisation afin de prédire l'effet des changements globaux sur la structure et le fonctionnement des écosystèmes. Cette synthèse permettra d'étudier l'effet de la perte d'habitat sur la structure et la stabilité des écosystèmes. La suite de ce document est divisée en trois chapitres qui s'articulent autour de mon objectif général (Figure 10) et qui abordent respectivement les trois problématiques mises en avant dans la section précédente. J'ai également placé en annexe un manuscrit qui ajoute une perspective intéressante à la notion de stabilité des écosystèmes, en montrant que les écosystèmes marins étaient structurés en réseaux trophiques dès le Dévonien (il y a 380 Ma).

Chapitre 1 : Quelles propriétés favorisent la stabilité des écosystèmes ?

L'objectif de mon premier chapitre de thèse est d'étudier la relation entre la complexité et la stabilité des écosystèmes en me basant sur des données empiriques. Ces données sont composées de 116 réseaux trophiques quantitatifs provenant de modèles Ecopath. Un modèle Ecopath décrit les flux d'énergie entre les compartiments d'un écosystème et constitue un outil très largement utilisé pour la gestion écosystémique des pêches. Grâce aux données disponibles dans ces modèles, c'est-à-dire la biomasse, le taux de consommation, l'efficacité de conversion de la ressource en biomasse et le régime alimentaire de chaque espèce, je suis en mesure d'estimer la complexité et la stabilité de chacun des réseaux trophiques Ecopath. La complexité correspond au produit de la richesse spécifique, de la connectance et de la variance

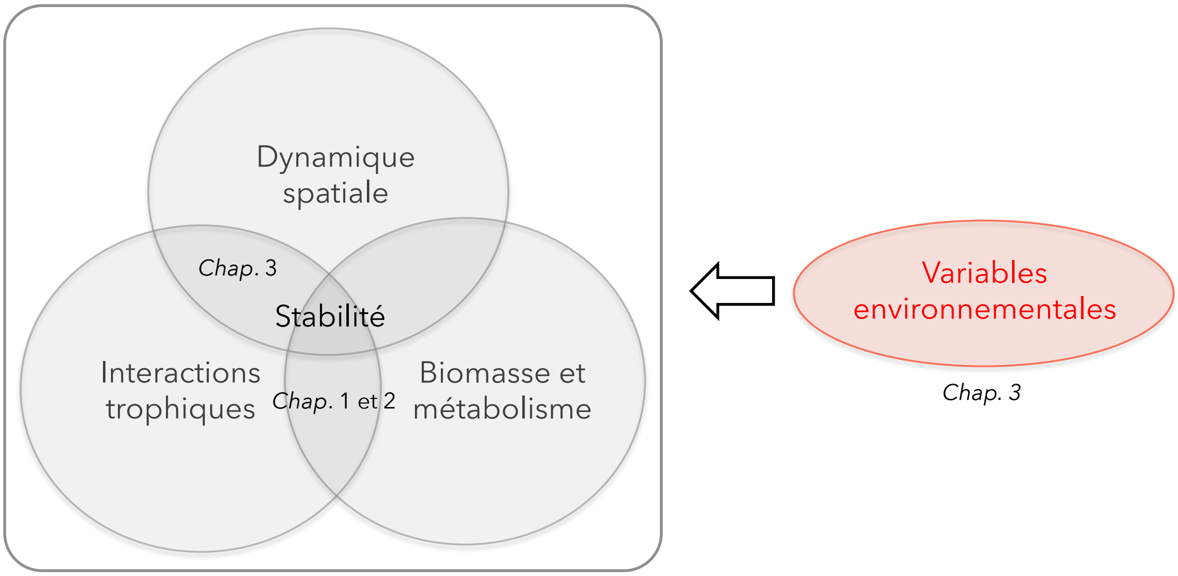

Figure 10: Représentation conceptuelle de la thèse. Le chapitre 1 étudie les propriétés stabilisantes des écosystèmes complexes. Le chapitre 2 relie la masse corporelle des espèces à la structure et aux flux de biomasse circulant dans un écosystème, permettant d'étudier sa stabilité à partir des caractéristiques des espèces qui le composent. Enfin, le chapitre 3 vise l'intégration de la structure des écosystèmes à la théorie de la biogéographie des îles, afin d'étudier l'influence de la taille et de l'isolement d'une zone d'habitat sur la composition des espèces qu'elle abrite.

de la force des interactions entre les espèces. À partir de ces données, j'étudie également les propriétés non aléatoires qui différencient les écosystèmes réels des écosystèmes théoriques à l'origine du débat sur la relation complexité-stabilité.

Chapitre 2 : Relier la stabilité des écosystèmes aux traits fonctionnels des espèces qui le composent

Dans mon second chapitre de thèse, je propose de relier ces propriétés non aléatoires à des caractéristiques mesurables à l'échelle de l'espèce. Différents modèles théoriques ont été développés dans le but de reproduire des écosystèmes possédant une structure réaliste. Une voie prometteuse semble être l'utilisation de la masse corporelle, à la fois pour déterminer la topologie d'un réseau trophique, mais également pour déterminer la force des interactions entre proies et prédateurs. J'utilise donc la masse corporelle pour construire des réseaux trophiques réalistes, et j'étudie comment la masse corporelle des espèces va influencer la structure et la stabilité de l'écosystème.

Chapitre 3 : Effet de la taille et de l'isolement de l'habitat sur la structure en taille des espèces d'un écosystème

Dans mon troisième chapitre de thèse, j'ai pour objectif de déterminer quels sont les mécanismes écologiques responsables de la variation spatiale de la masse corporelle des espèces présentent sur un fragment d'habitat de taille et d'isolement donné. Pour cela, je développe une approche qui prend en compte les traits fonctionnels des espèces ainsi que les interactions trophiques pour caractériser la dynamique spatiale et les probabilités de présence d'une espèce dans un fragment d'habitat. Pour étudier l'effet de l'espace sur la masse corporelle des espèces composant un assemblage local, j'utilise trois modèles biogéographiques, décrivant chacun des mécanismes écologiques différents. J'étudie les prédictions que font ces modèles concernant l'effet de la taille et de l'isolement de l'habitat sur la moyenne et l'écart type de la masse corporelle des espèces d'un assemblage local. Je compare ensuite ces prédictions aux distributions de masse des assemblages de poissons tropicaux. J'utilise un jeu de données dans lequel les tailles de 688 poissons piscivores et de 368 poissons herbivores, ainsi que leur présence/absence sur 134 sites sont disponibles. Pour chaque site, la taille du récif ainsi que son isolement ont été mesurés.

ARTICLE 1

QUELLES PROPRIÉTÉS FAVORISENT LA STABILITÉ DES ÉCOSYSTÈMES ?

1.1 TITRE DE L'ARTICLE

Pas de relation entre la complexité et la stabilité dans les écosystèmes empiriques

1.2 RÉSUMÉ

La compréhension des mécanismes responsables de la stabilité et de la persistance des écosystèmes est un défi majeur en écologie. Robert May a démontré que les écosystèmes complexes construits de façon aléatoire sont en général moins stables que les écosystèmes pauvres en espèces. Peu d'études ont tenté de tester cette prédiction de façon empirique, et nous ignorons toujours s'il existe une relation entre la stabilité et la complexité des écosystèmes naturels. Dans cette étude, nous analysons la stabilité de 116 réseaux trophiques quantitatifs échantillonnés à l'échelle mondiale. Nous trouvons que les descripteurs classiques de la complexité (richesse spécifique, connectance et force des interactions) ne sont pas liés à la stabilité des réseaux trophiques empiriques. Une analyse approfondie révèle que la corrélation entre l'effet des prédateurs sur leurs proies et celui des proies sur leurs prédateurs, combinée à une forte fréquence d'interactions de faible intensité, stabilise la dynamique des réseaux trophiques par rapport à ce qui est attendu pour des écosystèmes aléatoires. Nous concluons que les réseaux trophiques empiriques possèdent différentes propriétés non aléatoires qui contribuent à l'absence de relation entre la complexité et la stabilité des écosystèmes.

Cet article intitulé "*No complexity–stability relationship in empirical ecosystems*", fut corédigé par Charlotte Moritz, Lyne Morissette, Pierre Legagneux, François Massol, Philippe

Archambault, Dominique Gravel et moi-même. Il a été publié en août 2016 dans la revue *Nature Communications*.

En tant que première auteure, j'ai contribué à la conception de l'étude et au développement des outils analytiques utilisés. J'ai réalisé la recherche bibliographique, la compilation et l'analyse des données ainsi que les tests de permutations qui ont permis d'identifier les propriétés qui contribuent à la stabilité des écosystèmes. J'ai rédigé le manuscrit et réalisé les tableaux et les figures. Charlotte Moritz, seconde auteure, a contribué à la conception de l'étude, à l'analyse des données et à l'édition du manuscrit. Lyne Morissette, troisième auteure, a fourni la majorité des modèles Ecopath et a contribué à l'analyse des données. Pierre Legagneux, quatrième auteur, a contribué à la conception de l'étude, au développement des outils analytiques, a fourni les données empiriques provenant d'écosystèmes terrestres arctiques et a contribué à l'édition du manuscrit. François Massol, cinquième auteur, a contribué au développement des outils analytiques, à la rédaction et à l'édition du manuscrit. Le professeur Philippe Archambault, sixième auteur, a contribué à l'édition du manuscrit. Le professeur Dominique Gravel, dernier auteur, a fourni l'idée originale, a contribué au développement des outils analytiques, à la rédaction et à l'édition du manuscrit.

Cet article a obtenu le Prix *"Découverte scientifique de l'année BORÉAS"* du groupe de recherche sur les environnements nordiques BORÉAS en 2016. Il a fait l'objet de communiqués de presse du CNRS, de l'Université du Québec à Rimouski et de l'Université de Sherbrooke. J'ai également été invitée à présenter les résultats de ce travail de recherche au symposium annuel *"Current Themes in Ecology 2016"* organisé en novembre par le NERN (Netherlands Ecological Research Network) à Lunteren, Pays-Bas.

1.3 TITLE

No complexity–stability relationship in empirical ecosystems.

Nature Communications **7**, 12573 (2016).

1.4 ABSTRACT

Understanding the mechanisms responsible for stability and persistence of ecosystems is one of the greatest challenges in ecology. Robert May showed that, contrary to intuition, complex randomly built ecosystems are less likely to be stable than simpler ones. Few attempts have been tried to test May's prediction empirically, and we still ignore what is the actual complexity–stability relationship in natural ecosystems. Here we perform a stability analysis of 116 quantitative food webs sampled worldwide. We find that classic descriptors of complexity (species richness, connectance and interaction strength) are not associated with stability in empirical food webs. Further analysis reveals that a correlation between the effects of predators on prey and those of prey on predators, combined with a high frequency of weak interactions, stabilize food web dynamics relative to the random expectation. We conclude that empirical food webs have several non-random properties contributing to the absence of a complexity–stability relationship.

1.5 INTRODUCTION

The complexity–stability debate (McCann, 2000), initiated more than 40 years ago, stems from two apparently conflicting observations. On the one hand, complex ecosystems are ubiquitous in nature, as illustrated by diverse tropical forests, coral reefs or intertidal communities. These observations have inspired ecologists to hypothesize that complexity could stabilize ecosystems (MacArthur, 1955; Paine, 1966). On the other hand, theory states that complex random systems are less likely to recover from small perturbations than simpler ones (Levins, 1968; Gardner and Ashby, 1970; May, 1972). This prediction was put forth by Robert May (May, 1972), who studied the relationship between complexity and stability in random ecosystems. Ecosystem complexity was defined as $\sigma\sqrt{SC}$ where S is species richness, C is connectance (the probability that any two species will interact with each other) and σ is the s.d. of interaction strength. May (1972) predicted that a system could be stable only if the criterion $\sigma\sqrt{SC} < \bar{d}$ was satisfied, where $\bar{d}$ expresses the magnitude of intraspecific competition.

May (1972) analysed the local stability of randomly generated community matrices. A community matrix is obtained from the linearization around a feasible equilibrium of a system of equations describing the dynamics of the community. The entries of a community matrix quantify the impact of a change in abundance of one species on the dynamics of another species. The real part of the dominant eigenvalue of the community matrix indicates the rate at which a system returns to equilibrium (if negative) or moves away from it (if positive) after small perturbations. It does not guarantee stability following large perturbations (global stability), or that the perturbation will not first amplify before vanishing (reactivity) (Neubert and Caswell, 1997; Tang and Allesina, 2014).

The stability of a random community matrix can be predicted thanks to the generalization of the circular law (Tao et al., 2010). This theory states that the distribution of the eigenvalues of a $S \times S$ matrix, whose coefficients are independently sampled from a distribution of mean 0 and variance 1, converges to the uniform distribution in the unit circle in the complex plane, as $S \to \infty$. The centre of the circle $-\bar{d}$ corresponds to the mean of intraspecific interaction terms ($\bar{d} > 0$), provided that the variance in intraspecific interaction terms is not too large (Allesina and Tang, 2012). The radius R is related to interspecific interactions and is equal to $\sigma\sqrt{SC}$ in random ecosystems, that is May's complexity measure. Thus, local stability is determined by the combination of two components; one can increase the stability of a system by (i) moving the centre of the circle to more negative values along the real axis by increasing intraspecific competition or (ii) decreasing the radius of the circle by reducing the complexity of the system (Fig. 11c).

Tang et al. (2014) proposed that another quantity critically affects the stability of more realistic ecosystems, such as predator–prey communities, namely the correlation between coefficients across the diagonal of the community matrix ρ. They subsequently found that the stability criterion for large and random community matrices is $\sigma \sqrt{SC}(1+\rho) - E < \bar{d}$ where E is the mean of the elements of the community matrix (including zeros). In other words, the correlation between pairs of interactions decreases stability if positive ($\rho > 0$) but increases stability if negative ($\rho < 0$) with respect to May's case (Tang et al., 2014).

Here we attempt to solve the complexity–stability paradox with a local stability analysis of 116 quantitative food webs sampled worldwide from marine, freshwater and terrestrial habitats. This is the largest data set ever used to test May's prediction empirically. The complexity–stability relationship has been previously studied with direct observations of energy flows between species, but on a small number of food webs (from one to seven) (De Ruiter et al., 1995; Neutel et al., 2007; Emmerson and Raffaelli, 2004). Recently, Neutel and Thorne (2014) reported an absence of complexity–stability relationship in 21 soil food webs, while James et al. (2015) found a weak positive relationship based on 21 food webs from terrestrial and marine habitats. These studies, however, used heterogeneous methodologies, shared several networks, and in several cases, interaction strengths were derived from assumptions rather than from direct observations (Yodzis, 1981; Neutel et al., 2002).

The studied food webs were all compiled on the same standard methodology to satisfy the Ecopath modelling framework (Christensen, 1992). Ecopath is a trophic model, the most widely used tool for ecosystem-based fisheries management, and has also been used to characterize unexploited terrestrial ecosystems (Legagneux et al., 2014). It relies on a system of linear equations established with the aim of balancing the inflows and the outflows of each compartment (Christensen, 1992; Christensen et al., 2000). A large amount of information is included in Ecopath models, such as diet composition, biomass, production and consump-

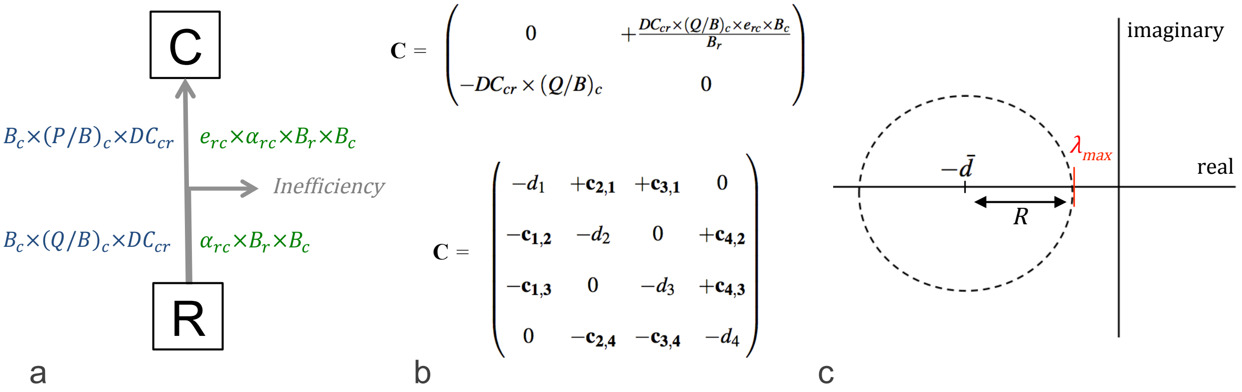

Figure 11: **Method summary:** (a) Equivalence between Ecopath and Lotka-Volterra models: simplified diagram of trophic flows between one consumer C and one resource R parameterized with Ecopath model (in blue) and Lotka-Volterra model (in green). B is biomass ($t\,km^{-2}$), $(P/B)_c$ and $(Q/B)_c$ are the production/biomass and consumption/biomass ratios of C respectively ($year^{-1}$), DC_{cr} is the proportion of resource R in the diet of consumer C, e_{rc} expresses the efficiency of a consumer to convert resource energy into biomass with $e_{rc} = \frac{(P/B)_c}{(Q/B)_c}$. (b) Community matrix construction: derivation of community matrix elements for the simplified food web presented in diagram A, and an example of community matrix structure observed in real food webs. (c) Measure of stability: the eigenvalues of a large community matrix are uniformly distributed on a circle on the complex plane (axes cross at the origin). On the real axis, the dominant eigenvalue $Re(\lambda_{max}) = R - \bar{d}$, where the center of the circle $-\bar{d}$ is equal to the mean of intraspecific interaction terms ($\bar{d} > 0$), and the radius R is related to interspecific interaction terms (i.e. off diagonal elements of the community matrix) and is equal to $\sigma\sqrt{SC}$ in random matrices. For predator-prey communities, the eigenvalues are uniformly distributed on an ellipse with an horizontal half axis $R = (1+\rho)\sigma\sqrt{SC}$ (Allesina and Tang, 2012).

tion rates of each species, providing an accurate representation of feeding interactions within food webs. Ecopath models provide a unique opportunity to build realistic community matrices with empirical data derived from a standardized protocol. The level of resolution of marine Ecopath models is, however, heterogeneous through food web compartments, with detailed compartments for collected fishes and more aggregated compartments for plankton and invertebrates.

We translated parameters of the Ecopath models into interaction coefficients of the Lotka–Volterra interaction model following the same approach as De Ruiter et al. (1995). Interaction coefficients from all pairwise interactions of a food web make the interaction matrix $\mathbf{A} = [\alpha_{ij}]$. Because of the equilibrium assumption of Ecopath models, a community matrix **C** can be constructed for each food web by multiplying the interaction matrix **A** with species biomass (Fig. 11b).

We measured food web stability using the real part of the dominant eigenvalue of the community matrix **C** to be directly comparable to May's approach. The diagonal elements of the community matrices were set to 0 to focus on the effect of interspecific interactions on stability. Note that $Re(\lambda_{max})$ will be positive, since $R > 0$ (Fig. 11c). This method is comparable to other studies that calculated stability by assessing the level of intraspecific interaction needed for all eigenvalues in a community matrix to have negative real parts (Neutel et al., 2007; Neutel and Thorne, 2014; Neutel et al., 2002).

We show that complexity is not related to stability in empirical ecosystems. We find that the intrinsic energetic organization of food webs creates a high frequency of weak interactions and a correlation between pairs of interactions. These non-random properties are highly stabilizing and contribute to the absence of a complexity–stability relationship.

1.6 RESULTS

1.6.1 Complexity–stability relationship in empirical ecosystems

We first investigated the relationship between stability and classic descriptors of ecosystem complexity, that is, species richness S, connectance C and s.d. of interaction strengths σ (May, 2001). We observed no relationship between food web stability and species richness, neither with connectance nor with s.d. of interaction strength (Fig. 12). Further analyses revealed that this result was robust to the variability of sampling intensity among the 116 food webs and to uncertainty related to Ecopath parameter estimates (Methods section, Supplementary Figs 15,16 and 17). We neither found significant complexity–stability relationship using the stability criterion derived by Tang et al. (2014) that integrates correlation between pairs of interactions and mean of interaction strengths (Supplementary Fig. 18). The absence of a complexity–stability relationship in empirical food webs demonstrates that the random matrices studied by May (1972) to derive stability criteria deviate significantly from empirical systems. As May (2001) stated in the re-edition of his book, his theory provides the baseline against which we should compare empirical systems and find the non-random features stabilizing them. We therefore investigated further the mechanisms preventing the negative relationship between complexity and stability to occur.

1.6.2 Correlation between complexity parameters

May's stability criterion $\sigma\sqrt{SC} < \bar{d}$ indirectly predicts for complex systems to persist, interaction strength should be weaker in species-rich and highly connected systems (May, 2001; Bastolla et al., 2005). In other words, complex ecosystems could persist in nature provided that S, C and σ are not independent. In the same way, the inequality derived by Tang et al. (2014), $\sigma\sqrt{SC}(1+\rho) < \bar{d} + E$, predicts that ρ and $\sigma\sqrt{SC}$ should be correlated in feasible ecosystems. We therefore hypothesized that, contrary to randomly built ecosystems,

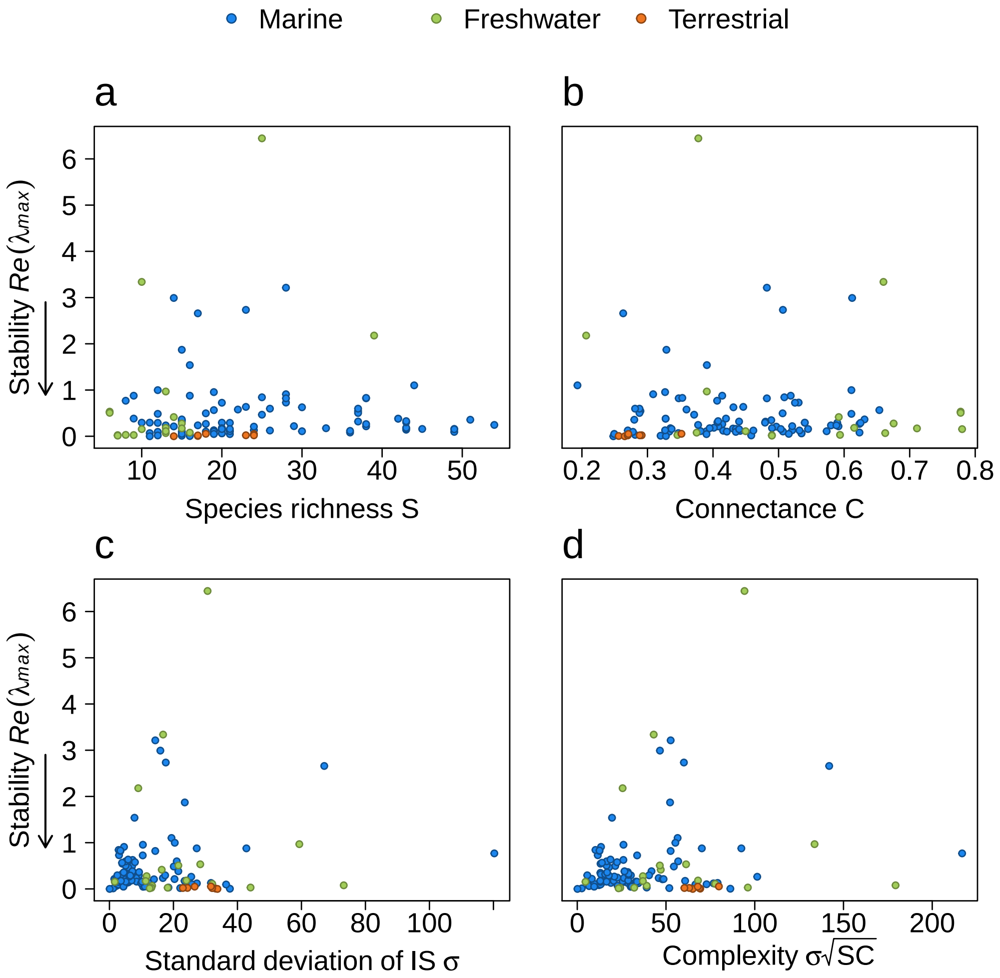

Figure 12: **Food web stability related to complexity parameters in 116 food webs.** (a) Number of species S (linear regression: $P = 0.97, R^2 < 10^{-5}$), (b) Connectance $C = (L/S^2)$ where L is the number of links ($P = 0.98, R^2 < 10^{-6}$), (c) Standard deviation of interaction strengths σ ($P = 0.1, R^2 = 0.02$), (d) May's complexity measure $\sigma\sqrt{SC}$ ($P = 0.02, R^2 = 0.04$). Stability is measured as $Re(\lambda_{max})$ for marine (blue), freshwater (green) and terrestrial ecosystems (orange). Food webs with eigenvalues close to zero are the most stable. All quantities are dimensionless.

parameters describing complexity are not independent in nature. We found that the s.d. of interaction strength σ across the 116 food webs was negatively correlated to the product of species richness and connectance $\sqrt{SC}$ (Fig. 13a) and contrary to expectations, we observed a slightly positive correlation between ρ and $\sigma\sqrt{SC}$ (Fig. 13b). The correlation between σ and $\sqrt{SC}$ decreased the overall complexity and confirmed the existence of feasibility constraints on communities. However, we still observed higher values of σ than predicted by May's stability criterion and this observation did not explain the absence of complexity– stability relationship in empirical systems.

1.6.3 Non-random properties of empirical community matrices

Random matrix theory supposes that interaction coefficients are independent and identically distributed in the community matrix. However, many studies on the complexity-stability relationship suggest that real ecosystems have non-random structural properties promoting their stability despite their complexity (Dunne, 2006). We focused on four non-random properties observed in our empirical community matrices, and then investigated their contribution to stability with randomization tests. *(i) Pyramidal structure of interaction strength (Yodzis, 1981; De Ruiter et al., 1995; James et al., 2015):* we found that interaction strength was related to trophic level, the occurrence of strong interactions being more likely at low trophic levels. Species biomass distribution affected the mean and variance of row i, since $c_{ji} = a_{ij} \times B_j$. Consequently, rows had different means and variance, a feature we call row structure. We hypothesized that food webs without this row structure are less stable than real food webs. *(ii) Interaction strength topology (Yodzis, 1981; Neutel et al., 2007; Emmerson and Yearsley, 2004):* trophic structure determines the position and the direction of interaction strength (that is, 'who eats whom'), and creates a non-random topology of interaction strengths. We hypothesized that food webs with a random topological structure are less stable than real food webs. *(iii) Correlation between pairs of predator-prey interactions (Tang et al., 2014; Montoya et al., 2006; De Angelis, 1975):* we found a correlation between pairs of interaction strengths c_{ij} and c_{ji} in community matrices, since $c_{ji} = (-c_{ij} \times e_{ij} \times B_j)/B_i$ (Fig. 11b). We therefore hypothesized that food webs with an empirical topological structure, but with a null correlation between pairs of interaction strengths, are less stable than

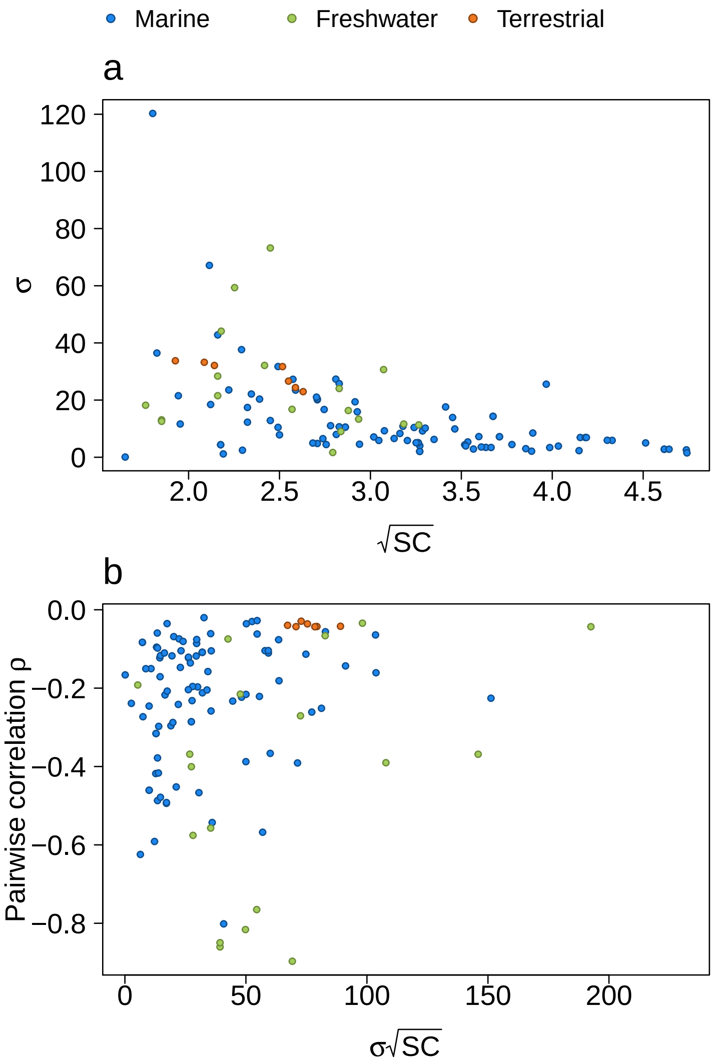

Figure 13: **Correlation between complexity parameters in real food webs.** (a) σ is the standard deviation of interaction strengths, S the number of species and C the connectance. The product $\sqrt{SC}$ was negatively correlated to σ (Spearman's rank correlation $P < 10^{-13}$, $r = -0.64$). (b) $\rho = corr(c_{ij}, c_{ji})$ is the correlation between pairwise interactions. The product $\sigma\sqrt{SC}$ was positively correlated to ρ ($P = 0.02$, $r = 0.22$).

real food webs. *(iv) Interaction strength frequency distribution:* in agreement with previous studies (De Ruiter et al., 1995; Paine, 1992; McCann and Hastings, 1998; Berlow, 1999), we observed a leptokurtic distribution of interaction strengths (high proportion of weak interactions). Consequently, we hypothesized that food webs with a highly peaked and long tailed distribution of interaction strengths are more stable than flatter distributions, such as the normal distribution.

Table 1: **Properties conserved by each randomization test (indicated by a ✓).** The column "row structure" specifies whether the pyramidal structure of interaction strength is conserved or not in randomization tests H1-H8. Similarly, "topology" corresponds to interaction strength topology ("who eat whom"), "pairwise interaction" corresponds to the correlation between pairs of predator-prey interactions and "frequency distribution" corresponds to the leptokurtic distribution of interaction strengths (high proportion of weak interactions).

Hypothesis	Row structure	Topology	Pairwise correlation	Frequency distribution
H1	×	✓	✓	✓
H2	×	×	✓	✓
H3	×	✓	×	✓
H4	×	✓	✓	×
H5	×	×	×	✓
H6	×	×	✓	×
H7	×	✓	×	×
H8	×	×	×	×

1.6.4 Randomization tests

We performed eight randomization tests to remove one or several properties of natural food webs and computed stability of the permuted community matrices (called H1-H8 at Table 1, see Methods section for details). We used this method to determine whether these properties had a significant effect on the distribution of eigenvalues across the 116 food webs, and their impact on the complexity–stability relationship. Randomization tests removed some non-random features of empirically built community matrices, generating matrices more similar to the ones expected under the random matrix theory, in which elements are drawn from a standardized distribution.

The distribution of eigenvalues of the permuted food webs was compared to stability of the original food webs. We found that each of the four structural properties enhanced food web stability (Fig. 14a). The removal of the empirical distribution of interaction strengths (with many weak interactions, H4) had the strongest impact on stability, followed by the removal of correlation between pairs of interactions (H3). Note that in all the randomization tests, the pyramidal structure of interaction strength was removed. Stability decreased when only this property was removed, keeping empirical topology, pairwise correlation and interaction strength distribution (H1). The randomization of interaction strength topology (H2) was also destabilizing, but to a very lesser extent compared with others non-random properties (Fig. 14a).

Randomization tests resulted in some cases in a negative complexity–stability relationship, although weaker than one should expect from the random matrix theory. Even if randomized matrices conserved the same S, C and σ^2 than as original ones (and thus their correlation, presented in Fig. 13a), we found a negative complexity–stability relationship when we normalized interaction strength distribution (H4, linear regression: $P < 10^{-16}$, $R^2 = 0.64$) and removed correlation between pairs of interactions (H3, linear regression: $P = 10^{-7}$, $R^2 = 0.2$, Fig. 14c). The removal of the pyramidal structure of interaction strengths and the topology found in empirical ecosystems did not affect the relationship between complexity and stability (linear regressions, H1: $P = 0.38$, $R^2 = 0.002$, H2: $P = 0.20$, $R^2 = 0,006$, Fig. 14c).

All food web properties contributed to stability, but clearly, the leptokurtic distribution of interaction strength had the strongest impact on the complexity–stability relationship. We found a significant negative relationship between stability and complexity when we removed this property (H4, Fig. 14c). Conversely, when we only kept the empirical distribution of in-

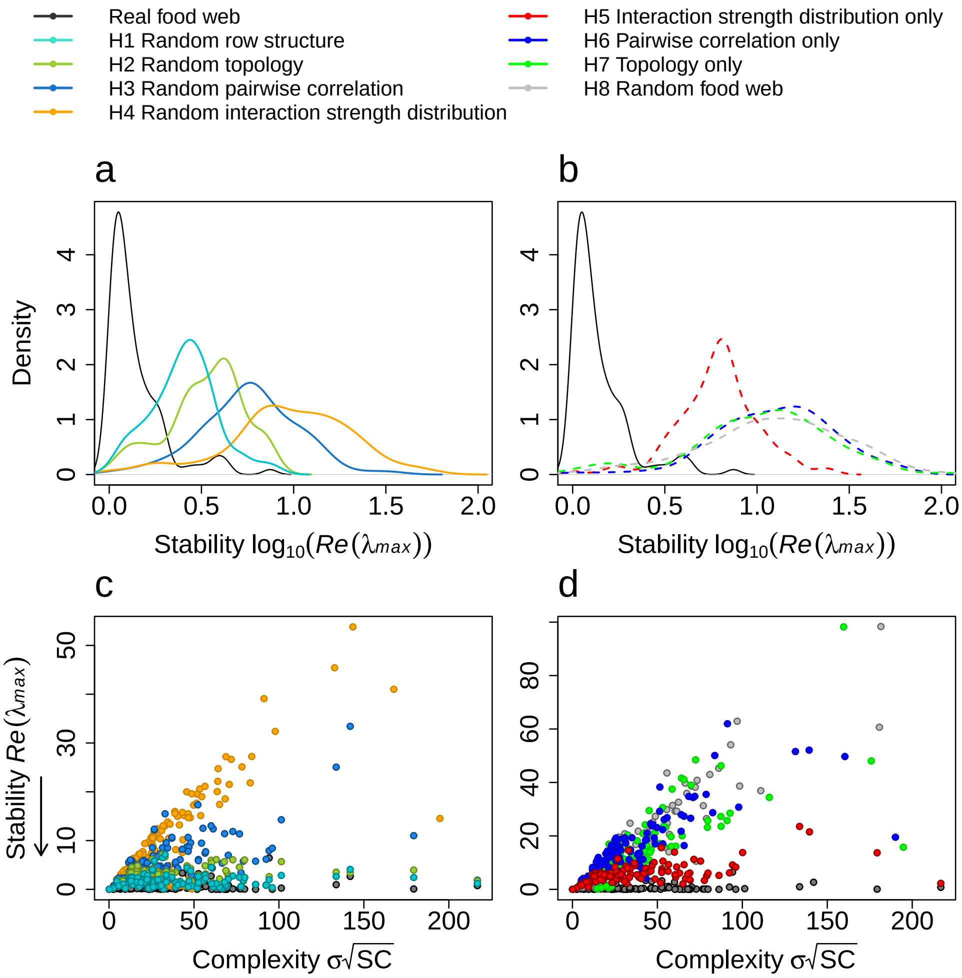

Figure 14: **Complexity-stability relationship in empirical and permuted food webs** (a-b) Frequency distributions of eigenvalues of real and permuted food webs. Eigenvalues are on a logarithmic scale and dimensionless. Permutation tests were carried out 1,000 times for each food web. Eigenvalue distributions were smoothed using a kernel density estimate of 0.28. (c-d) Stability of real and permuted food webs related to complexity. Stability is measured as $Re(\lambda_{max})$ and $\sigma\sqrt{SC}$ corresponds to complexity. Statistics of the linear regression between complexity and stability: real food webs (slope = 0.005, $P = 0.02, R^2 = 0.04$), H1: random row structure (slope = 0.003, $P = 0.38, R^2 = 0.002$), H2: random topology (slope = 0.006, $P = 0.2, R^2 = 0.006$), H3: random pairwise correlation (slope = 0.06, $P = 10^{-7}, R^2 = 0.2$), H4: random interaction strength distribution (slope=0.23, $P < 10^{-16}, R^2 = 0.64$). H5: just empirical distribution of interaction strengths (slope = 0.05, $P = 10^{-9}, R^2 = 0.23$). H6: just pairwise correlation (slope = 0.3, $P < 10^{-16}, R^2 = 0.62$). H7: just topology (slope = 0.05, $P < 10^{-16}, R^2 = 0.63$). H8: random food webs (slope = 0.4, $P < 10^{-16}, R^2 = 0.73$).

teraction strengths (H5), the slope of the complexity–stability relationship was significantly flatter than in the random case (H8). Topology of interaction strengths (H7) or pairwise correlation (H6) alone did not significantly affect the complexity–stability relationship (Fig.14d).

We conclude that May's stability criterion does not apply to empirical ecosystems because of their structure, which has several stabilizing non-random properties. First, the high frequency of weak interactions balanced the destabilizing effect of complexity (H4). Interestingly, we observed a strong positive correlation between the kurtosis κ (index of the peakedness of the interaction strength distribution) and species richness in real food webs (Supplementary Fig. 19). Thus the probability of having many weak interactions increased with species richness. The negative correlation between pairs of interaction strengths c_{ij} and c_{ji} is also a strong stabilizing property of empirical community matrices (H3). Finally, the non-random topology of interaction strengths (H2) was also stabilizing, as suggested by previous studies(Yodzis, 1981; De Ruiter et al., 1995; Neutel et al., 2007; Neutel and Thorne, 2014).

1.7 DISCUSSION

The relevance of local stability analysis to study real ecosystems may be questioned. More general and realistic definitions of stability have been introduced during the complexity–stability debate, such as persistence, variability, resilience or resistance Grimm (1997). Indeed, local stability analysis only tests the impact of small perturbations on ecological dynamics, and may not apply to large and/or cumulative perturbations typical of most empirical studies. It neither considers the covariance among species and thus the stability of the aggregated properties of the community De Mazancourt et al. (2013). However, it allows the use of analytically tractable community matrices, and thus the investigation of May's complexity–stability relationship on real ecosystems.

Our study yields new insight on the complexity–stability debate. Random matrix theory cannot predict the stability of real ecosystems because interaction strengths are not independent and identically distributed in empirically derived community matrices. Trophic structure creates a negative correlation between pairs of interactions and a non-random distribution of interaction strengths, with many weak interactions and few strong ones at the bottom of the food webs. The likely explanation for the strong effect of the leptokurtic distribution of interaction strengths is the size of the community matrices we investigated. Random matrix theory is performed in the limit of infinitely large matrices and all distributions are expected to converge in systems of several hundreds of species (Allesina and Tang, 2012). The community matrices we investigated had between 6 and 54 species. A detailed investigation of some community matrices revealed that small modules (two to five species) were often responsible for extreme eigenvalues. These modules could drive strong negative or positive feedbacks16 and thus dominate the dynamics of the entire system. Random matrix theory could provide a sufficient approximation for large ecosystems, but needs to be refined for smaller and realistic food webs such as the ones we investigated.

The study of small community matrices might require a different theoretical framework. For instance, Neutel and Thorne (2014) showed that the stability of a dynamical system could be predicted from the analysis of feedback loops. However, this approach requires knowledge of all of the elements of the community matrix and does not provide a statement about the expected relationship between S, C, σ and the occurrence of feedback loops. Such a theory would be needed to make quantitative predictions about the stability of a system with estimates of only few state variables.

Our food web dataset provided a great opportunity to study the effect of interspecific interactions on the relationship between complexity and stability and to demonstrate the existence of a negative correlation between S, C and σ in empirical ecosystems. We had, however, no information about the strength of intraspecific interactions, which is a strong stabilizing mechanism. Our analysis thus focused on the radius of the distribution of eigenvalues in the complex plane, ignoring the location of the centre (Fig. 11c). It is possible that the absence of relationship between complexity and stability results from a positive correlation between the strength of intraspecific interactions ($\bar{d}$) and complexity ($\sigma\sqrt{SC}$). Here we hypothesized that the food webs we studied were mainly top-down controlled, and that the strength of intraspecific interactions was negligible in comparison to interspecific interactions. Nonetheless, we valuated the sensitivity of our findings to the addition of intraspecific interaction terms proportional to species equilibrium biomass, since $c_{ii} = \alpha_{ii} \times B_i$. In agreement with random matrix theory and previous studies (Allesina and Tang, 2012; Neutel et al., 2007, 2002), the addition of intraspecific interactions was stabilizing, but had no effect on the correlation between complexity and stability (Methods section, Supplementary Fig. 20). Our results emphasize that further empirical investigations should better consider the relationship between ecosystem complexity and density dependence.

The analysis of empirically derived community matrices, combined with the observation of a complexity–stability relationship when their non-random structural properties were removed, demonstrates that the properties captured by Ecopath models contribute to the stability of complex food webs. Further empirical investigations are necessary to better approach real ecosystems and to study the stabilizing effect of the properties ignored or poorly described in Ecopath models, such as species age structure, energy flows from detrital pool or external inputs.

We showed that complexity is not related to stability in empirical ecosystems, a question that has stimulated ecological research for four decades. We found that the intrinsic energetic organization of food webs is highly stabilizing and allows complex ecosystems to recover from perturbations. Coexistence also constrains the feasibility of ecosystems, imposing a non-random structure of interactions and a correlation between S, C and σ that decreases the overall complexity (Bastolla et al., 2005). The non-random structure of food webs occurs from the successive addition of consumers having an increasingly large diet, which causes a growing frequency of weak interactions. The complexity–stability debate has contributed to the development of productive research that have pointed out the key role of the structural properties of real ecosystems.

1.8 METHODS

1.8.1 Ecopath modelling framework

We compiled 116 Ecopath food web models from published studies (Supplementary Table 1). Ecopath provides a quantitative overview of how species interact in a food web. Species sharing the same prey and predators and having similar physiological characteristics are aggregated in trophic species. The dynamics of each species i is described by the difference between biomass production and biomass losses due to harvesting, predation or other unspecified sources. It can be expressed as:

$$\frac{dB_i}{dt} = B_i \times (P/B)_i - Y_i - \sum_j [B_j \times (Q/B)_j \times DC_{ji}] - M_{0i} \times B_i \tag{1.1}$$

where B_i $(t\,km^{-2})$ and $(P/B)_i$ $(year^{-1})$ are biomass and production/biomass ratio of species i respectively, Y_i $(t\,km^{-2}\,year^{-1})$ corresponds to fishery yields, $(Q/B)_j$ $(year^{-1})$ is consumption/biomass ratio of predator j and DC_{ji} is the proportion of species i in the diet of predator j. Other mortality sources, M_{0i} $(year^{-1})$, can be expressed as $(1 - EE_i) \times (P/B)_i$, where EE_i is called the "ecotrophic efficiency" of i, corresponding to the fraction of the production that is used in the food web. The Ecopath model assumes mass-balance, meaning that all species biomass are at equilibrium ($dB_i/dt = 0$).

Input parameters (i.e. biomass, production/biomass and consumption/biomass ratios, fishery yields, and diet composition) can have different origins: field sampling (e.g. trawl survey), derived from similar Ecopath models, or known empirical relationships. Ecopath with Ecosim software includes routines that estimate missing parameters based on the mass-balance hypothesis and the generalized inverse method for a system of n linear equations and m unknowns (see Christensen et al. (2000), p. 12-15). In general, the biomasses, production/biomass and consumption/biomass ratios are entered for all groups in order to estimate ecotrophic efficiency, which is difficult to measure in the field Christensen and Walters (2004). The Ecoranger module, also included in Ecopath with Ecosim software, can be used to explore the effect of uncertainty in input data on estimated parameters. This module calculates probability distributions of output parameters based on the confidence intervals of input parameters specified by the users Christensen and Walters (2004). Full details of the Ecopath modelling approach and the Ecopath with Ecosim software can be obtained from www.ecopath.org.

1.8.2 Parameterization of Lotka-Volterra interaction coefficients

We used the method from De Ruiter et al. (1995) to derive the Jacobian matrices from Ecopath models: sssuming direct dependence of feeding rates on predator population density, we calculated the per capita effect of predator j on the growth rate of prey i as $\alpha_{ij} = -((Q/B)_j \times DC_{ji})/B_i$. Effects of prey on their predator are defined as predator growth resulting from this predation. Consequently, effect of the prey i on the predator j is related to effect of the predator on the prey according to: $\alpha_{ji} = -e_{ij} \times \alpha_{ij}$, where B is biomass, DC_{ji} is the proportion of species i in the diet of predator j, e_{ij} is the efficiency with which j converts food into biomass, from feeding on i: $e_{ij} = \frac{(P/B)_j}{(Q/B)_j}$ and $(P/B)_j$ and $(Q/B)_j$ are predator production/biomass and consumption/biomass ratios respectively. We obtained the following Lotka-Volterra interaction equation:

$$\frac{dB_i}{dt} = B_i\Big(b_i + \sum_{j=1}^{S}(\alpha_{ij} \times B_j) - \alpha_{ii} \times B_i\Big) \tag{1.2}$$

where b_i is the intrinsic growth rate (i.e., the intrinsic rate of increase for autotrophs, and natural mortality and losses for heterotrophs), B_i and B_j are respectively biomass of species i and j, interaction strength α_{ij} corresponds to the per capita effect of species j on the growth rate of species i and α_{ii} represents the per capita self limitation of species i. Assuming mass-balance, we obtain the following expression for intrinsic growth rate: $b_i = -\sum(\alpha_{ij} \times B_j) + \alpha_{ii} \times B_i$.

1.8.3 Correlation between pairs of interactions

Pairwise correlation ρ was calculated using the formula from Tang et al. (2014): $\rho = corr(c_{ij}, c_{ji}) = \frac{E(c_{ij}c_{ji}) - E(c_{ij})^2}{V}$ where $E(c_{ij})$ is the mean of the off-diagonal elements c_{ij} of the community matrix, their variance is V and $E(c_{ij}c_{ji})$ is the mean of the products of the pairs $c_{ij}c_{ji}$.

1.8.4 Randomization tests

Reported dominant eigenvalues of randomized food webs correspond to the mean of 1,000 replicates. All permutation tests conserve S, C and σ. To randomize the pyramidal structure of interaction strengths ($H1$), we swap pairs of predator-prey interactions (the pair $-c_{ij}/+c_{ji}$ is replaced by the pair $-c_{kl}/+c_{lk}$). This permutation only changes row structure (mean and variance) and does not change topology, frequency distribution of interaction strengths nor correlation between pairs of interactions. To randomize interaction strength topology ($H2$), we swap the element of the community matrix c_{ij} with the element c_{ji}. This permutation only removes food web topology and do not change the frequency distribution of interaction strengths or pairwise correlation. To remove correlation between pairs of predator-prey interactions ($H3$), we permute off-diagonal elements of the community matrix, keeping the topological structure and the frequency distribution of interaction strengths. Positive and negative terms are permuted separately in order to keep the same the mean of positive and negative interactions. For randomization of interaction strength distribution ($H4$), we created a random community matrix in which off-diagonal elements were picked from a bivariate normal distribution $N_2(\mu, \Sigma)$ where the mean vector μ is composed of the mean of positive (μ_+)

and the mean of negative (μ_-) terms, and Σ is the covariance matrix between positive and negative terms of the original community matrix. Original pairs of positive/negative terms were replaced by positive/negative terms from the bivariate normal distribution. For large random community matrices, the correlation between pairwise interactions is expected to be identical to the original community matrix. Randomization test $H5$ only keeps frequency distribution of interaction strengths. This test is a combination of permutation $H2$, that randomizes the topology of interaction strengths, and permutation $H3$, that removes pairwise correlation. Randomization test $H6$ only keeps pairwise correlation, this test is a combination of permutation $H2$ and randomization $H4$, that create a random community matrix in which off-diagonal elements are picked from a bivariate normal distribution. Randomization test $H7$ only keeps the topology of interaction strengths, which is a combination of tests $H3$ and $H4$. Randomization test $H8$ creates community matrices in which elements are identically and independently distributed, that is food webs with a random topology, a normal distribution of interaction strengths and no pairwise correlation. This test corresponds to test $H2$, that randomizes the topology of the community matrix, combined to a randomization that creates a community matrix in which positive and negative off-diagonal elements are picked from a normal distribution $N(\mu_+, \sigma_+^2)$ and $N(\mu_-, \sigma_-^2)$, where μ_+ and μ_- are the mean and σ_+^2 and σ_-^2 the variance of positive/negative elements of the original community matrix.

1.8.5 Parameter uncertainty

We investigated the impact of parameter uncertainty on our findings. In the section ‘Interspecific interaction terms of the community matrix’, we evaluated the sensitivity of our results to variability in interspecific interaction terms. The parameters used to build empirical community matrices come from Ecopath data and each of them bears some uncertainty (Christensen et al., 2000). Consequently, we tested whether the introduction of variability in input parameters could bias the complexity–stability relationship.

In the section ‘Intraspecific interaction terms of the community matrix’, we evaluated the robustness of our results to the addition of density dependence. Because Ecopath models depict exclusively trophic interactions between species, we had no empirical information about the strength of intraspecific interactions and we decided not to model density dependence in the Lotka–Volterra model. Our method is comparable to other studies that calculated stability by assessing the level of intraspecific interaction needed for all eigenvalues in a community matrix to have negative real parts (diagonal dominance) (May, 1972; Neutel et al., 2002; Neutel and Thorne, 2014). These studies assumed that all diagonal elements c_{ii} of the community matrix are the same. However, to obtain the community matrix, the interaction matrix **A** is multiplied by species biomass, which means that diagonal elements are non-constant: $c_{ii} = \alpha_{ii} \times B_i$. We therefore evaluated the robustness of our results to the addition of diagonal elements structured by species biomass.

Finally, in the section 'Food web resolution', we assessed the impact of food web resolution level on the complexity–stability relationship. Ecopath model is mainly used for ecosystem-based fisheries management and the level of resolution of several food webs is not homogeneous through all ecological compartments. Harvested fishes are generally resolved at the species level, while species at the bottom of the food web, such as plankton and invertebrates, are highly aggregated. We therefore analysed the complexity–stability relationship on a subset of the best resolved Ecopath food webs.

Overall, we found the same qualitative results than our main study. We conclude that our findings are robust to (i) input parameter uncertainty, (ii) addition of non-zero diagonal elements in community matrices and (iii) differences in food web resolution level.

1.8.6 Interspecific interaction terms of the community matrix.

We ran sensitivity analyses to determine how uncertainties in parameter estimates could affect the results of the study. For each input parameter, we tested if uncertainty biases (that is, overestimates or underestimates) food web stability and the variables determining complexity, and if our findings are qualitatively affected by this bias.

We used the following parameters from Ecopath data to determine the interspecific terms of a community matrix: (i) biomass B, (ii) consumption/biomass ratio (Q/B), (iii) production/biomass ratio (P/B) and (iv) diet composition DC. Uncertainty in these parameters could influence our results through the dominant eigenvalue $Re(\lambda_{max})$, through the standard deviation of interaction strength σ (related to May's complexity criterion $\sigma\sqrt{SC}$), or through the pairwise correlation ρ (related to Tang's complexity criterion $\sigma\sqrt{SC}(1+\rho)-E$).

We used a resampling procedure to evaluate the sensitivity of our results to parameter uncertainty. For each of the 116 Ecopath models, we proceeded as follows: we resampled each parameter, B, (Q/B) and (P/B), 1,000 times from a normal distribution $N(\mu,\sigma)$ with $\mu = X_i$, $\sigma = X_i/10$ (corresponding to a $CV = 10\%$) and X_i is the reported value of parameter X for species i. We chose a CV of 10% because higher values could lead to negative P/B. We built a matrix of diet composition in which predators have no prey preferences (that is, they are opportunistic feeders, attacking prey in proportion to their availability). The proportion of prey i in the diet of predator j corresponds to the ratio between biomass of i and total biomass of all j's prey species.

(i) Biomass: for each of the 116 Ecopath models, 1,000 community matrices were built from the resampled values of B. Diet composition, production/biomass and consumption/biomass ratios were kept constant and corresponded to the values reported in Ecopath data.

(ii) Consumption/biomass ratio: for each of the 116 Ecopath models, 1,000 community matrices were built from the resampled values of Q/B. Biomass, diet composition and production/biomass ratio corresponded to the values reported in Ecopath data.

(iii) Production/biomass ratio: for each of the 116 Ecopath models, 1,000 community matrices were built from the resampled values of P/B. Biomass, diet composition and consumption/biomass ratio corresponded to the values reported in Ecopath data.

(iv) Diet composition: for each of the 116 Ecopath models, a community matrix was built using the matrix of diet composition in which predators have no prey preferences. Biomass, production/biomass and consumption/biomass ratios corresponded to the values reported in Ecopath data. We used a resampling procedure to evaluate the sensitivity of our results to parameter uncertainty.

We calculated the dominant eigenvalue $Re(\lambda_{max}$, the standard deviation of interaction strengths σ and the correlation between pairwise interactions ρ of these community matrices and compared their values to the ones found in the original community matrices (Supplementary Fig. 16). We found that uncertainty in the estimation of B, P/B and Q/B had no effect on food web stability or the variables determining complexity. The absence of diet preferences was destabilizing and also decreased s.d. of interaction strength. However, we found that the deviation between the original leading eigenvalues and the ones obtained after the addition of variability in input parameters was not correlated to complexity (Supplementary Fig. 17). The complexity–stability relationship would have been biased if, for instance, the addition of variability in the biomass estimates would have a more profound impact on the leading eigenvalue of highly complex webs than the one of simpler food webs. In agreement with Barabás and Allesina (2015). these results demonstrate that our findings are robust to the addition of variability in interspecific interaction terms of the community matrices

1.8.7 Intraspecific interaction terms of the community matrix

The diagonal elements c_{ii} of the community matrix express the strength of density dependence, which is highly stabilizing as it moves the dominant eigenvalue to more negative values: $Re(\lambda_{max}) = R - \bar{c_{ii}}$, where the radius of the unit circle R corresponds to $\sigma\sqrt{SC}$ in random matrices and $\bar{c_{ii}}$ is the mean of diagonal elements (Introduction and Fig. 11c). Our aim was not to assess the local stability of empirical food webs but to investigate the relationship between stability and complexity using realistic community matrices on a large gradient of complexity. In the main text, we therefore set all the diagonal elements to 0 to focus on the effect of interspecific interactions on stability. Our method is comparable to other studies that calculated stability by assessing the level of intraspecific interaction needed for all eigenvalues in a community matrix to have negative real parts (diagonal dominance) (May, 1972; Neutel et al., 2002; Neutel and Thorne, 2014). These studies assumed that all diagonal elements c_{ii} of the community matrix are the same. However, to obtain the community matrix, the interaction matrix **A** is multiplied by species biomass and the diagonal of an empirically derived community matrix should be structured by species biomass, as $c_{ii} = \alpha_{ii} \times B_i^*$. Here, we investigated how a non-constant diagonal, in which elements c_{ii} are proportional to species biomass, affect the dominant eigenvalues reported in our analysis. We compared the dominant eigenvalues of community matrices with $\alpha_{ii} = 0$ (original food webs) and $\alpha_{ii} = 0.01$ or 0.1 (Supplementary Fig. 20). We found that the addition of the intraspecific interaction terms was stabilizing, but had no effect on the absence of complexity-stability relationship

1.8.8 Food web resolution

Ecopath is mainly used for ecosystem-based fisheries management. Consequently, the structure of food webs parameterized with Ecopath is often biased, with detailed compartments for harvested fishes and more aggregated compartments for species at the bottom of the food web (that is, plankton and invertebrates). Food web resolution influences the estimation of species richness, connectance and interaction strength. To assess the robustness of our analysis, we investigated the complexity–stability relationship on a subset of the best resolved Ecopath models. We measured the amount of aggregation of each model, based on the criterion that groups with taxonomic name were more resolved than groups with trophic function names. We defined four resolution levels and qualified one level for each species with the following indices: taxonomic species (that is, greenland turbot, index = 1), family/class (that is, whales, gadoids; index = 0.7), trophic function (that is, small demersal fish; index = 0.4) and general name (that is, benthos, fish; index = 0.1). Resolution indices *RI* of Ecopath models correspond to the mean resolution index of species within each food web and are listed in Supplementary Table 1. We studied the complexity–stability relationship on a subset of the 37 best resolved models (with $RI \geq 0.7$) and found results similar to the overall analysis (Supplementary Fig. 15).

1.9 DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author on request.

1.10 ACKNOWLEDGMENTS

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1.11 SUPPLEMENTARY FIGURES

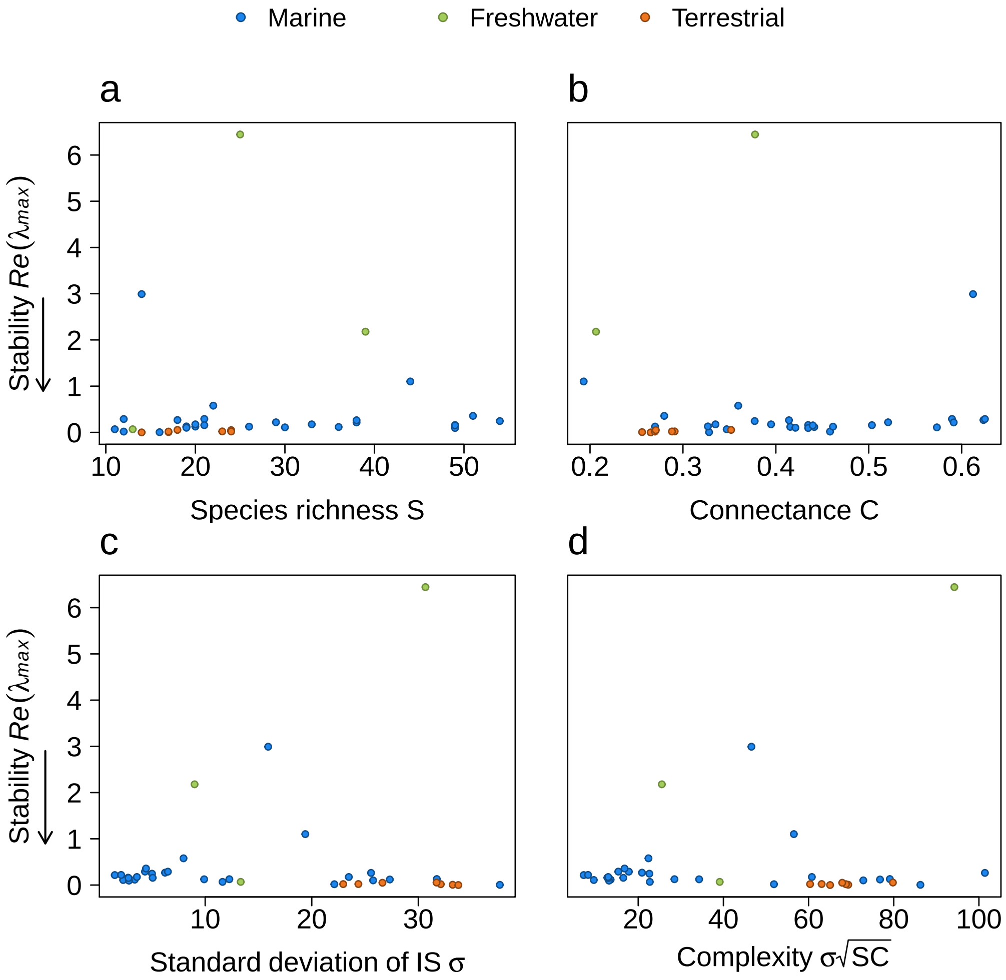

Figure 15: Food web stability related to complexity parameters for the 37 best resolved food webs. (a) Number of species S (linear regression: $P = 0.41, R^2 = 0.008$), (b) Connectance $C = L/S^2$ where L is the number of links ($P = 0.92, R^2 = 0.03$), (c) Standard deviation of interaction strengths σ ($P = 0.16, R^2 = 0.03$), (d) May's complexity criterion $\sigma\sqrt{SC}$ ($P = 0.05, R^2 = 0.02$). Stability is measured as $Re(\lambda_{max})$, for marine (blue), freshwater (green) and terrestrial ecosystems (orange). Food webs with eigenvalues close to zero are the most stable. All quantities are dimensionless.

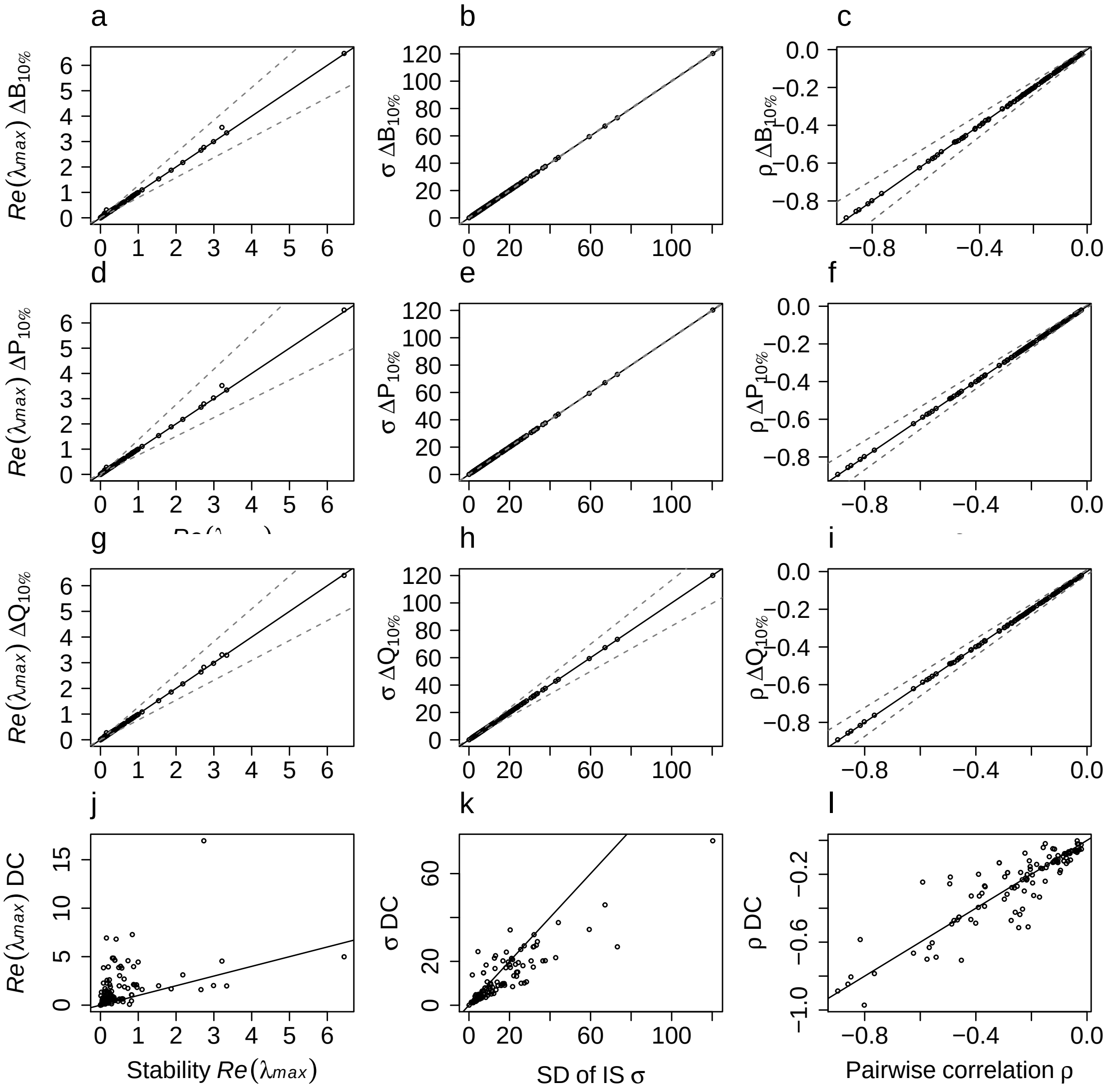

Figure 16: Effect of input parameter variability on stability and descriptors of complexity. Output parameters: $Re(\lambda_{max})$ corresponds to stability (first column), σ is standard deviation of interaction strength (second column) and ρ represents correlation between pairs of interactions (third column). Input parameters are biomass B (a-c), production/biomass ratio P/B (d-f), consumption/biomass ratio Q/B (g-i) and diet composition DC (j-l). Points represent the mean value of 1,000 replicates of the resampling procedure, dotted lines correspond to the 2.5% and 97.5% quantile regressions. Black lines correspond to 1:1 ratio between the original output parameter estimates (x-axis) and the resampled ones (y-axis).

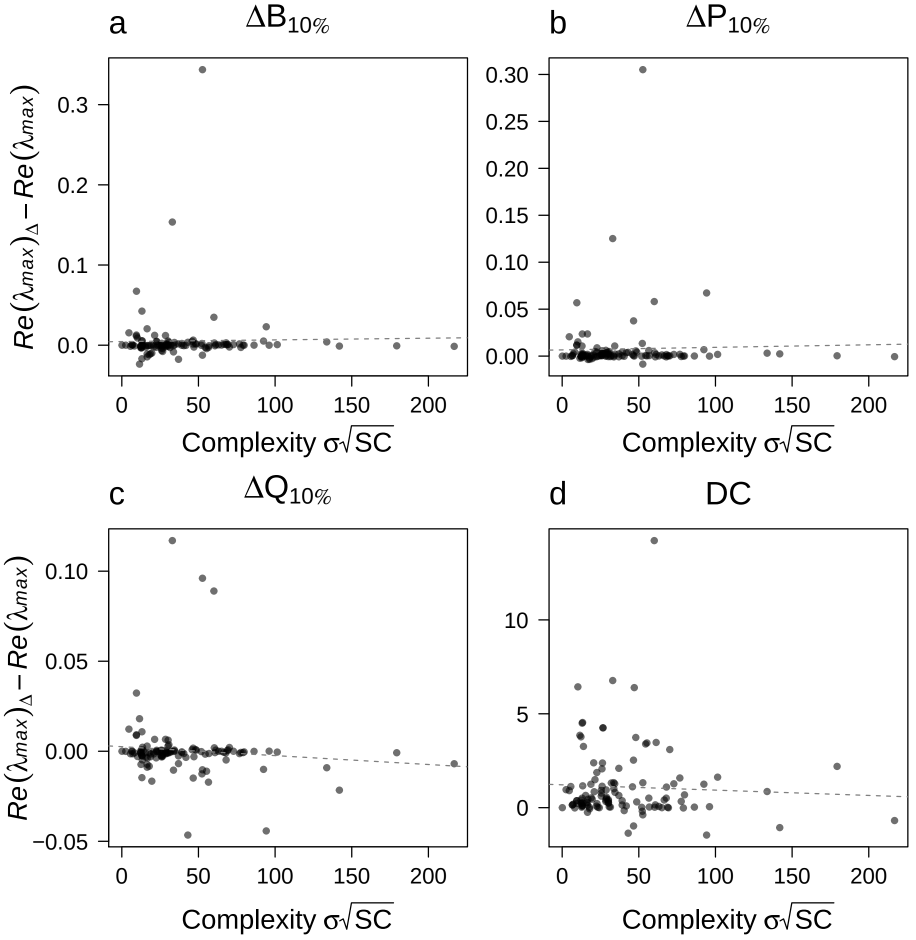

Figure 17: Effect of complexity on the deviation between the stability of empirical or resampled community matrices. $Re(\lambda_{max})_\Delta$ and $Re(\lambda_{max})$ correspond to the stability of resampled and original community matrices respectively. Dotted lines illustrate the linear regression between complexity $\sigma\sqrt{SC}$ and $Re(\lambda_{max})_\Delta - Re(\lambda_{max})$. The resampled community matrices are drawn from the resampling of (a) species biomass B ($P = 0.82$, $R^2 = 10^{-4}$), (b) production/biomass ratio P/B ($P = 0.75$, $R^2 = 10^{-3}$) or (c) consumption/biomass ratio Q/B with a CV of 10% ($P = 0.32$, $R^2 = 10^{-2}$). (d) The community matrices are drawn from a diet composition matrix in which predators have no prey preferences ($P = 0.59$, $R^2 = 10^{-3}$).

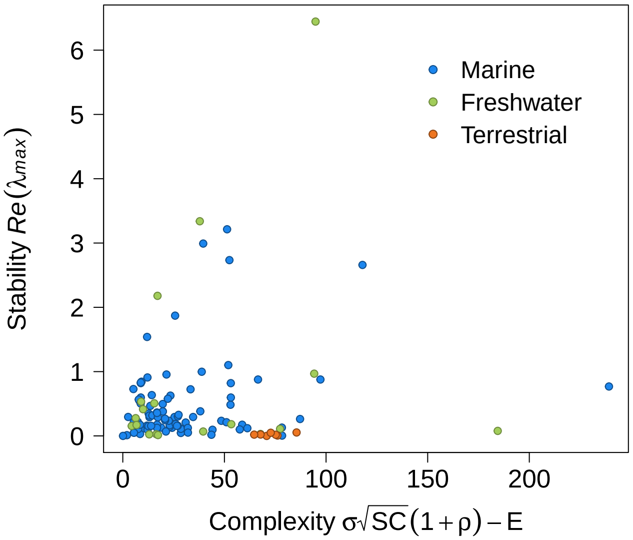

Figure 18: Complexity-stability relationship in 118 food webs with Tang's complexity criterion. Complexity is defined as $\sigma\sqrt{SC}(1+\rho)-E$, where E is the mean (including zeros) and ρ is the correlation between pairs of interactions. Stability is measured as $Re(\lambda_{max})$, for marine (blue), freshwater (green) and terrestrial ecosystems (orange). Linear regression: $P = 0.02, R^2 = 0.053$. Food webs with eigenvalues close to zero are the most stable. All quantities are dimensionless.

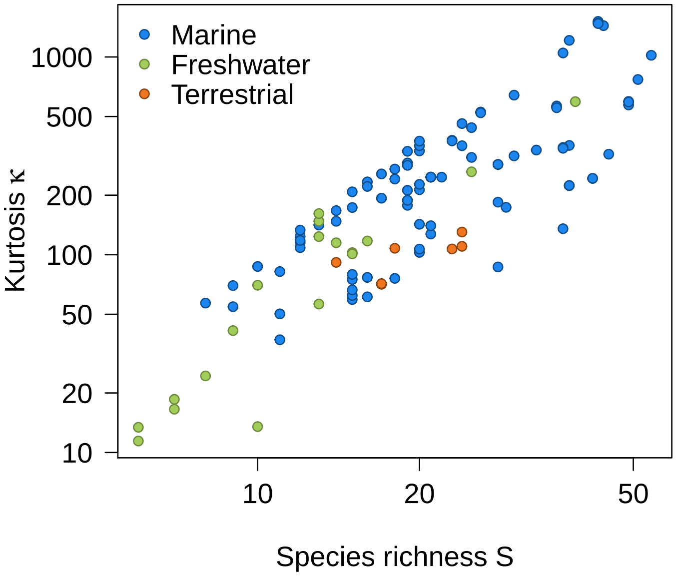

Figure 19: Relationship between species richness and the shape of interaction strength distribution. The kurtosis κ is an index of the peakedness of the interaction strength distribution, for a normal distribution $\kappa = 0$. Kurtosis increases linearly with species richness on a logarithmic scale (linear regression: $P < 10^{-15}, R^2 = 0.71$). All quantities are dimensionless.

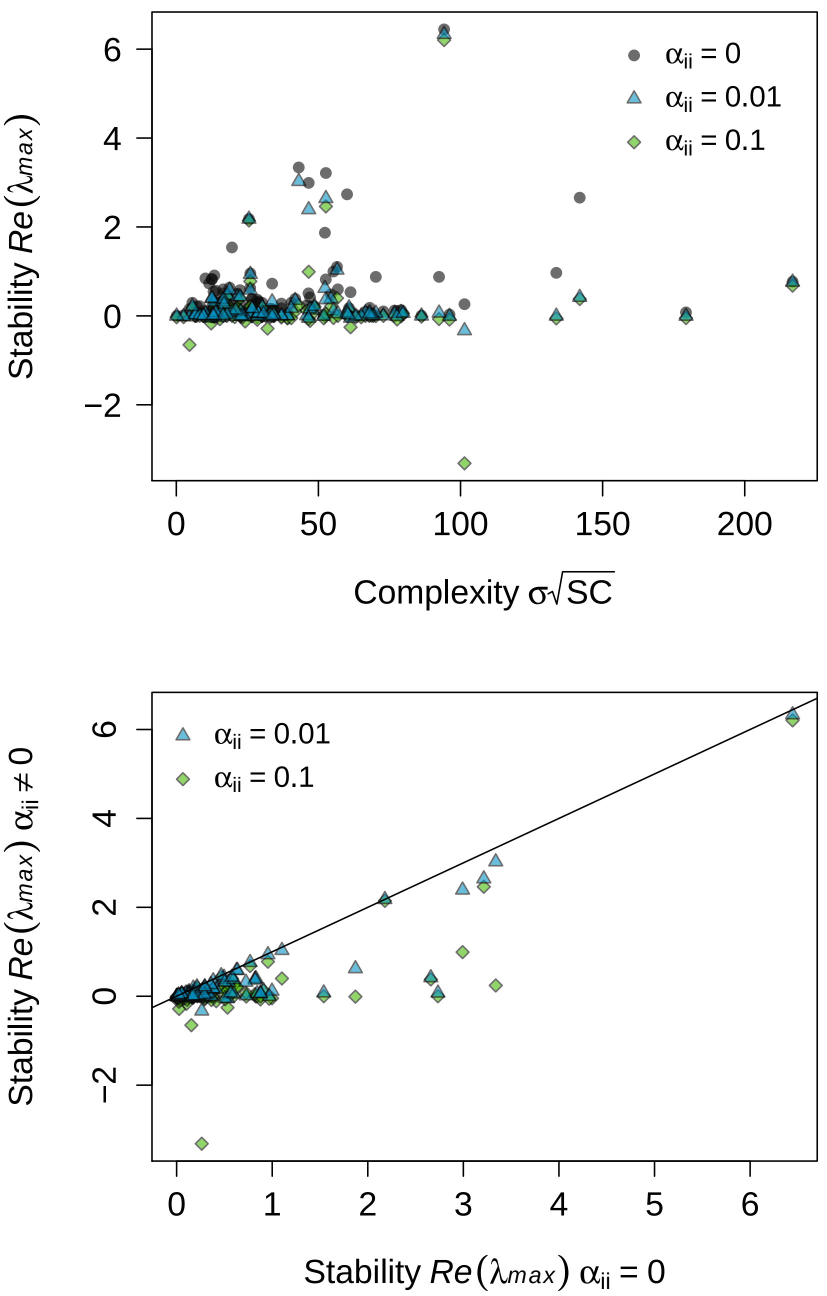

Figure 20: Effect of diagonal elements on the complexity-stability relationship. (a) Complexity-stability relationship in 118 food webs with no intraspecific interaction (black circles, $P = 0.02, R^2 = 0.04$), with $\alpha_{ii} = 0.01$ (blue triangles, $P = 0.1, R^2 = 0.01$) or $\alpha_{ii} = 0.1$ (green diamonds, $P = 0.34, R^2 = 10^{-3}$). Complexity is defined as $\sigma\sqrt{SC}$ and stability is measured as $Re(\lambda_{max})$. (b) Relationships between stability of food web matrices with zero (x-axis) or non-zero diagonal elements (y-axis, α_{ii}= 0.01 or 0.1). The black line corresponds to 1:1 ratio between the x-axis and y-axis.

1.12 SUPPLEMENTARY TABLE

List of the 116 Ecopath models with references, habitat types, number of species S, connectance C, standard deviation of interaction strengths σ, and resolution index RI.

Model Name	Reference	Habitat	S	C	σ	RI
Alaka Prince William Sound OM	Okey and Pauly (1999)	marine	18	0.35	12.63	0.62
Alto Golfo De California	Morales-Zarate et al. (2004)	marine	28	0.55	2.99	0.63
Antarctica Weddel Sea	Jarre-teichmann et al. (1997)	marine	19	0.26	4.31	0.57
Arctic islands, Alert	Legagneux et al. (2014)	terrestrial	17	0.26	33.22	0.86
Arctic islands, Bylot	Legagneux et al. (2014)	terrestrial	18	0.35	31.71	0.85
Arctic islands, Herschel	Legagneux et al. (2014)	terrestrial	24	0.27	26.63	0.85
Arctic islands, Nenetsky	Legagneux et al. (2014)	terrestrial	24	0.29	22.95	0.83
Arctic islands, Svalbard	Legagneux et al. (2014)	terrestrial	14	0.27	33.76	0.76
Arctic islands, Yamal	Legagneux et al. (2014)	terrestrial	23	0.29	24.38	0.84
Arctic islands, Zackenberg	Legagneux et al. (2014)	terrestrial	17	0.27	32.11	0.86
Bali Strait	Buchary and Alder (2002)	marine	13	0.6	16.38	0.51
Bay Of Biscay 1998	Ainsworth et al. (2001)	marine	36	0.64	2.56	0.42
Bay Of Somme	Rybarczyk et al. (2003)	marine	8	0.41	120.28	0.33
Black Sea	Orek (2000)	marine	9	0.43	21.23	0.43
Brunei Darussalam, China Sea	Silvestre and Selvanathan 1993 (1993)	marine	12	0.65	19.54	0.45
Campeche Bank, Golf of Mexico	Vega-Cendejas (1993)	marine	18	0.51	7.09	0.6

Table 2 – continued from previous page

Model Name	Reference	Habitat	S	C	σ	RI
Campeche Sound	Manickchand-Heileman et al. (1998)	marine	24	0.52	5.34	0.61
Cape Verde	Stobberup et al. (2004)	marine	24	0.5	13.86	0.61
Caribbean	Morissette et al. (2010b)	marine	28	0.32	4.45	0.68
Celestun	Chavez et al. (1993)	marine	15	0.53	4.37	0.6
Central Atlantic 50s	Vasconcellos and Watson (2004)	marine	37	0.3	3.95	0.56
Central Chile 1992	Neira et al. (2004)	marine	20	0.28	12.1	0.93
Central Gulf Of California	Arreguin-Sanchez et al. (2002)	marine	25	0.38	5.83	0.63
Central Pacific, sharks	Kitchell et al. (2002)	marine	21	0.6	4.31	0.8
Chesapeake Present	Christensen et al. (2009)	marine	44	0.19	19.32	0.79
Darwin Harbour, Australia	Martin (2005)	marine	20	0.51	6.47	0.5
Eastern Scotian Shelf 90s	Bundy (2004)	marine	38	0.6	1.5	0.72
Eastern Tropical Pacific	Olson and Watters (2003)	marine	38	0.42	25.39	0.81
Etang de Thau, France	Palomares et al. (1993)	marine	10	0.84	2.04	0.52
Gambia 1986	Mendy (2003)	marine	21	0.39	10.5	0.63
Gambia 1992	Mendy (2004)	marine	21	0.39	10.5	0.63
Gambia 1995	Mendy (2004)	marine	21	0.38	10.63	0.63
Gironde Estuary, France	Lobry (2004)	marine	16	0.42	7.58	0.56
Golfo Dulce, Costa Rica	Wolff et al. (1996)	marine	20	0.56	9.1	0.6
Guinee 1985	Guénette and Diallo (2004)	marine	43	0.44	5.85	0.66

Table 2 – continued from previous page

Model Name	**Reference**	**Habitat**	**S**	**C**	σ	**RI**
Guinee 1998	Guénette and Diallo (2004)	marine	43	0.44	5.89	0.66
Guinee Bissau 1991	Amorim et al. (2003)	marine	30	0.44	7.19	0.57
Gulf of Salamanca, Upwelling	Duarte and Garcia (2004)	marine	17	0.61	8.2	0.54
High Barents Sea AllJuvs1990	Blanchard et al. (2002)	marine	15	0.52	4.71	0.54
High Barents Sea Final 1990	Blanchard et al. (2002)	marine	38	0.36	3.4	0.66
Huizache Caimanero, Mexico	Zetina-Rejon (2004)	marine	25	0.52	2.89	0.64
Iceland Fisheries	Buchary (2001)	marine	20	0.54	2.04	0.69
Icelandic Shelf	Buchary (2001)	marine	20	0.54	2.02	0.69
Jalisco y Colima	Galvan-Pina (2005)	marine	36	0.46	3.33	0.7
Kuala Terengganu, Malaysia	Liew and Chan (1987)	marine	12	0.66	19.71	0.4
Kuosheng Bay, Taiwan	Lin et al. (2004)	marine	16	0.29	18.15	0.49
Lagoon of Venice	Opitz (1996)	marine	15	0.34	1.14	0.48
Laguna De Bay, Philippines, 1950	Delos Reyes (1995)	marine	20	0.34	23.31	0.73
Laguna De Bay, Philippines, 1980	Delos Reyes and Martens (1994)	marine	16	0.33	37.43	0.76
Laguna De Bay, Philippines, 1990	Delos Reyes (1995)	marine	19	0.33	31.61	0.73
Lake Aydat, France	Reyes-Marchant et al. (1993)	freshwater	10	0.69	16.4	0.49

Table 2 – continued from previous page

Model Name	Reference	Habitat	S	C	σ	RI
Lake Chad, Africa	Palomares et al. (1993)	freshwater	14	0.62	15.94	0.55
Lake George, Uganda	Moreau et al. (1993a)	freshwater	13	0.7	13	0.72
Lake Kariba, Africa	Machena et al. (1993)	freshwater	9	0.36	17.88	0.67
Lake Kinneret, Israel	Walline et al. (1993)	freshwater	13	0.41	58.05	0.52
Lake Malawi 2, Africa	Degnbol (1993)	freshwater	8	0.61	43.53	0.63
Lake Malawi, Africa	Nsiku (1999)	freshwater	25	0.39	30.29	0.7
Lake Tanganyka, Africa, 1975	Moreau et al. (1993c)	freshwater	6	0.92	26.08	0.5
Lake Tanganyka, Africa, 1981	Moreau et al. (1993c)	freshwater	6	0.92	19.83	0.5
Lake Turkana, Kenya, 1973	Kolding (1993)	freshwater	7	0.53	12.59	0.57
LakeTurkana, Kenya, 1987	Kolding (1993)	freshwater	7	0.53	12.09	0.57
Lake Victoria, Africa, 1971	Moreau et al. (1993b)	freshwater	15	0.71	11.37	0.62
Lake Victoria, Africa, 1985	Moreau et al. (1993b)	freshwater	15	0.74	11.09	0.62
Looe Key, Florida, USA	Venier and Pauly (1997)	marine	19	0.55	10.62	0.51
Low Barents Sea 1995	Blanchard et al. (2002)	marine	38	0.36	3.38	0.69
Low Barents Sea Juvs 1995	Blanchard et al. (2002)	marine	15	0.51	4.85	0.54
Mandinga Lagoon, Mexico	Cruz-Aguero (1993)	marine	19	0.33	10.37	0.65
Maputo Bay, Mozambique	Silva et al. (1993)	marine	9	0.6	39.66	0.5

Table 2 – continued from previous page

Model Name	Reference	Habitat	S	C	σ	RI
Mid Atlantic Bight	Okey and Pugliese (2001)	marine	54	0.38	4.98	0.7
Monterey Bay, California	Olivieri et al. (1993)	marine	15	0.36	22.71	0.36
Moorea Barrier reef	Arias- Gonzalez et al. (1997)	marine	45	0.34	8.64	0.54
Moorea Fringing reef	Arias- Gonzalez et al. (1997)	marine	42	0.33	7.17	0.56
Morocco 1984	Stanford and Pitcher (2004)	marine	37	0.45	3.87	0.52
Newfoundland Grand Banks 1900	Heymans and Pitcher (2002b)	marine	49	0.44	2.75	0.72
Newfoundland Grand Banks mid-1980s	Bundy (2001)	marine	30	0.58	2.29	0.76
Newfoundland Grand Banks mid-1980s	Heymans and Pitcher (2002a)	marine	49	0.44	2.83	0.76
Newfounland Grand Banks mid-1990s	Heymans and Pitcher (2002a)	marine	49	0.44	3.87	0.76
North Atlantic 1950s	Vasconcellos and Watson (2004)	marine	37	0.3	4.97	0.59
North Atlantic 1990s	Vasconcellos and Watson (2004)	marine	37	0.3	4.98	0.59
Northeastern Venezuela shelf	Mendoza (1993)	marine	15	0.57	23.47	0.54
Northwest Africa	Morissette et al. (2010a)	marine	26	0.28	20.92	0.69
Orbetello Lagoon	Ceccarelli et al. (2005)	marine	11	0.37	11.25	0.73

Table 2 – continued from previous page

Model Name	**Reference**	**Habitat**	**S**	**C**	σ	**RI**
Pallude Della Rosa Lag Venice	Carrer and Opitz (1999)	marine	11	0.25	0.07	0.4
Patos Lagoon Estuary	Betito (2006)	marine	23	0.52	17.39	0.65
Peruvian upwelling system 1950s	Jarre-teichmann (1998)	marine	19	0.43	26.81	0.7
Peruvian upwelling system 1960s	Jarre-teichmann (1998)	marine	19	0.44	25.28	0.7
Ria Formosa	Gamito and Erzini (2005)	freshwater	13	0.65	23.39	0.58
Sakumo Lagoon, Ghana	Pauly (2002)	marine	12	0.29	35.58	0.65
San Pedro Bay, Leyte, Philippines	Campos (2003)	marine	15	0.68	9.09	0.48
Seine Estuary	Rybarczyk and Elkaim (2003)	marine	14	0.41	20.34	0.64
Sene-Gambia	Samb and Mendy (2003)	marine	16	0.42	27.15	0.56
Sierra Leone 1964	Heymans and Vakily (2002)	marine	43	0.41	6.86	0.61
Sierra Leone 1978	Heymans and Vakily (2002)	marine	43	0.41	6.84	0.61
Sierra Leone 1990	Heymans and Vakily (2002)	marine	43	0.42	6.84	0.61
Sonda Campeche	Manickchand-Heileman et al. (1998)	marine	18	0.64	6.18	0.7
South Pacific, marine mammals	Morissette (unpublished data)	marine	42	0.33	7.17	0.55

Table 2 – continued from previous page

Model Name	**Reference**	**Habitat**	**S**	**C**	σ	**RI**
Southern Brazil	Vasconcellos and Gasalla (2001)	marine	12	0.49	21.66	0.73
Southern Gulf St Lawrence 1980	Savenkoff et al. (2004)	marine	29	0.53	2.1	0.7
Southwest Coast Of India	Vivekanandan et al. (2003)	marine	10	0.62	16.26	0.4
SriLanka Lake Prakrama Samudra	Moreau et al. (2001)	freshwater	16	0.39	71.76	0.63
Strait Of Georgia	Martell et al. (2002)	marine	26	0.47	9.81	0.73
Subantartic Plateau New Zealand	Bradford-Grieve et al. (2003)	marine	17	0.28	64.77	0.54
Tamiahua Lagoon, Golf of Mexico	Abarca-Arenas and Valero-Pacheco (1993)	marine	12	0.63	6.46	0.7
Tampa Bay	Walters et al. (2005)	marine	51	0.28	4.42	0.86
Tampamachoco Lagoon, Mexico	Rosado-Solórzano and del Próo (1998)	marine	22	0.36	7.95	0.7
Terminos Lagoon, Gulf of Mexico	Manickchand-Heileman et al. (1998)	marine	19	0.67	3.89	0.6
Terminos Lagoon, seagrass	Rivera-Arriaga et al. (2003)	marine	15	0.53	10.9	0.56
UK Virgin Islands, Caribbean	Opitz (1996)	marine	20	0.57	9.96	0.45
Upper Parana River Floodplain	Angelini and Agostinho (2005)	freshwater	39	0.21	8.95	0.82
Veli Lake, India	Aravindan (1993)	freshwater	13	0.45	32.13	0.58

Table 2 – continued from previous page

Model Name	**Reference**	**Habitat**	**S**	**C**	σ	**RI**
Weddell Sea	Jarre-teichmann et al. (1997)	marine	19	0.26	4.31	0.57
West Coast of Greenland	Pedersen and Zeller (2001)	marine	21	0.52	4.98	0.74
West Coast of Sabah	Garces and Alias (2003)	marine	28	0.49	14.18	0.6
West Coast of Sarawak	Garces and Alias (2003)	marine	28	0.49	14.18	0.6
West Coast of Vancouver Island	Martell (2002)	marine	14	0.64	15.59	0.83
West Greenland, Shrimp Pound	Pedersen (1994)	marine	11	0.54	2.34	0.59
Western Bering Sea	Aydin et al. (2002)	marine	33	0.4	3.56	0.72
Western Gulf of Mexico	Arreguin-Sanchez (1993)	marine	23	0.45	5.84	0.65
Yucatan shelf, Gulf of Mexico	Vega-Cendejas (2001)	marine	20	0.53	10.33	0.63

ARTICLE 2

RELIER LA STABILITÉ DES RÉSEAUX TROPHIQUES AUX TRAITS FONCTIONNELS DES ESPÈCES QUI LE COMPOSENT

2.1 TITRE DE L'ARTICLE

Effet de la distribution de la masse corporelle des espèces sur la structure et la stabilité des réseaux trophiques complexes

2.2 RÉSUMÉ

La stabilité des réseaux trophiques est influencée par la topologie et la force des interactions entre les prédateurs et leurs proies. Il est très difficile de mesurer la force des interactions empiriquement, c'est pourquoi notre capacité à généraliser et à prédire l'effet de perturbations sur la stabilité des communautés complexes est toujours limitée. La masse corporelle semble être un trait fonctionnel clé pour la détermination de la topologie et de la force des interactions trophiques. Ce trait a été utilisé pour paramétrer des modèles de topologie des réseaux trophiques et a été également combiné à la théorie métabolique de l'écologie pour modéliser la dynamique consommateur-ressource. Bien qu'il ait été démontré que la relation entre taux métabolique et masse corporelle a un impact sur la stabilité des modules proie-prédateur, l'effet des propriétés de la distribution de la masse corporelle (moyenne et variance) sur la stabilité de réseaux trophiques riches en espèces n'a pas encore été exploré. Dans cette étude, nous relions la structure et la stabilité des réseaux trophiques à la distribution de la masse corporelle des espèces, en supposant que ce trait fonctionnel correspond à la dimension principale qui structure les réseaux d'interactions. Nous dérivons des matrices de communautés basées sur la masse corporelle qui décrivent la force et la topologie des

interactions trophiques entre les espèces d'un écosystème. Nous trouvons que l'ensemble des réseaux trophiques modélisés possèdent une forte stabilité asymptotique, quel que soit leur niveau de complexité, tandis que l'effet à court terme des perturbations a tendance à être plus faible dans les réseaux trophiques générés à partir d'une distribution de masse corporelle ayant une moyenne et un écart type élevés.

Cet article intitulé "*Effect of species body-mass distribution on the structure and stability of complex food webs*", fut corédigé par Dominique Gravel et moi-même. Le manuscrit est actuellement en préparation pour publication dans la revue *Ecology*.

En tant que première auteure, j'ai contribué à la conception de l'étude et au développement des outils analytiques utilisés. J'ai réalisé la recherche bibliographique, l'expression analytique des matrices d'interaction en fonction de la masse corporelle, la calibration du modèle, les simulations informatiques et l'analyse des résultats. J'ai également rédigé le manuscrit et réalisé les tableaux et les figures. Le professeur par Dominique Gravel, second auteur, a contribué à la conception de l'étude, au développement des outils analytiques et à la rédaction du manuscrit.

2.3 TITLE

Effect of species body-mass distribution on the structure and stability of complex food webs.

In preparation for *Ecology*.

2.4 ABSTRACT

The stability of complex food webs is influenced by the topology and the strength of interactions between predators and their prey. Because interaction strength is extremely difficult to measure empirically, our ability to generalize and predict the effect of perturbations on the stability of complex communities is still limited. One key functional trait that has been explored in determining food web topology and interaction strengths is body mass. It has been successfully used to parameterize models of food web topology and has also been combined with the metabolic theory of ecology to model consumer-resource dynamics. While the scaling of metabolic rate with body mass has been shown to impact the stability of predator-prey modules, the effect of the properties of the body mass distribution (average and variance) on the stability of large food webs has not been investigated yet. Here, we link food web structure and stability to species body mass distribution, assuming that this trait corresponds to the main dimension of interaction networks. We derive mass-based community matrices describing the strength and the topology of trophic interactions between species within a network. We find that all the modeled food webs have a high asymptotic stability regardless of their complexity, while short-term effects of perturbations tend to be lower on food webs generated from a species body mass distribution with high mean and standard deviation.

Keywords:

Trophic interactions, asymptotic stability, reactivity, community matrix, allometric relationships.

2.5 INTRODUCTION

Ecosystems are composed of hundreds of interacting species dependent on one another for energy and nutrients, creating complex dynamic food webs (Dunne et al., 2002). Despite decades of research on ecosystem stability, our ability to predict ecosystem responses to perturbations is still limited. It has been demonstrated that modeled food webs as large and complex as the ones observed in nature, but in which species interact at random, have a probability of persisting close to zero (May, 1972). This paradox, known as the complexity-stability debate, suggests that real communities have non-random properties that promote their stability despite their complexity. Yodzis (1981) was the first to outline the importance of the non-random organization of food webs. He showed that community matrices with empirically derived topology and realistic estimates of interaction strengths were more stable than randomly assembled ones (Yodzis, 1981). However, a process-based explanation to the existence of structured food webs was missing to solve the complexity-stability debate. This challenge led to the development of models able to capture the general mechanisms responsible for (i) the topology and (ii) the strength of the feeding interactions observed in real food webs.

In this context, the importance of metabolism and body-mass of organisms in structuring predator-prey interactions has been widely recognized (Peters and Wassenberg, 1983; Woodward et al., 2005; Brown et al., 2004). Several models generating realistic food web topology are based on simple feeding hierarchy rules (Cohen and Newman, 1985; Williams and Martinez, 2000; Allesina et al., 2008), but do not include body mass explicitly. The exception is the allometric niche model (Gravel et al., 2013), which assumes that body mass is the single dimension of the niche model, as consumer species tend to feed on prey smaller than themselves (Williams et al., 2010). Contrary to the original niche model, connectance is not an input parameter but instead emerge from species richness, predator–prey body mass relationships and body-mass frequency distribution. Body mass has also been used to generate realistic food webs in models based on foraging theory (Petchey et al., 2008) or ecological and evolutionary rules (Loeuille and Loreau, 2005).

Regarding the strength of feeding interactions, empirical food web studies have reported a skewed distribution of interaction strengths, characterized by many weak and few strong interactions, which has been shown to be highly stabilizing (De Ruiter et al., 1995; Paine, 1992; McCann and Hastings, 1998; Berlow, 1999; Jacquet et al., 2016). Again, body mass, and specifically predator-prey mass ratios, have been widely used as a shortcut for estimating per capita interaction strengths and studying food web stability (Emmerson and Raffaelli, 2004; Wootton and Emmerson, 2005; Reuman and Cohen, 2005; Otto et al., 2007; Berlow et al., 2009; O'Gorman and Emmerson, 2009; Riede et al., 2011). Finally, body-mass scaling theory has recently been used to derive realistic interaction strength distributions (Tang et al., 2014; Pawar, 2015).

Bioenergetic models has been developed that combined models of food web topology (i.e. niche, cascade or nested hierarchy) to a nonlinear bioenergetic model of population dynamics that use the allometric scaling of biological rates with body mass to determine species interaction strengths (Brose et al., 2005a, 2006a, 2005b, 2006b; Cheung et al., 2008; Berlow et al., 2009; O'Gorman and Emmerson, 2009; Allesina et al., 2015). According to the metabolic theory of ecology (Brown et al., 2004), metabolic, consumption and production rates are all supposed to follow a negative-quarter power–law relationship with body mass (Brose et al., 2005b, 2006b). Investigations of these models suggest that allometric scaling does indeed stabilize predator-prey dynamics (Otto et al., 2007)).

Despite the increasing number of food web models based on allometric constraints, the influence of the properties of the body-mass frequency distribution on food web structure and stability has not been investigated. Yet species body-mass distribution experiences important pressure in many ecosystems, such as marine food webs, where fisheries primarily target large species and global warming may reduce average body mass (Fisher et al., 2010; Cheung et al., 2012; Daufresne et al., 2009).

Here we explore the impact of the body-mass frequency distribution on emergent properties related to food web structure and stability. We integrate the topological and the quantitative description of food webs within a common mass-based approach in order to build realistic community matrices from body-mass frequency distribution and allometric scaling related to body mass. We investigate the effects of the average and variance of the body mass distribution on asymptotic stability and reactivity. We only fix these properties and species richness, letting all other aspects of food web structure (e.g. predator-prey mass ratio, connectance, topology, frequency distribution of interaction strengths) emerge from these variables.

2.6 METHODS

In the following we describe how we model species population dynamics and how we build mass-based community matrices from the body-mass distribution. We then describe the metrics we use to explore the effect of body-mass distribution on food web structure and stability.

2.6.1 Population dynamics

We consider the generalized Lotka-Volterra interaction equation to model population dynamics:

$$\frac{dB_i}{dt} = B_i\Big(b_i + \sum_{j=1}^{S}(\alpha_{ij} \times B_j) - \alpha_{ii} \times B_i\Big) \tag{2.1}$$

where b_i is the intrinsic rate (i.e., the intrinsic rate of increase for autotrophs, and natural mortality and losses for heterotrophs), B_i and B_j are respectively biomass of species i and j, interaction strength α_{ij} corresponds to the per capita effect of species j on the growth rate of species i and α_{ii} represents the per capita self-limitation of species i. As we will see below, we derive these quantities using allometric relationships and elements of the bioenergetic models.

2.6.2 Mass-based community matrices

We study the emergent structure and stability of a community matrix **C**, constructed in the following way. A first step is to determine the structure of an interaction network of size $S \times S$ from the niche model (Williams and Martinez, 2000), parameterized with the method presented in Gravel et al. (2013). We note the occurrence of a feeding interaction between species j and species i as $L_{ij} = 1$ in the interaction matrix **L**. The allometric niche model considers that body mass is the main niche axis, determining species feeding interactions. The model assigns each consumer species a feeding range along that niche axis, which can overlap with itself (allowing cannibalism) and even larger species (allowing loops), generating realistic food web topology. Based on empirical data, the optimal prey mass and the range of the feeding niche both increase with body mass Gravel et al. (2013). This approach has a unique feature relative to the original niche model: connectance, predator-prey mass ratio and degree distribution are not input parameters, but instead emerge from species richness, predator–prey body mass relationship and body- mass frequency distribution. Comparatively, previous studies based on allometric relationships use the body mass of a species to determine its energetic needs and derive food web structure from topological models using species richness and connectance as input parameters. Then, the same *a priori* predator- prey body mass ratio is assigned to all the community (Brose et al., 2005a, 2006a, 2005b, 2006b; Iles and Novak, 2016).

We use the formulation of De Ruiter et al. (1995) and mass-based constraints related to energy acquisition to calculate the strength of per capita predator-prey interactions. Assuming direct dependence of feeding rates on predator population density, we denote:

$$\alpha_{ij} = -\frac{\Phi_{ij}}{B_i \times B_j} \tag{2.2}$$

where Φ_{ij} corresponds to the biomass flux between predator species j and prey i ($kg/year$). We then assume that equilibrium biomass density B_i^* of each species i scales with body mass M_i in the logarithmic scale:

$$B_i^* = x_B \times M_i^{1/4+\theta_i} \tag{2.3}$$

where $\theta_i = log(\epsilon_i)/log(\rho_i)$. The term ϵ_i corresponds to the efficiency of species i to convert the resource on its own biomass and ρ_i is mean body-mass ratio between species i and its prey (Brown and Gillooly, 2003; Brown et al., 2004; Trebilco et al., 2013). According to the metabolic theory of ecology, the consumption rate of an individual of species j, noted Q_j, follows a negative-quarter power–law relationships with its body mass M_j (Peters and Wassenberg, 1983; Brown and Gillooly, 2003; Brown et al., 2004):

$$Q_j = x_Q \times M_j^{-1/4} \tag{2.4}$$

The predation required to cover all the energetic needs Φ_j of species j is split between all of its prey, in proportion to their relative abundance. From the topology matrix $\mathbf{L}$, we can determine the diet breadth g_j of each predator j and the set of its prey Γ_j. We suppose that DC_{ji}, the proportion of species i (where $i \in \Gamma_j$) in the diet of j, corresponds to the ratio between i's biomass density B_i and total prey biomass density $\sum_{k\in\Gamma}^{g_j} B_k$:

$$DC_{ji} = \frac{B_i}{\sum_{k\in\Gamma}^{g_j} B_k} \tag{2.5}$$

The consumption rate of an individual of species j feeding on i is therefore $Q_{ij} = Q_j \times DC_{ji}$. From equation (2.2), the per capita effect of predator j on prey i corresponds to:

$$\alpha_{ij} = -\frac{\Phi_{ij}}{B_j \times B_i} = -\frac{Q_{ij}}{B_i} = -\frac{x_\alpha \times M_j^{-1/4}}{\sum_{k\in\Gamma_j}^{g_j} M_k^{(1/4+\theta_k)}} \tag{2.6}$$

where $x_\alpha = x_Q/x_B$ is a normalization constant. Effects of prey on their predator are defined as predator growth resulting from this predation. Consequently, effect of the prey i on the predator j is related to effect of the predator on the prey according to: $\alpha_{ji} = -e_{ij} \times \alpha_{ij}$, where e_{ij} is the efficiency with which j converts food into biomass, from feeding on i.

We study the stability of food webs under equilibrium. Per capita interaction strength from all pairwise interactions of the topology matrix $\mathbf{L}$ make the interaction matrix $\mathbf{A} = [\alpha_{ij}]$. A community matrix $\mathbf{C}$ is obtained by multiplying the interaction matrix $\mathbf{A}$ with equilibrium biomass densities derived from the metabolic theory (Eq. 2.3), imposing the condition that all species at equilibrium have positive and finite densities (Bastolla et al., 2005). Thus, given classic measures of feasibility, all the food webs built with this approach would be feasible. Following Emmerson and Raffaelli (2004), we provide a further check on our model and include constraints on the signs of the intrinsic rate b_i, with consumer species having negative intrinsic rates and basal species positive ones. All the parameters used to build a community matrix come from the literature and are listed in Table 3.

2.6.3 Descriptors of food web structure

An increasingly wide variety of metrics is employed to describe and compare the structure of ecological networks, such as connectance, degree distribution, modularity or compartmentalization (Vermaat et al., 2009; Dunne et al., 2002; Williams and Martinez, 2000; Guimerà et al., 2010), but few of them address the strength of interactions (but see Bersier et al. (2002); Banasek-Richter et al. (2009)). Within this study, we focus on the properties related to food web complexity as defined by random matrix theory (May, 1972) in order to investigate the effect of body mass on the emergence of stable and complex food webs. We therefore measure the effect of the mean and variance of body mass on connectance, average and variance of interaction strength (May, 1972; Yodzis, 1981; Pimm, 1984; De Ruiter et al., 1995; Paine, 1992; McCann and Hastings, 1998; Berlow, 1999). Connectance determines the density of interactions in a food web, while average and variance of interaction strength quantify the magnitude of feeding interactions.

Furthermore, we measure the ratio between the shortest positive and negative feedback loops (Neutel and Thorne, 2014). This metric goes beyond pairwise interactions as it relies both on the topology and the strength of feeding interactions to describe food webs in terms of feedback loops (Levins, 1974; Dambacher et al., 2003; Neutel and Thorne, 2016). The ratio between 3-link positive and 2-link negative feedback loops is measured as $\sqrt[3]{\frac{|a_3|}{|a_2|}}$ where a_2 and a_3 correspond to the sum of all the 2-link and 3-link loops respectively and is thought to be negatively correlated to stability (Neutel and Thorne, 2014, 2016). We also study the average predator-prey mean ratio (PPMR), as an allometric scaling between this metric and per capita interaction strengths has been reported in several studies on food web stability (Emmerson and Raffaelli, 2004; Wootton and Emmerson, 2005; Reuman and Cohen, 2005; Otto et al., 2007; Berlow et al., 2009; O'Gorman and Emmerson, 2009; Riede et al., 2011).

2.6.4 Food web stability

The entries of a community matrix quantify the impact of a change in the density of one species on the dynamics of another species and several stability metrics can be derived from the study of its eigenvalues. The real part of the eigenvalues of the community matrix indicates the rate at which the different species converge toward the equilibrium after a small pulse perturbations to their density. Usually called asymptotic stability, the dominant real part of eigenvalues corresponds to the asymptotic rate at which a community returns to equilibrium (if negative) or moves away from it (if positive).

The reactivity of a food web can also be assessed from the community matrix (Neubert and Caswell, 1997). It corresponds to the maximal initial amplification rate of a pulse perturbation. It is computed as the dominant eigenvalue $\lambda_{max}(\mathbf{H})$ of the symmetric part $\mathbf{H} = (\mathbf{C} + \mathbf{C}^T)/2$ of the community matrix $\mathbf{C}$. It is a measure of instability: perturbations grow faster and communities temporarily move farther away from the equilibrium as reactivity increases. Together, the reactivity and the asymptotic stability describe the short and long-term response of a system to a perturbation.

The diagonal elements of the community matrix express the strength of density dependence, which is highly stabilizing as it moves the dominant eigenvalue to more negative values. In this study, the diagonal elements of the community matrices were set to 0 in order to focus on the effect of interspecific interactions on stability. Note that $Re(\lambda_{max})$ will be positive. This method is comparable to other studies that calculated stability by assessing the level of intraspecific interaction needed for all eigenvalues in a community matrix to have negative real parts (diagonal dominance) (May, 1972; Neutel et al., 2002; Neutel and Thorne, 2014).

2.6.5 Simulations

We run several simulations in order to study the influence of the mean and the standard deviation of species body mass distribution on properties of food web structure and stability. Range values for these variables are shown in Table 3. For each set of parameters, we take S species with body masses drawn from a log normal distribution of mean μ_M and standard deviation σ_M and build a community matrix. We only keep community matrices composed of 10% to 15% of basal species. We also remove the ones corresponding to unrealistic food webs, in which consumer or basal species have positive or negative intrinsic rates respectively. All species interact with at least one species in the remaining community matrices.

We built multiple polynomial regression models to assess the relative effect of mean body mass, s.d. of body mass and their interaction on the metrics describing food web structure and stability.

2.7 RESULTS

We first investigate the influence of species body mass distribution on connectance, average predator-prey mass ratio (PPMR) and the ratio between positive and negative feedback loops of the emergent food webs. We find that connectance decreases with mean body mass while it increases with the s.d. of body mass (Figure 21a, b). Conversely, PPMR increases with mean body mass and decreases with the s.d. of body mass (Figure 21c, d). The interaction between the mean and s.d. of body mass has a significant effect on PPMR (Table 4). As for connectance, the ratio between 3-link positive and 2-link negative feedback loops decreases with mean body mass and increases with the s.d. of body mass (Figure 21e, f).

We then study the interaction strength distribution (ISD) using the mean, s.d. and kurtosis. The mean ISD decreases with mean body mass only when associated to a small standard deviation of body mass (Figure 22a, $\sigma = 0.3$, in blue) and is strongly correlated to

Table 3: Parameters of the mass-based food web model and range of values used in the simulations. The allometric niche model (topology) is implemented with predator-prey body-size relationships derived from data on a Mediterranean food web (Gravel *et al.* 2013). Trophic efficiency is assumed constant across trophic levels and is derived from literature (Ware, 2000; Jennings et al., 2002). We choose normalization constants that generate feasible community matrices (i.e. positive densities and realistic intrinsic rates).

	Parameter	Values	Dimensions	Description
Body mass	S	100	–	Species richness
	μ	[3 : 6], step: 10^{-3}	*mass*	Mean body mass (log)
	σ	[0.25 : 0.5], step: 10^{-4}	*mass*	Standard deviation (log)
Topology	α_1	0.53	–	Slope of the regression line
	α_0	0.2	–	Intercept of the regression line
	$\beta_{1,low}$	0.19	–	Slope of the 5% quantile regression
	$\beta_{0,low}$	0.27	–	Intercept of the 5% quantile regression
	$\beta_{1,high}$	0.9	–	Slope of the 95% quantile regression
	$\beta_{0,high}$	-0.07	–	Intercept of the 95% quantile regression
Species biomass	x_B	10^3	$mass^{0.25}$	Normalization constant of eq. 2.3
Energetic needs	x_Q	10^4	$mass^{0.25} \times time^{-1}$	Normalization constant of eq. 2.4
	ϵ	0.1	–	Trophic efficiency

the s.d. of body mass (Figure 22b, Table 4). We observe the opposite trend for the s.d. of ISD (Figure 22c, d), with a strong negative effect of the s.d. of body mass (Table 4). A striking result is the high values of kurtosis of the ISD (Figure 22e, f, average of 236). Kurtosis is an index of the peakedness of the interaction strength distribution and equals zero for normal distributions. Kurtosis decreases with mean body mass and increases with s.d. of body mass, but these parameters only explain a small part of the variability of the kurtosis (Figure 22e,f and Table 4, $R^2 = 0.11$).

We finally investigate the influence of species body mass distribution on the asymptotic stability and reactivity of food webs, which describe the short and long-term response of food webs to a perturbation. We find that asymptotic stability depicts a very small range of values among all the simulated food webs (values between 1.3×10^{-5} and 0.34 for 2,720 community

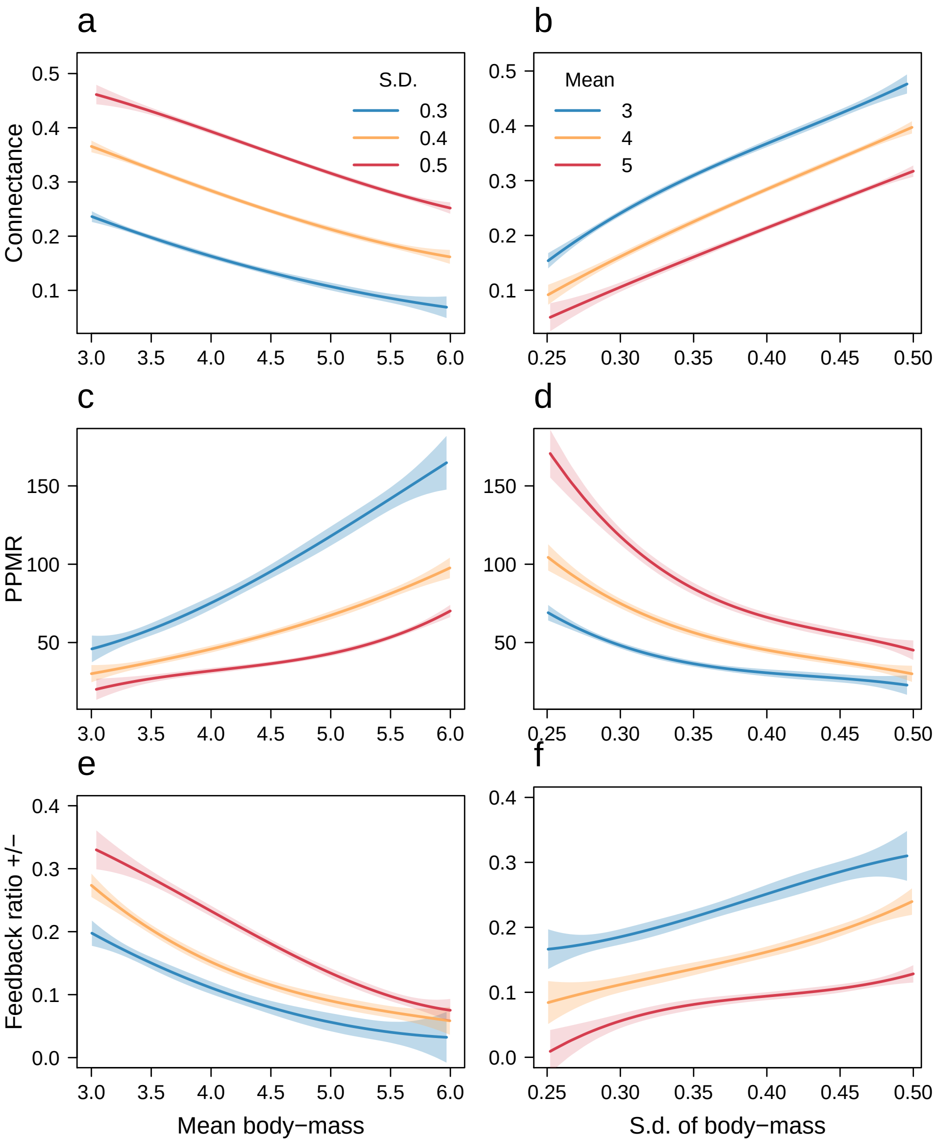

Figure 21: Effect of body mass distribution on food web structure. a-b) Relationship between connectance and a) mean body mass or b) s.d. of body mass. c-d) Relationship between average predator-prey mass ratio (PPMR) and c) mean body mass or d) s.d. of body mass. e-f) Relationship between the ratio between 3-link positive and 2-link negative feedback loops and e) mean body mass or f) s.d. of body mass. Lines correspond to the polynomial regressions fitted for different values of s.d. of body mass (a, c, e) or different values of mean body mass (b, d, f). Colored areas give the 95% confidence intervals.

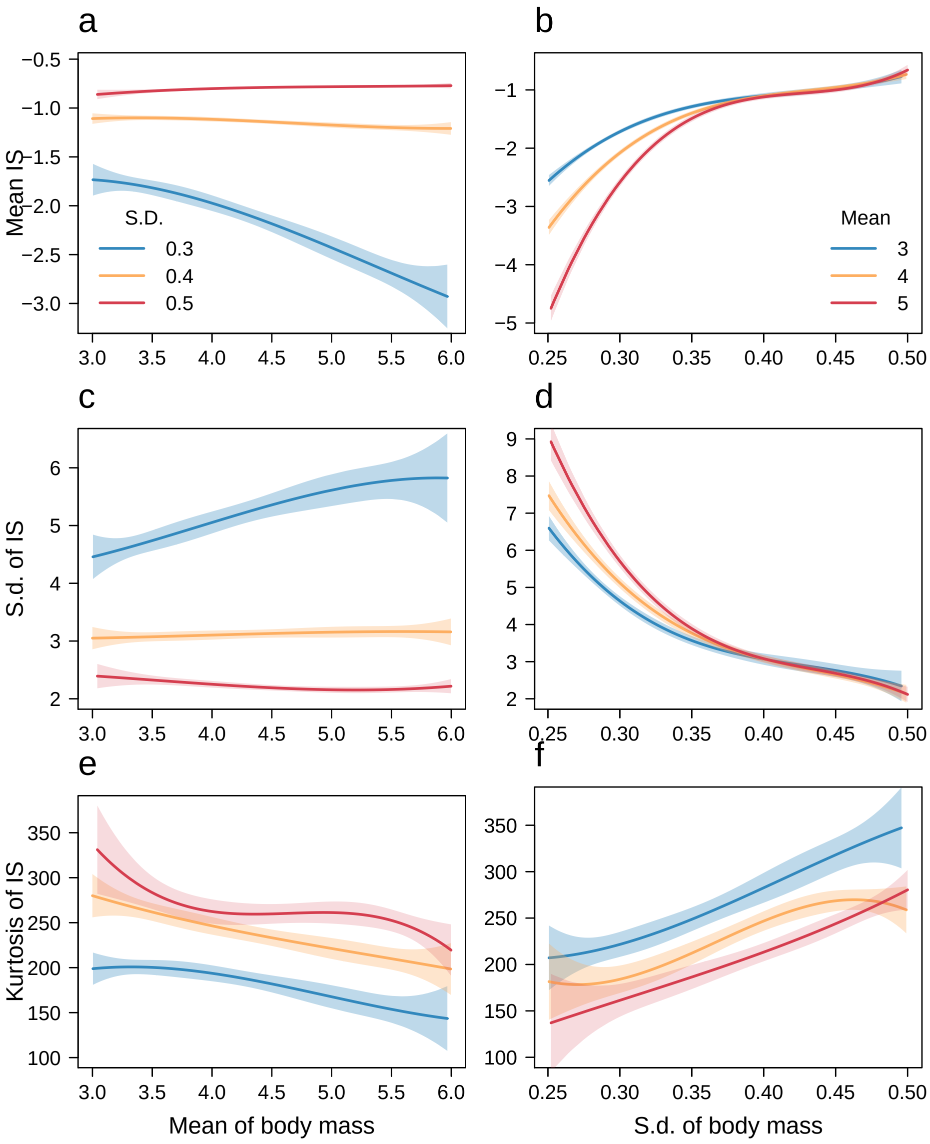

Figure 22: Effect of body mass distribution on interaction strength distribution (ISD). a-b) Relationship between interaction strength mean and a) mean body mass or b) s.d. of body mass. c-d) Relationship between the s.d. of interaction strengths and c) mean body mass or d) s.d. of body mass. e-f) Relationship between the kurtosis of the ISD and e) mean body mass or f) s.d. of body mass. Lines correspond to the polynomial regressions fitted for different values of s.d. of body mass (a, c, e) or different values of mean body mass (b, d, f). Colored areas give the 95% confidence intervals.

Table 4: Analyses of variance for polynomial multiple regression models accounting for mean body mass, s.d. of body mass and their interaction. Response variables are connectance, average predator-prey mass ratio (PPMR), ratio between positive and negative feedback loops (feedback ratio), mean, s.d. and kurtosis of the interaction strength distribution (ISD), asymptotic stability and reactivity. F-values in bold illustrate a significant effect of the explanatory variable (P-value<0.01).

	F-value			
Variable	Mean body mass	S.D. of body mass	Interaction	R^2
Connectance	**3,359**	**6,244**	**21**	0.81
PPMR	**1,458**	**1,318**	**157**	0.57
Feedback ratio	**1,852**	**421**	**75**	0.52
Mean ISD	**58**	**5,334**	**185**	0.72
S.D. of ISD	**94**	**2,727**	**31**	0.56
Kurtosis of ISD	**89**	**183**	0.3	0.11
Asymptotic stability	**1,095**	**142**	**36**	0.37
Reactivity	**2,815**	**227**	**37**	0.58

matrices). The asymptotic stability increases with mean body mass while it decreases with the s.d. of body mass, but these relationships are not very strong (Figure 23a, b and Table 4). Again, the interaction between these parameters influences the strength of the relationships (Table 4). The effect of mean or s.d. of body mass on reactivity is much stronger than for asymptotic stability (values between 1 and 263). Both mean body mass and s.d. of body mass are negatively correlated to reactivity, with a stronger effect of mean body mass (Figure 23c, d).

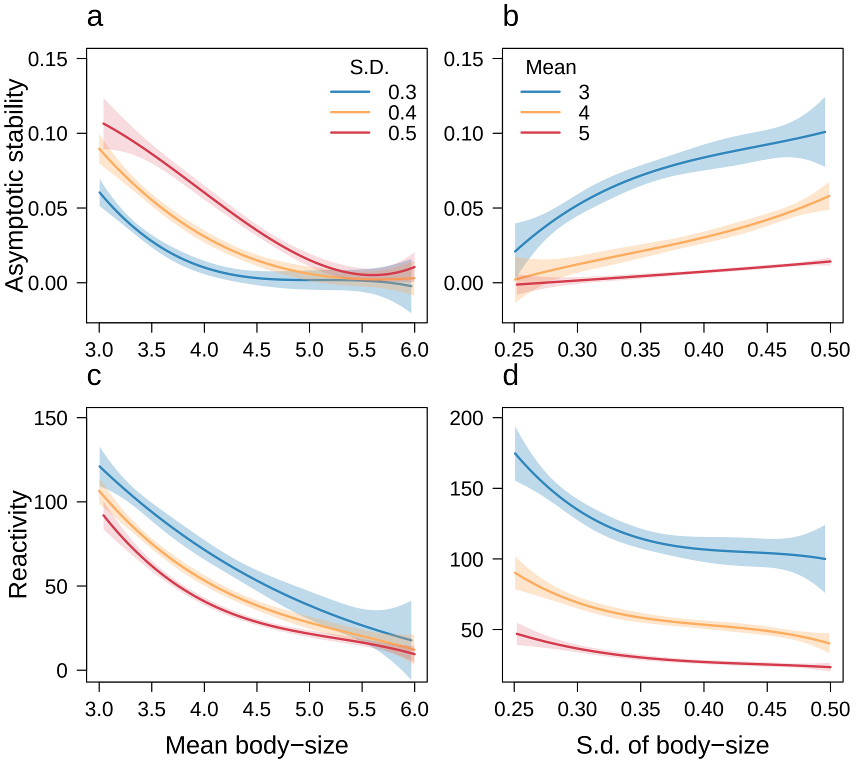

Figure 23: Effect of body mass distribution on food web stability. a-b) Relationship between asymptotic stability, measured as the dominant real part of the eigenvalues, and a) mean body mass or b) s.d. of body mass. Food webs with values closed to zero are the most stable. c-d) Relationship between reactivity, computed as the dominant eigenvalue of the symmetric part of the community matrix, and c) mean body mass or d) s.d. of body mass. Food webs with values close to zero are the less reactive. Lines correspond to the polynomial regressions fitted for different values of s.d. of body mass (a, c) or different values of mean body mass (b, d). Colored areas give the 95% confidence intervals.

2.8 DISCUSSION

Overall, these results demonstrate that the relative effects of mean and s.d. of the body mass distribution differ between food web properties. They can be categorized into three groups: (i) the properties that are equally affected by mean and s.d. of body mass (ii) those that are mainly affected by mean body mass and (iii) those that are mainly affected by the s.d. of body mass.

Connectance and average predator-prey mass ratio (PPMR) correspond to the first category, as shown in Table 4 and Figure 21. Asymptotic stability and reactivity, which measure food web stability, along with the ratio between positive and negative feedback loops fall into the second category. We find that strong negative feedback loops, a high asymptotic stability and a low reactivity characterize food webs with a high mean of body mass (and a high s.d. of body mass to a lesser extent). The stabilizing effect of mean body mass could be related to its effect on the variables related to May's stability criterion, namely connectance and the standard deviation of interaction strengths. We observe that mean body mass is negatively correlated to connectance, but has little effect on interaction strength distribution (relative to the s.d. of body mass, see Table 4). Thus, mean body mass tends to decrease the overall complexity, which is stabilizing.

All the properties describing the distribution of interaction strengths (ISD) fall into the third category. Counter-intuitively, a higher s.d. of body mass generates less extreme interactions, with a mean of the ISD closer to zero (illustrating a balance between positive and negative interactions) and with a smaller s.d. of the ISD (Figure 22). The positive effect of the s.d. of body mass on the kurtosis is, however, not very strong (Table 4). Again, we refer to connectance to explain the relationship of s.d. of body mass with stability. A strong positive correlation is observed between connectance and the s.d. of body mass (Figure 21). Consequently, connectance and the s.d. of IS are negatively correlated in mass-based community matrices, which is stabilizing as it decreases the overall complexity of the system.

In this study, we derived community matrices from a single trait, assuming that body mass corresponds to the main dimension of the trophic niche space. Although this assumption is unlikely, this approach provides interesting insights on the effect of body mass distribution on food web structure and the stabilizing properties of real food webs. Indeed, this approach provides a process-based explanation to the absence of complexity stability relationship observed in empirical ecosystems. We find that connectance and s.d. of interaction strengths, which determine complexity (May, 1972), are negatively correlated in mass-based community matrices, a trade-off that has been observed in empirical food webs (Jacquet et al., 2016). Furthermore, the mass-based community matrices are characterized by an interaction strength distribution with a high kurtosis. This non-random frequency distribution of interaction strengths, with many weak and few strong interactions, is thought to be the primary driver of the absence of a complexity-stability relationship in real ecosystems (De Ruiter et al., 1995; Paine, 1992; McCann and Hastings, 1998; Berlow, 1999; Jacquet et al., 2016).

Our approach assumes that food webs are close systems and that predators only feed on the species present in the community. Large predators are more mobile than small species and often feed on several sub-food webs. This mechanism could decrease the per capita effect of mobile predators on their prey, allowing to sustain larger biomass of predator species. The method we presented here could be easily developed to account for these mobility- dependent interaction strengths by specifying the amount of external resource into the diet composition of each predator (equation 2.5).

In conclusion, mass-based community matrices generate food webs with a high asymptotic stability, while large mean and s.d. of body mass generate less reactive food webs. Human-induced changes in body mass distributions, generally related to a depletion of large sized species (Pauly and Zeller, 2016; Cardillo et al., 2005), could therefore increase the reactivity of an ecosystem, leading to a higher initial amplification of a disturbance in population densities.

2.9 ACKNOWLEDGEMENTS

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ARTICLE 3

EFFET DE LA TAILLE ET DE L'ISOLEMENT DE L'HABITAT SUR LA STRUCTURE EN TAILLE DES ESPÈCES D'UN ÉCOSYSTÈME

3.1 TITRE DE L'ARTICLE

Prédire la variation de la distribution de taille des espèces avec la théorie allométrique et trophique de la biogéographie des îles

3.2 RÉSUMÉ

La Théorie de la Biogéographie des Îles (TBI) prédit comment la taille et l'isolement, à travers les dynamiques de colonisation et d'extinction, influencent la richesse spécifique à l'équilibre des habitats insulaires. Toutefois, la TBI demeure silencieuse concernant la distribution de la taille corporelle au sein d'un assemblage d'espèces, qui est un aspect clé du fonctionnement des écosystèmes. Pour combler cette lacune, nous développons des modèles de biogéographie des îles qui prédisent la distribution de la taille corporelle des espèces en fonction de l'aire et de l'isolement de l'habitat. Ces modèles intègrent le potentiel de dispersion, la vulnérabilité aux extinctions et la position trophique des espèces, qui varient en fonction de la taille corporelle et influencent la dynamique spatiale des populations. Nous comparons ensuite les prédictions des modèles aux distributions de taille corporelle des poissons piscivores et herbivores des récifs tropicaux à l'échelle mondiale. Nous trouvons que les récifs petits et isolés possèdent une plus grande proportion d'espèces de grande taille comparativement aux récifs grands et très connectés. Nous montrons également que la connaissance de la taille corporelle et de la position trophique des espèces améliore les prédictions de la probabilité de présence des poissons sur les récifs tropicaux, ce qui supporte la théorie

allométrique et trophique de la biogéographie des îles. L'intégration de l'écologie fonctionnelle à des modèles de biogéographie est applicable à d'autres traits fonctionnels et propose une approche générale probabiliste pour étudier la variation de la distribution d'un trait fonctionnel en fonction de la taille et de l'isolement d'une zone d'habitat.

Cet article intitulé "*Predicting the scaling of species body-size distribution with the allometric and trophic theory of island biogeography*", fut corédigé par David Mouillot, Michel Kulbicki, Dominique Gravel et moi-même. Il a est actuellement en révisions dans la revue *Ecology Letters*.

En tant que première auteure, j'ai contribué à la conception de l'étude et au développement des outils analytiques utilisés. J'ai réalisé la recherche bibliographique, l'analyse statistique des données, les simulations des modèles de biogéographie et l'analyse des résultats. J'ai rédigé le manuscrit et réalisé les tableaux et les figures. Le professeur David Mouillot, second auteur, a contribué à la conception de l'étude, au développement des outils analytiques utilisés et à la rédaction du manuscrit. Michel Kulbicki, troisième auteur, a fourni les données empiriques concernant les poissons des récifs tropicaux et a contribué à la rédaction du manuscrit. Le professeur Dominique Gravel, dernier auteur, a contribué à la conception de l'étude, au développement des outils analytiques utilisés et à la rédaction du manuscrit.

J'ai présenté ses résultats lors de la conférence annuelle du CSBQ (Centre de la Science de la Biodiversité du Québec) en octobre 2015 à Montréal (Canada), ainsi qu'à la conférence annuelle de l'ESA (Ecological Society of America) en août 2016 à Fort Lauderdale (États-Unis).

3.3 TITLE

Predicting the scaling of species body-size distribution with the allometric and trophic theory of island biogeography.

In revision for *Ecology Letters*.

3.4 ABSTRACT

The Theory of Island Biogeography (TIB) predicts how area and isolation, through colonization and extinction dynamics, influence species richness equilibrium on insular habitats. However, the TIB remains silent about the body-size distribution within species assemblages, a key aspect of ecosystem functioning and services. To fill this gap, we develop models of island biogeography that predict species body-size distribution as a function of habitat area and isolation. These models integrate species dispersal potential, vulnerability to extinction and trophic position, which are known to scale with body-size and to influence spatial population dynamics. We then compare model predictions to the body- size distributions of piscivorous and herbivorous fishes found on tropical reefs worldwide. We find that small and isolated reefs have a higher proportion of large-sized species than large and connected ones. We also show that knowledge of species body-size and trophic position improves the predictions of fish occupancy on tropical reefs, supporting the predictions of the allometric and trophic theory of biogeography. The integration of functional ecology to island biogeography models is broadly applicable to any functional traits and provides a general probabilistic approach to study the scaling of trait distribution with habitat area and isolation.

3.5 INTRODUCTION

Human activities have caused widespread degradation of natural landscapes through habitat destruction, fragmentation and homogenization (Haddad et al., 2015; Newbold et al., 2015). Understanding the effect of habitat area and isolation on biodiversity is therefore a central question in ecology and conservation (Tscharntke et al., 2012; Newbold et al., 2015). Although most of the early studies on biogeography have focused on the ecological processes determining species richness distribution (e.g. Arrhenius (1921); MacArthur and Wilson (1963)), other aspects of biodiversity, such as functional or phylogenetic diversity, are increasingly investigated (Gaston and Blackburn, 2000; Mazel et al., 2015; Whittaker et al., 2014). Body-size distribution within species assemblages is also a critical aspect of biodiversity since productivity, energy flows and biomass storage are all size-based constrained (McMahon, 1973; Peters and Wassenberg, 1983; Brown et al., 2004; Woodward et al., 2005; Brose et al., 2006a; Vucic-Pestic et al., 2010). Hence, species body-size has been successfully used to parameterize food web models (Yodzis and Innes, 1992; Williams and Martinez, 2000; Allesina et al., 2008; Williams et al., 2010; Gravel et al., 2013) but the biogeography of species body-size distribution still lacks a mechanistic explanation. The present study aims to develop a framework bringing new insights upon the effect of habitat area and isolation on the body- size distribution of local species assemblages with an application to tropical reef fishes worldwide.

The frequency distribution of species body-size in a local assemblage is not a random sample of the regional species body-size distribution (Gaston and Blackburn, 2000). It has been demonstrated that the right skewed species body-size distribution of North American mammals, observed at the continental scale, becomes progressively flatter until being nearly uniform with decreasing area (Brown and Nicoletto, 1991; Brown, 1995; Bakker and Kelt, 2000). The biogeography of species body-size distributions has also been studied for South American (Marquet and Cofre, 1999; Bakker and Kelt, 2000) and African mammals (Kelt and Meyer, 2009).

Other studies, focusing on the relationship between extreme body-size and habitat area, show that, in general, smaller habitat patches have fewer taxa of extreme sizes (Marquet and Taper, 1998; Burness et al., 2001; Okie and Brown, 2009; Millien and Gonzalez, 2011). In marine ecosystems, the scaling of larval-stage duration and fish mobility with body-size has been hypothesized to primarily drive the global variation of species body-size distribution across assemblages (Connell, 1983; Mora et al., 2003; Jetz et al., 2004; Rooney et al., 2008; Luiz et al., 2013; Stier et al., 2014; Nash et al., 2015). Despite a long lasting interest in size-based approaches, we still lack a theoretical framework explaining species body-size distribution in assemblages as a function of habitat area and isolation.

Here, we develop two process-based models from the theory of island biogeography to derive how the mean and the standard deviation of species body-size distribution are expected to scale with area and isolation. We consider islands as a general representation of isolated systems, such as lakes, ponds, forest fragments or coral reefs, surrounded by a desert of unsuitable habitat (Diamond, 1975; Losos and Ricklefs, 2009; Warren et al., 2015). We use this framework to determine the influence of species dispersal potential, vulnerability to extinction and trophic position on the variation of body-size distribution across islands, along a gradient of area and isolation. Then, we compare theoretical predictions to the empirical distributions of body-size in fish assemblages across 134 tropical reefs of various area and isolation. We finally highlight the importance of considering trophic position to explain the global variation of body-size distribution in reef fish assemblages.

3.6 CONCEPTUAL FRAMEWORK

3.6.1 Probabilistic estimation of local trait distribution

A local assemblage, composed of S species, is a sub-sample of a regional pool composed of R species, whose composition is determined by various ecological mechanisms. The species body-size distribution of this sub-sample can be expressed in the following way: let the random variable X_i indicate the occurrence of species i in a given island or local assemblage, with $X_i = 0$ when species i is absent and $X_i = 1$ when present. The probability of picking a species i with a body-size M_i in this local assemblage is:

$$P(X_i, M_i) = P(X_i = 1|M_i) \times P(M_i) \tag{3.1}$$

where $P(M_i)$ corresponds to the probability of observing a species with body-size M_i in the regional pool, which depends on the moments of the regional body-size probability distribution $f(M)$. $P(X_i = 1|M_i)$ is the occupancy of species i, that is the probability for species i to occupy the island knowing its body-size M_i. This probability expresses the influence of ecological processes on species occupancy and varies according to the ecological hypotheses tested by the model. We then derive the density function of body-size, $g(M)$, observed in a local assemblage as:

$$g(M) = P(M|X = 1) = \frac{(P(X = 1|M) \times f(M))}{P(X)} \tag{3.2}$$

where $P(X) = S/R$. This illustrates how the regional body-size distribution $f(M)$ and ecological processes, determining $P(X_i = 1|M_i)$, shape the species body-size distribution of local assemblages (Figure 24). Note that the probabilistic expression, used here for the expected body-size distribution in a local community, can be applied to any functional trait. The strength of this approach is to clearly distinguish the influence of both ecological processes and the composition of the regional pool on the local distribution of body-size $g(M)$.

3.6.2 Theory of Island Biogeography (TIB)

The Theory of Island Biogeography (TIB) provides a process-based explanation to the general observation that larger islands have more species than smaller ones, and islands closer

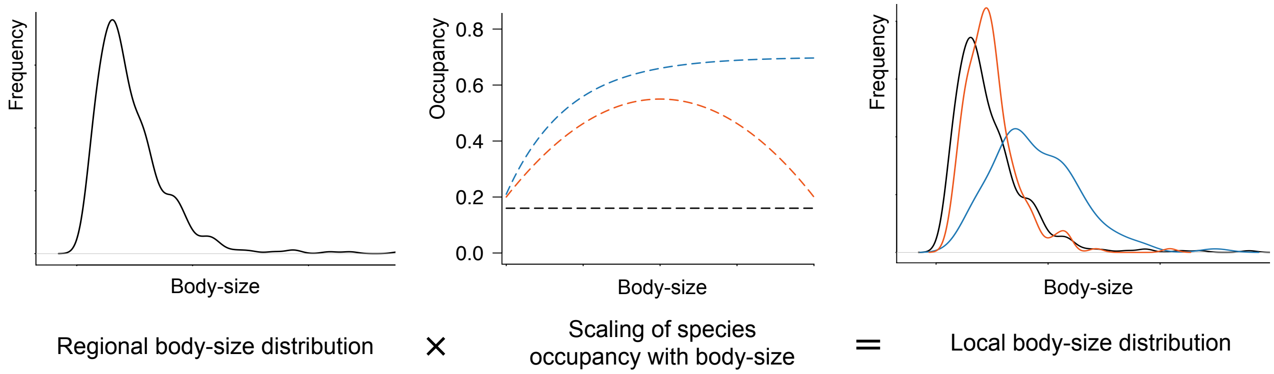

Figure 24: Conceptual framework. The regional body-size distribution and the scaling of species occupancy with body-size determine species body-size distribution in the local assemblage. The models of island biogeography suppose different relationships between species occupancy and body-size. The TIB assumes functional equivalence between species: occupancy is influenced by island area and isolation only. The ATIB assumes that occupancy is species-specific and depends on species body-size in addition to island area and isolation. Finally, the occupancy of predatory species also depends on resource availability in the ATTIB.

to the mainland have more species than isolated ones (MacArthur and Wilson, 1963; Losos and Ricklefs, 2009). Local species richness, i.e. within an island, results from the balance between colonization and extinction dynamics. Colonization rate c, that is species's colonization probability per unit time, is assumed inversely proportional to the distance to the mainland hosting the regional species pool. Extinction rate e (species's extinction probability per unit time) is assumed inversely proportional to island area, as this geographical characteristic directly affects population size and thus species sensitivity to demographic stochasticity (Hanski, 1989). In the TIB, species interactions have no impact on colonization and extinction rates. All species are assumed to be functionally equivalent and have the same probability of occupying the island. Consequently, $P(X_i = 1|M_i) = P(X_i = 1) = c/(c + e)$ (Gravel et al., 2011) and the species body-size distribution in a local assemblage is a random sample of S species drawn from the body-size probability distribution of the regional pool: $g(M) = f(M)$.

3.6.3 Allometric Theory of Island Biogeography (ATIB)

The TIB assumes that all species are equally influenced by island area and isolation in their probability of occurrence. However, body-size is likely to influence both colonization and extinction rates. Owing to the negative relationship between species abundance and body- size (Damuth, 1981; Nee et al., 1991; Blackburn, 1999; White et al., 2007), extinction rate has been hypothesized to be positively correlated to body-size. Consequently, we should consider $e_i \propto M_i^b$, meaning that large-bodied species will be more impacted by decreasing island area than small-bodied species. The link between species extinction rate and body- size is however not straightforward with multiple factors acting together, such as minimum viable population size, dependence to habitat complexity or diet generality (Gaston and Blackburn, 2000; Graham et al., 2011). For example, some studies proposed that intermediate body-sized species could be the less prone to extinction in small areas as they are more generalists than small species and have higher densities than large species, leading to a U- shape relationship between extinction rate and body-size: $e_i \propto -M_i(\frac{x-M_i}{x})$ (Marquet and Taper, 1998; Brown et al., 1993; Okie and Brown, 2009).

In contrast, the scaling of colonization rate with body-size is supported by many empirical studies (Peters and Wassenberg, 1983; Wieters et al., 2008). In marine systems, home range, pelagic larval duration, number of larvae produced per adult, mobility and diet generality increase with fish body-size (Mora et al., 2003; Luiz et al., 2013; Nash et al., 2015). The positive relationship between species body-size and their dispersal potential is thought to primarily influence the body-size distribution of reef fishes at the biogeographical scale (Cornell and Karlson, 2000; Mora et al., 2003; Luiz et al., 2013; Stier et al., 2014).

The scaling of extinction and colonization rates with body-size can be easily integrated into the TIB, leading to an Allometric Theory of Island Biogeography (ATIB). A general model of the equilibrium occurrence probability should be species-specific, with $P(X_i = 1|M_i) = c_i/(c_i + e_i)$. The net effect of area and isolation on the resulting distribution will be dependent on the functions specified for c_i and e_i. In the following analyses, we make different assumptions regarding the scaling of extinction rate with body-size, leading to three versions of the ATIB that we consider representative of most situations: extinction rate is independent of body-size ($ATIB_{H0}$), extinction rate increases with body size ($ATIB_{H1}$) and intermediate body-sized species are less prone to extinction than small and large species ($ATIB_{H2}$).

3.6.4 Allometric and Trophic Theory of Island Biogeography (ATTIB)

Another plausible hypothesis is that colonization and extinction dynamics are influenced by resource availability (Holt, 2002, 2009; Cirtwill and Stouffer, 2015). Under this assumption, species spatial dynamics depend not only on island characteristics and species traits but also on the composition of the local assemblage. The Trophic Theory of Island Biogeography is an extension of the TIB that takes into account the effect of trophic interactions on colonization (Gravel et al., 2011). It relies on two assumptions translating the concept of a bottom-up sequential dependency of predators on their prey (Holt, 1997, 2009): (i) a predator species colonizing a local assemblage will persist only if at least one of its potential prey species is present and (ii) a predator species losing its last potential prey in a local assemblage goes extinct (Gravel et al., 2011). Diet breadth is therefore a key trait influencing predator occurrence, with generalist species more likely to find prey species at colonization and persist then after. This theory predicts that consumers at the top of the food web have a lower occupancy than basal species as they rely on the presence of species at each intermediate trophic level. The TTIB is a first step toward the integration of resource availability constraints to species spatial dynamics. The hypothesis of "at least one prey species present" should be considered as an easily computable way to represent resource availability rather than a strict assumption related to the presence/absence of a particular prey species. We build an Allometric and Trophic Theory of Island Biogeography (ATTIB) that combines the ATIB and the TTIB. The equilibrium occurrence probability is $P(X_p = 1|M_p) = c_p/(c_p + e_p)$ for predatory species, where colonization and extinction rates c_p and e_p depend on the body-size of predator species p but also on its diet breadth g_p and its trophic position with respect to primary resources. Note that the spatial dynamics of basal species (noted b), located at the bottom of the food web and feeding on primary resources, are independent of assemblage composition and correspond to the ATIB: $P(X_b = 1|M_b) = c_b/(c_b + e_b)$.

The ATTIB requires an a priori knowledge of the regional food web structure (who eats whom). This kind of information is only available for a limited number of species and remains challenging to collect over large geographic scales or for species-rich assemblages. We used predator-prey allometric relationships observed in marine ecosystems and the method presented in Gravel et al. (2013) to parameterize the niche model of food web structure (Williams and Martinez, 2000). The niche model assigns to each consumer species a feeding range on a niche axis that can overlap with itself (allowing cannibalism), generating realistic food web structure at least for marine fishes (Gravel et al., 2013). Body-size is the niche position of every species and the optimal prey size is determined by the regression of prey size against predator size, and the range by quantile regressions (section 1 of Supporting Information). The parameters of the niche model were derived from data on marine food webs (Figure 32, Gravel et al. 2013, Barnes et al. 2010) and are presented in Table 7.

The diet breadth of a predatory species i depends on the probability of feeding on the species present in the regional species pool. Let the random variable L_{ij} indicate the occurrence of a trophic interaction between species i and species j, with $L_{ij} = 0$ when species do not interact and $L_{ij} = 1$ when species i can feed on species j. The expected number of prey items can then be expressed from the species body-size distribution as:

$$g_i = \int_0^\infty P(L_{ij} = 1|M_i, M_j) \times P(M_j) \tag{3.3}$$

where $P(L|M_i, M_j)$ is the probability that species i feeds on species j knowing their body-sizes M_i and M_j while $P(M_j)$ corresponds to the probability to observe a species with body-size M_j in the regional pool (Williams et al., 2010; Gravel et al., 2013; Bartomeus et al., 2016). The ATTIB thus predicts the interactive effect of biogeography and trophic position on the species body-size distribution in local assemblages from the relationship between diet breadth and body-size of species composing the regional pool. We consider three versions of the ATTIB assuming different relationships between extinction rate and body-size ($ATTIB_{H0}$, $ATTIB_{H1}$ and $ATTIB_{H2}$).

3.7 PREDICTIONS

3.7.1 From species occupancy to local body-size distribution

The TIB, the ATIB and the ATTIB predict different size-occupancy relationships and consequently different body-size distributions $g(M)$. We use species richness, the mean and the standard deviation (s.d.) of $g(M)$ to describe the local body-size distribution. We then run stochastic simulations to study the effect of island area and isolation on these metrics and compare the predictions of the TIB, the ATIB and the ATTIB.

3.7.2 Simulations

We consider a regional species pool composed of 200 species. The body-size M_i of any species i is randomly drawn from a log-normal distribution $f(M)$ of mean μ and standard deviation σ. This distribution roughly represents the observed distributions at large spatial scale (Cohen et al., 1993; Brown, 1995; Allen et al., 2006). Mean and s.d. are derived from the global body-size distribution of tropical reef-associated piscivorous fishes (Kulbicki et al. (2013); Parravicini et al. (2013) - see next section). We ran simulations for 2,500 pairs of c and e that vary between 0.01 and 0.99. Simulations were run over 1,000 time steps. All the model parameters are presented in section 1 of Supporting Information (Table 7, Figure 30, 31,32).

We use a discrete time stochastic version of the ATTIB to simulate the dynamics of species occupancy in local assemblages. The stochastic version of the model was found to better fit empirical data because it takes into account the effect of trophic level and the way that each species is connected to the food web (Gravel et al., 2011). At each time step, a predator species absent from the local assemblage colonizes it with a probability c_p if there is at least one prey or cannot otherwise. A predator species present in the local assemblage goes extinct with a probability e_p. Further, a predator species losing its last prey species during a time step goes automatically extinct. The probability that a basal species colonizes the local assemblage or goes extinct is c_b and e_b, respectively, irrespective of the assemblage composition. We consider that herbivorous species are not food limited and consequently have the dynamics of basal species. Herbivorous species make half of the regional species pool.

3.7.3 Island area and isolation shape species body-size distribution

As predicted by the classic TIB, we find that species richness increases with island area (Figure 25a) and decreases with island isolation (Figure 25b) using the ATIB and the ATTIB. We then explore the relationships between island characteristics and species body-size distribution in local assemblages. Under the TIB, the expected body-size distribution in assemblages has the same mean and s.d. as in the regional species pool (Figure 25c, d). The three versions of the ATIB predict a decrease of mean body-size with island area and an increase with island isolation (Figure 25c-d, in red). The effects of island area and isolation are stronger for $ATIB_{H2}$, in which the scaling of extinction rate with body-size is U-shaped, and weaker when extinction rate increases with body-size ($ATIB_{H1}$). The variation (s.d.) of species body-size within assemblages is not strongly influenced by island area or isolation (Figure 25e-f, in red, $1.04 < \sigma < 1.08$). Under the ATTIB, the regional food web is characterized by a positive relationship between body-size and diet breadth g_p, which determines the occupancy of predatory species $P(X_p|M_p)$. Large predatory species have a higher probability of finding prey species on a small and isolated island, and persist then after, than small predatory species. At the assemblage level, the ATTIB predicts that island area and isolation bias the local body-size distribution of predatory species towards larger and less variable body-sizes on small or isolated islands. This is illustrated in Figure 25c and d where mean body-size of predatory species decreases with area and increases with isolation. On small or isolated islands, the variation (s.d.) of body-size is lower than expected from the regional species pool, suggesting a lower proportion of extreme-sized predatory species as island geographic constrains increases (Figure 25e-f, in blue, $0.88 < \sigma < 1.04$). The three versions of the ATTIB predict similar effects of island area and isolation on the body-size distribution of local assemblages.

3.8 APPLICATION TO TROPICAL REEF FISHES

Fishes play key functional roles on tropical reefs (Bellwood et al., 2012; Bozec et al., 2016) and provide protein for several hundred million people, especially in the developing world (Teh et al., 2013). This provision of eatable biomass is not only promoted by fish species richness but also by the diversity of fish traits (Duffy et al., 2016). The body-size spectrum or the distribution of body-size within fish assemblages has been recognized as a primary operative factor in determining ecosystem functioning and the production of biomass (Fisher et al., 2010). At small scale, the structural complexity of coral reef habitat, i.e. the number and size of caves and crevices, determines the frequency distribution of body-size (Rogers et al., 2014). At the regional scale, species poor assemblages tend to have larger mean body-size (Stier et al., 2014; Kulbicki et al., 2015). However, we still lack a theoretical and mechanistic framework to explain this pattern.

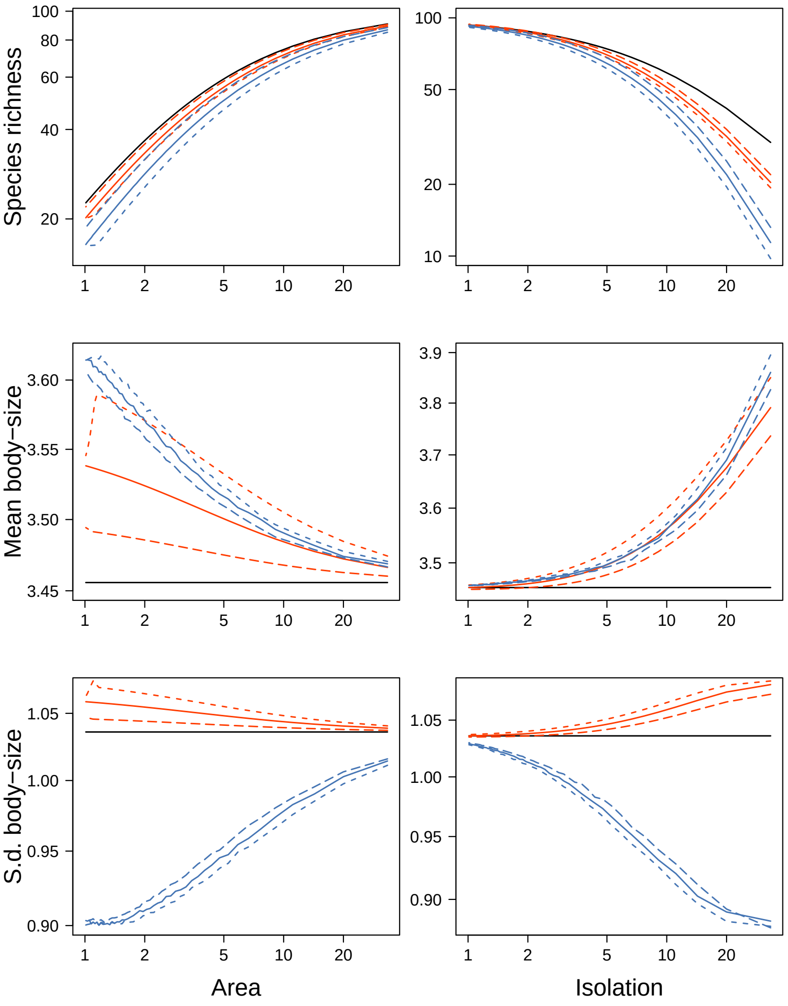

Figure 25: Influence of island area and isolation on species body-size distribution predicted by the TIB (in black) and different versions of the ATIB and the ATTIB. Red lines correspond to the ATIB and blue lines to the ATTIB. Full lines correspond to H_0 (extinction rate independent of body-size), wide dotted lines to H_1 (extinction rate increases with body-size) and small dotted lines to H_2 (U-shaped relationship). Island area corresponds to $1/e$ where e is species extinction rate and colonization rate is fixed to 0.13. Island isolation corresponds to $1/c$ and extinction rate is fixed to 0.13. a-b) Relationship between species richness S at equilibrium and habitat area or isolation in local assemblages. c-d) Relationship between average body-size at equilibrium and island area (c) or isolation (d) in local assemblages. e-f) Relationship between standard deviation of body-size at equilibrium and island area (e) or isolation (f) in local assemblages.

3.8.1 Empirical data and statistical tests

We investigate the influence of area and isolation of tropical reefs on the mean and s.d. of fish body-size distribution in local assemblages. We then downscale our analysis at the species-level and study the relative contribution of reef characteristics (area and isolation), body-size and trophic position on species occurrences across tropical reefs. We use a published database of 991 piscivorous and herbivorous tropical reef-associated fishes and their presence/absence in 134 locations worldwide (Kulbicki et al., 2013; Parravicini et al., 2013). These locations correspond to tropical reefs in areas with a minimum monthly sea surface temperature of 17° C. Twenty-two sites are located in the Atlantic Ocean, 40 in the Indian Ocean, 63 in the Pacific Ocean, and 9 in the Tropical Eastern Pacific. The database is composed of information from published studies, regional checklists, monographs and reports. We use total reef area (km^2) to estimate reef area of each location (range: 6.3×10^{-3} km^2 to 19,166 km^2, mean: 917 km^2, (Andréfouët et al., 2006). We use the relative distance of each location to other patches of reef habitat to quantify reef isolation (km) using a nearest neighbour approach: for each location, the mean distance from the location to the ten nearest reef patches is calculated (range: 209 km to 1,708 km, mean: 527 km, (Parravicini et al., 2013). The database contains average body-size and occurrence of 652 piscivorous fishes and 339 herbivorous fishes (feeding on undefined organic material, turf or filamentous algae). Body-size ranges between 3 and 400 cm for piscivorous fishes and between 2.4 and 120 cm for herbivorous fishes. In order to distinguish the predictions of the ATIB and the ATTIB, we choose to study species with marked different diets only (i.e. piscivorous vs herbivorous species). The ATTIB considers omnivores in a similar way to herbivores, because they are little constrained by prey distribution; we however removed them from the analysis to maximize the contrast between types of diet.

We test three predictions at the assemblage-level derived from the models of island biogeography: (i) species richness is influenced by reef area and isolation (derived from the TIB, ATIB and ATTIB), (ii) mean fish body-size decreases with area and increases with

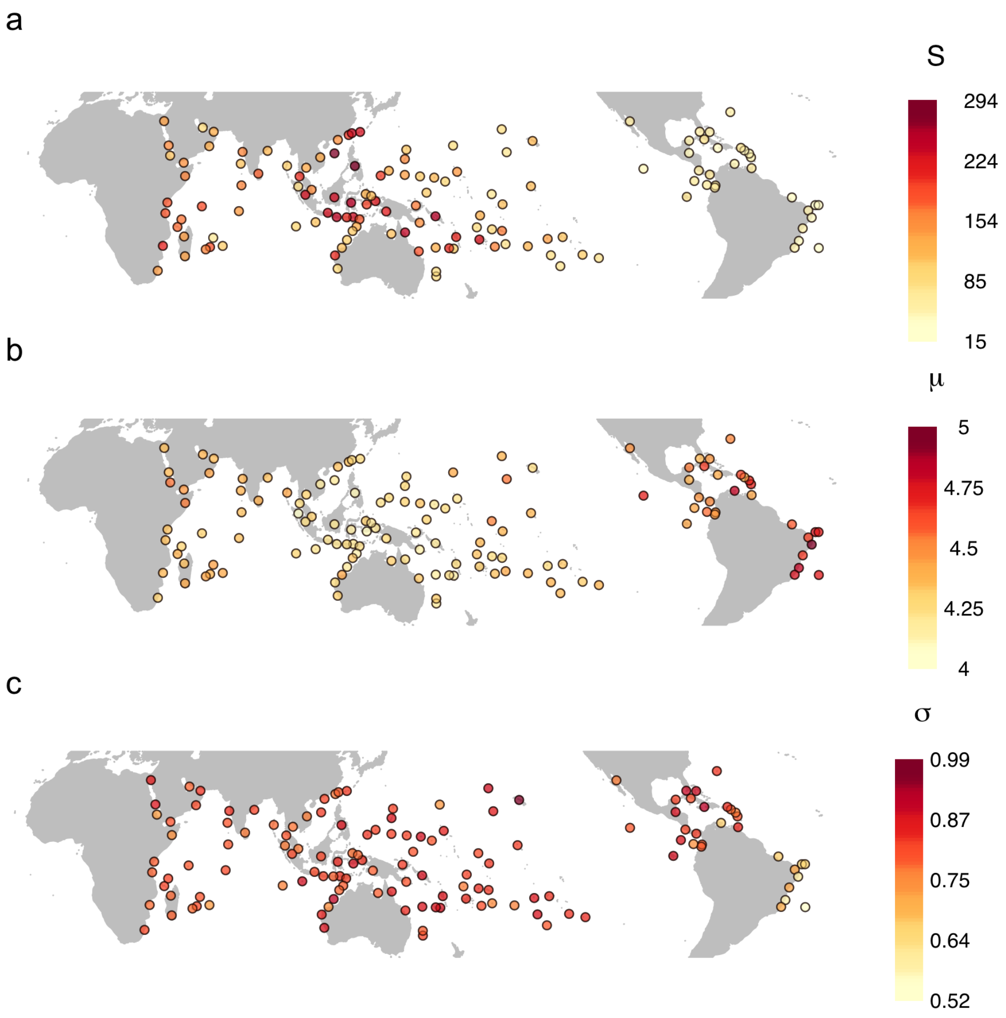

Figure 26: Global variation of body-size distribution in piscivorous fish assemblages observed across 134 locations on tropical reefs.. Circle color is proportional to the three metrics describing piscivorous fish assemblages at each location: species richness (a), mean body-size (b) and standard deviation (c) of species body-size.

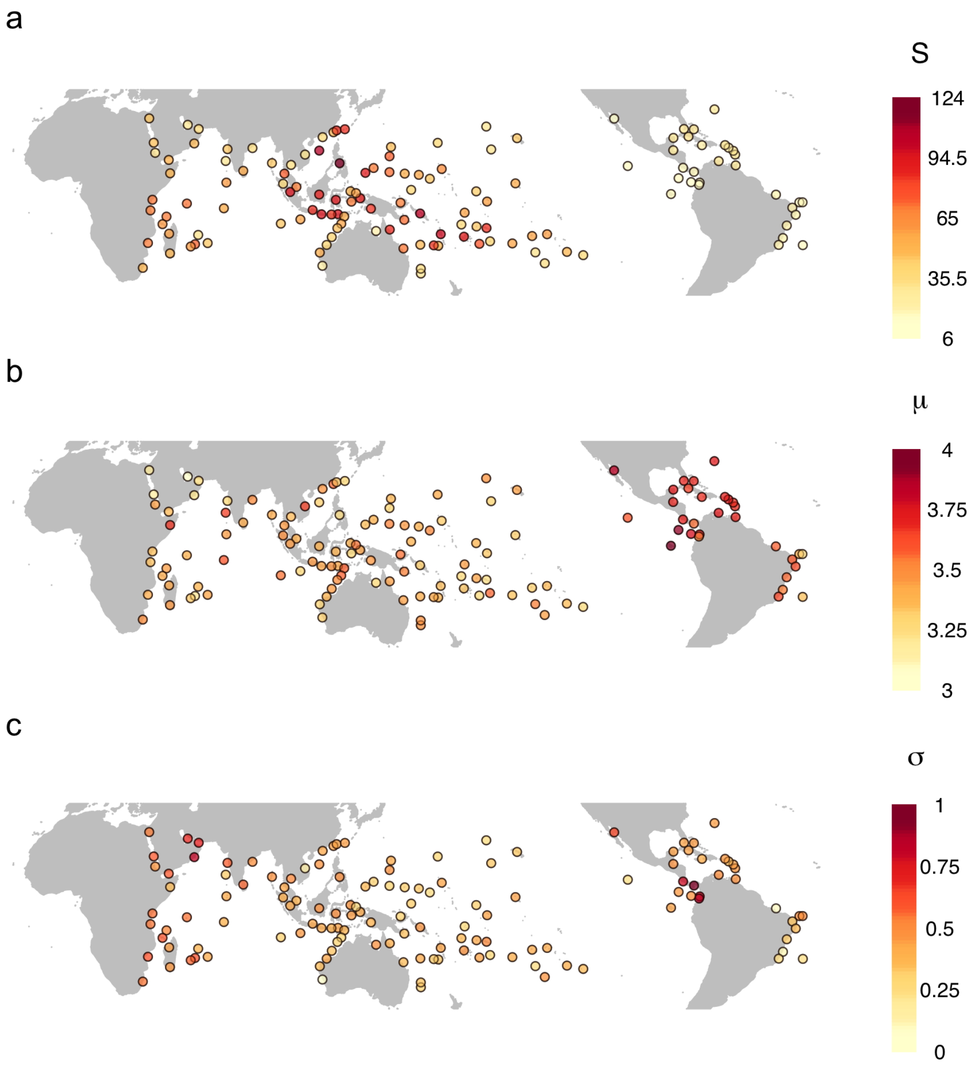

Figure 27: Global variation of body-size distribution in herbivorous fish assemblages observed across 134 locations on tropical reefs. Circle color is proportional to the three metrics describing herbivorous fish assemblages at each location: species richness (a), mean body-size (b) and standard deviation (c) of species body-size.

isolation (derived from the ATIB and ATTIB), (iii) variation (s.d.) of body-size of piscivorous fishes increases with area and decreases with isolation (derived from the ATTIB). We use ordinary least-squares regressions on log-transformed data to characterize the relationships between species richness and (i) area and (ii) isolation. We build second-order regression models and use a stepwise algorithm based on Akaike's Information Criterion to determine which regressions fit the data best (i.e. linear or quadratic relationships). We use the same method to characterize the relationships between the mean and the s.d. of fish body-size and (i) area or (ii) isolation. We also build multiple polynomial regression models to evaluate the relative contribution of reef area, reef isolation, their quadratic form and their interaction on the body-size distribution of reef fish assemblages.

At the species-level, we focus on the following predictions: (i) species occurrence (i.e. occupancy) is influenced by reef area and isolation (derived from the TIB, ATIB and ATTIB), (ii) occupancy is influenced by species body-size (derived from the ATIB and ATTIB) and (iii) occupancy is influenced by species trophic position (TTIB, ATTIB). We build corresponding logistic regression models to test these predictions. We compare their capacity to predict species occupancy based on (i) island characteristics, (ii) body-size and (iii) trophic position (predatory or basal species) using Akaike's Information Criterion corrected for small sample size (AICc ; Burnham and Anderson (2003). Models with the lowest AICc value were considered to provide the best fit.

3.8.2 Global variations across reef fish assemblages

Tropical reef locations contain on average 121 piscivorous and 48 herbivorous species. Local species richness varies between 15 and 294 species for piscivorous fishes (Figure 26 a), and between 6 and 124 species for herbivorous ones (Figure 27a). Species richness of both piscivorous and herbivorous fishes increases with reef area and decreases with reef isolation (Figure 28a-b), consistently with the predictions of the TIB, ATIB and ATTIB (Figure 25a-b). We then analyze the relationships between reef characteristics and mean body-size within fish assemblages. On small and isolated reefs, the mean body- size of piscivorous and herbivorous fishes is significantly higher than on large and connected reefs (Figure 28c-d). Reef area and isolation are negatively correlated (Spearman's rank correlation: $r = -0.42, P = 3.8 \times 10^{-7}$, Figure 33), their interaction contributes to explain the variation of mean body-size across assemblages for herbivorous fishes only (Table 5). Further, we find that the proportion of piscivorous fishes smaller than 30 cm decreases on small and isolated reefs, while the proportion of piscivorous fishes larger than 80 cm increases (Figure 29a, c). These observed relationships for piscivorous and herbivorous fishes are consistent with the ATIB and the ATTIB.

Table 5: Analyses of variance for second-order polynomial regression models accounting for log_{10}(reef area), log_{10}(reef isolation) and their interaction. Response variables are species richness, mean and standard deviation (s.d.) of log_{10}(body-size) for piscivorous and herbivorous fishes. F-values in bold illustrate a significant effect of the explanatory variable ($P - value < 0.01$).

	F-value ($P_{v}alue$)					
Variable	Area	Isolation	Area^2	Isolation^2	A × I	R^2
S pisc.	**110.87** (10^{-16})	**172.19** (10^{-16})	0.06 (0.8)	**16.45** (10^{-5})	0.1 (0.75)	0.81
S herb.	**75.68** (10^{-14})	**36.71** (10^{-8})	0.3 (0.58)	2.78 (0.1)	1.78 (0.19)	0.57
Mean BS pisc.	**38.44** (10^{-9})	**91.9** ($< 10^{-16}$)	1.56 (0.2)	**4.77** (0.03)	0.37 (0.54)	0.52
Mean BS herb.	**6.73** (0.01)	**25.51** (10^{-7})	1.35 (0.25)	0.06 (0.8)	**12.1** (10^{-3})	0.72
s.d. BS pisc.	**17.06** (10^{-5})	**14.38** (10^{-4})	0.06 (0.8)	**15** (10^{-4})	2.6 (0.1)	0.56
s.d. BS herb.	0 (0.99)	6.35 (0.02)	0 (0.99)	0.2 (0.65)	1.57 (0.21)	0.11

We observe a positive relationship between reef area and the s.d. of body-size among piscivorous fishes but not for herbivorous ones (Figure 28e, Table 5). As reef isolation increases, the s.d. of body-size decreases for piscivorous fishes (Figure 28f). We also observe a relationship between reef area or isolation and extreme sizes of piscivorous fishes. The maximum fish size increases with reef area while the minimum size decreases (Figure 29b). Conversely, the range between the minimum and the maximum fish size decreases with reef

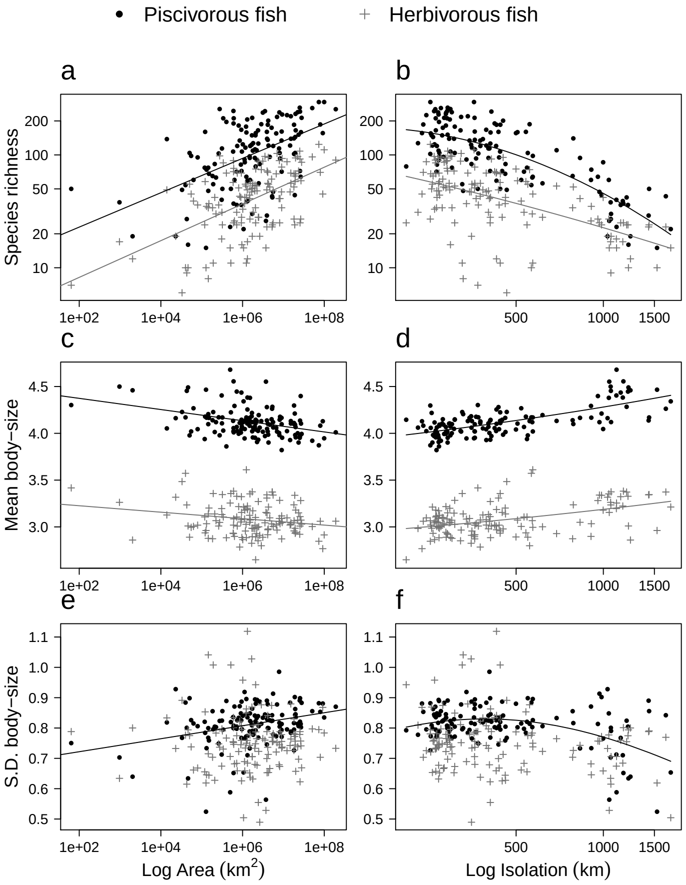

Figure 28: a) Relationship between species richness of piscivores (black circles) and herbivores (grey crosses), and reef area observed in 134 tropical reef locations (in km^2), least-square ordinary regression statistics for piscivorous species ($R^2 = 0.26$, p-value = 10^{-10}) and for herbivorous species ($R^2 = 0.31$, p-value = 10^{-12}). b) Relationship between species richness and reef isolation (relative proximity to the 10 nearest reefs; piscivorous species: $R^2 = 0.61$, p-value $\leq 10^{-16}$, herbivorous species: $R^2 = 0.31$, p-value = 10^{-12}). c) Relationship between reef area and mean μ of species body-size (piscivorous species: p-value = 10^{-6}, $R^2 = 0.14$, herbivorous species: $R^2 = 0.04$, p-value = 0.02). d) Relationship between reef isolation and mean μ of species body-size (piscivorous species: p-value $\leq 10^{-16}, R^2 = 0.47$, herbivorous species: p-value = 10^{-7}, $R^2 = 0.19$). e) Relationship between reef area and standard deviation σ of species body-size (piscivorous species: $R^2 = 0.1$, p-value = 10^{-4}, herbivorous species: $R^2 = 0$, p-value = 0.89). f) Relationship between reef isolation and standard deviation σ species body-size (piscivorous species: $R^2 = 0.20$, p-value $\leq 10^{-7}$, herbivorous species: $R^2 = 0.03$, p-value = 0.06).

isolation (Figure 29d). The s.d. of herbivorous fish body-sizes is not influenced by reef area or isolation, which supports the predictions of the ATTIB (Table 5).

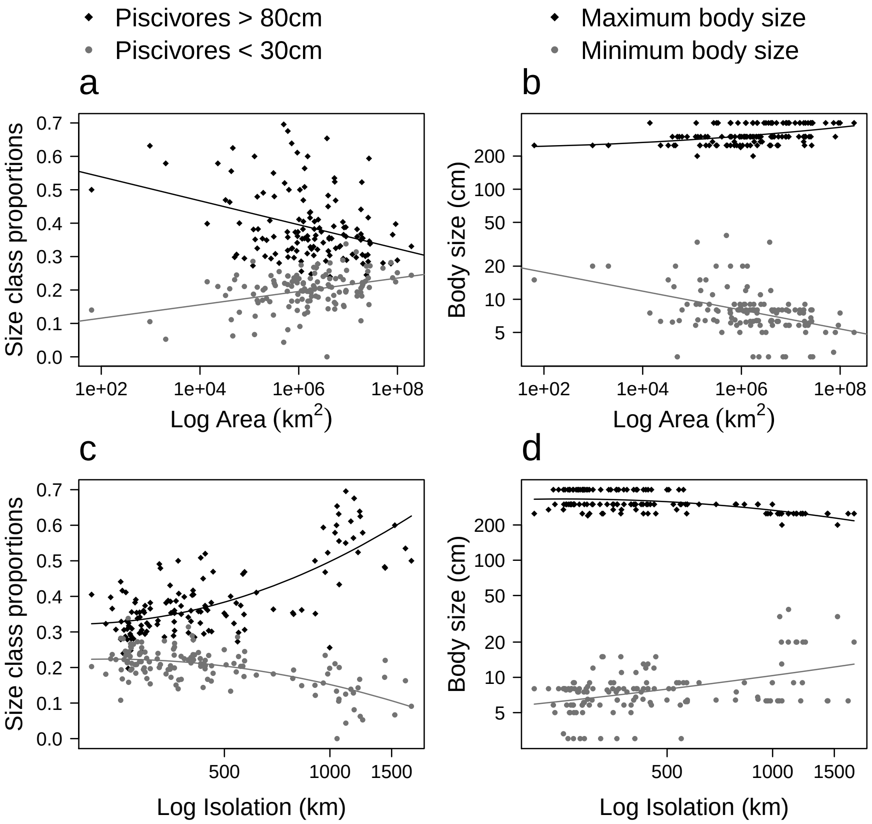

Figure 29: a) Relationship between reef area and body-size classes observed in piscivorous fish assemblages: proportion of piscivorous fishes <30 cm (R^2 = 0.12, p-value = 10^{-5}) and proportion of piscivorous fishes > 80 cm (R^2 = 0.11, p-value = 10^{-5}). b) Relationship between reef area and extreme body-sizes observed in piscivorous fish assemblages: minimal body-size (R^2 = 0.18, p-value = 10^{-7}) and maximal body-size (R^2 = 0.15, p-value = 10^{-6}). c) Relationship between reef isolation and body-size classes observed in piscivorous fish assemblages: proportion of piscivorous fishes < 30 cm (R^2 = 0.35, p-value = 10^{-14}) and proportion of piscivorous fishes > 80 cm (R^2 = 0.51, p-value < 10^{-16}). d) Relationship between reef isolation and extreme body-sizes observed in piscivorous fish assemblages: minimal body-size (R^2 = 0.18, p-value < 10^{-7}) and maximal body-size (R^2 = 0.3, p-value = 10^{-11}). Reef area, reef isolation and body-size are on a logarithmic scale. The interaction of reef area and isolation has not significant effect on these relationships.

At the species level, we find that knowledge of reef area and isolation improves the predictions of species occurrences, as the logistic regression model integrating these explanatory variables has a significantly lower corrected Akaike's Information Criterion (AICc) than the null expectation (Table 6). Additionally, we find that logistic regression models integrating species body-size and trophic position (piscivore or herbivore) have significantly lower AICc than the models based on reef area and isolation only (Table 6). We conclude that body-size and trophic position are key to predict fish species occupancy on tropical reefs, according to the ATTIB.

Table 6: Corrected Akaike's Information Criterion (AIC_c) for the different logistic regression models based on the occurrence of 991 species over 134 locations. The variable X indicates species occurrence, with $X_i = 0$ when species i is absent from the reef and $X_i = 1$ when it is present. The random sampling model supposes that species are distributed randomly in each location. The explanatory variables of the TIB are island A, isolation I and their interaction. The TTIB adds trophic position G (piscivorous or herbivorous species) and its interactions with A and I as explanatory variables, while the ATIB adds body-size M and its interactions. Finally, the explanatory variables of the ATTIB are island area, isolation, body-size, trophic position and all their interactions. The model with the lowest AIC_c value (in bold) is considered to fit the data best.

Model	GLM formula	AIC_c
Random sampling	glm(X ~ 1)	121 542
TIB	glm(X ~ $A \times I$)	116 747
TTIB	glm(X ~ $A \times I$)	116 238
ATIB	glm(X ~ $(A \times I \times M)^2$)	114 887
ATTIB	**glm(X** ~ $(A \times I \times M \times G)^3$	114 473

3.9 DISCUSSION

3.9.1 A step forward in the biogeography of species body-size

Based on the theory of island biogeography, we develop a theoretical framework that links species occupancy to body-size. We analyze how species body-size distribution depends on a range of ecological processes linking species-specific occupancy to body-size. We then study the predictions made by two models of island biogeography: (i) the ATIB, where colonization and extinction rates scale with body-size and (ii) the ATTIB, which further assumes that diet generality and trophic position scale with body size. Contrary to the null expectation of the traditional model of island biogeography (TIB), our models provide a process-based explanation to the observed body-size distribution at a locality that can differ from a random sample of the regional species pool.

The allometric scaling theory proposed by (Marquet and Taper, 1998) predicts a positive power-law relationship between maximum species body-size and land area. This relationship has been reported for mammals, birds and reptiles (Marquet and Taper, 1998; Burness et al., 2001; Okie and Brown, 2009; Millien and Gonzalez, 2011). According to these authors, extreme-sized species have higher extinction rates than intermediate-sized species in smaller islands since their populations are approaching minimal viable population sizes. They hypothesize that intermediate-sized species are more generalist than small-sized species and have higher densities than large-sized species, thus preventing their stochastic extinctions in the smallest areas (Okie and Brown, 2009). Our observations show that the allometric theory also holds for tropical-reef fishes, although extreme body-sizes only provide a partial picture of the influence of reef area on species body-size distribution. As illustrated in Fig. 29b, we find a positive relationship between maximum body-size and reef area that supports the allometric scaling theory. The relationship is however negative for the proportion of large-bodied piscivorous fishes (Fig. 29a), since mean body-size decreases with area (Fig 29c).

A positive relationship between species body-size and diet generality enhances the persistence of large-sized species on small and isolated islands. However, a regional food web in which small or medium-sized species are the most trophically general can generate very different spatial distributions of body-size. The slope of the predator-prey size relationship influences the scaling of diet generality with body size, and thus further shapes the body-size occupancy relationship (Gravel et al., 2011, 2013). However, the predator-prey body-size ratio varies across ecosystems. For example, (Barnes et al., 2010) studied 21 marine food webs worldwide and found that the slope of the predator-prey size relationship ranged between 0.44 and 3.08. Further, using the same dataset, (Gibert and DeLong, 2014) found that the slope decreases with temperature. Interestingly, we find that the body-size occupancy relationship does not promote the persistence of large predators for steeper predator-prey body-size relationships since medium-sized species are the most general in this case (Fig. 34). Our analysis therefore reveals that the trophic structure of the regional species pool could also influence the effect of insularity on the local body-size distribution.

3.9.2 Implications for tropical reef fishes

The ATTIB provides a mechanistic explanation to the variability of body-size distributions across reef-associated fish assemblages reported by previous studies (Stier et al., 2014; Kulbicki et al., 2015). We find that small and isolated reefs support a higher mean fish body-size than large and connected ones. In tropical reef ecosystems, a relatively flat slope ($\alpha_1 = 0.44 - 0.47$) for the allometric relationship between predator and prey body-size has been reported (Barnes et al., 2010), in agreement with observations across some of our reefs (Fig. 32). The consequent scaling of diet generality with body-size is a possible driver of occupancy of reef-associated piscivorous fishes, explaining why fewer species of extreme sizes are observed in species-poor tropical reef assemblages. The ATTIB is also supported by the maximum likelihood analysis for logistic regression models, showing that knowledge of fish body-size and trophic position improves the predictions of species occupancy.

The influence of diet generality on the ability of fishes to colonize isolated islands could be due to alternative processes related to body-size, a trait that is well-known to correlate with many aspects of life history and demography (Brown et al., 2004; Woodward et al., 2005; Brose et al., 2016). For instance, small-bodied species are more dependent on reef habitat complexity (Graham et al., 2011) compared to large-bodied species, which are more generalist and can thus colonize small and isolated islands. In addition, large-bodied species would be at advantage when confronted to major environmental changes (bleaching events or climate stress) as they can reach more favorable environments (including resource availability) owing to a wider home range and higher dispersal ability. A negative correlation between reef isolation and fishing pressure (Maire et al., 2016) could also explain why the mean body-size of fish assemblages increases with reef isolation. Under this assumption, we would however expect an increase of maximum fish body-size with isolation, while our observations show the opposite relationship (Fig. 28f, 29d). Finally, our results suggest that fish assemblages on small reefs, which are composed of larger species, are highly vulnerable to fisheries since large sized individuals are primarily targeted. These reefs deserve conservation priority with the creation of well enforced (no-take) marine protected areas to avoid the irreversible depletion of fish taxonomic and functional biodiversity.

3.9.3 Generality of the framework

The Allometric and Trophic Theory of Island Biogeography assumes that: (i) the frequency distribution of species body-size is log-normal, (ii) generalists are more likely to find prey species than specialists and (iii) all islands share the same source of species (island-mainland approach to metacommunity dynamics). We assume a log-normal distribution in our simulations, which corresponds to the regional body-size distribution observed in our dataset (section 1 of Supporting Information). Several studies report a log-lognormal distribution for species body-size, meaning that the distribution remains skewed after a logarithmic transformation (Etienne and Olff, 2004; Smith and Lyons, 2013). Supplementary simulations using a log-lognormal body-size distribution for the regional species pool nonetheless show similar results than the ones reported in the main analysis (Figure 35).

The ATTIB further assumes that species with large diets are more likely to find resources than specialists. If specialists preferentially feed upon widely distributed species while generalists preferentially feed upon narrowly distributed species, this assumption could be violated (Srinivasan et al., 2007). The stochastic version of the ATTIB capture this phenomenon, since a specialist feeding on prey with high occupancy will be more likely to persist than a predator feeding on rare prey species. As a consequence, the theory also predicts that consumers at the top of the food web have a lower occupancy than basal species as they rely on the presence of species at each intermediate trophic levels.

Finally, the Theory of Island Biogeography is a particular case of the metacommunity theory (Leibold et al., 2004), as it assumes a unidirectional flow of migration, from the mainland to the islands. Consequently, all islands share the same species pool, represented by the same body-size distribution. In more complex and realistic spatial structures, migration flows between islands are bidirectional. Determining the effect of migration from various patches on a local body-size distribution would require further development of the ATTIB. In a metacommunity system, we expect that the body-size distribution of the source pool is itself dynamic and responds to island characteristics. If an island is connected to large islands occupied by many species, the body-size distribution of its migration source will be very different in comparison to an island connected to small and species poor islands.

The intraspecific variations in body-size are not captured by our theory, thus ignoring ontogeny and evolutionary dynamics (such as the ones expected by the island rule - Foster (1964); Faurby and Svenning (2016)). Body-size, trophic position, colonization and extinction rates are species-specific and are supposed to be similar among the individuals of a given species. We consider here the mean adult body-size, but the scaling of colonization rates with body-size covers all the dispersal strategies of a species, from larval production and dispersal to adult mobility. Body-size has a positive effect on dispersal abilities through all the ontogenetic stages of tropical reef fishes. However, for a given taxonomic group, we may observed opposite effects of body-size on colonization rate through ontogenetic growth.

In this study, we applied the ATIB and the ATTIB to tropical reef fishes and the scaling of colonization and extinction rates were defined from knowledge on this particular taxonomic group. The scaling of body-size with extinction and colonization rates is, however, not universal and is expected to differ between (i) taxonomic groups (ii) habitat types (iii) the matrix surrounding habitat patches and (iv) the geographic structure of patches. These factors must be considered when applying this framework to other insular systems such as forest fragments, mountain tops, lakes or ponds. We assumed a positive relationship between colonization rate and body-size because all the life-history traits increasing colonization are positively correlated to fish body-size, such as fecundity, home range, mobility or diet generality (Luiz et al., 2013; Kulbicki et al., 2015; Nash et al., 2015). Inferring this scaling is less straightforward in taxonomic groups where these traits scale differently with body-size. For example, fecundity decreases with body-size for birds and mammals while mobility increases (Marquet et al., 2005). On the other hand, the variation of population density between taxonomic groups could influence the minimum area required to sustain a viable population. The density of tropical reef fishes weighing 100 kg is around 100 ind./km^2 and the density of fishes weighing 0.1 kg is approximately 10,000 ind./km^2 (Barneche et al., 2016; Kulbicki et al., 2015). In our dataset, the ten smallest reefs have a surface area of 3 km^2 on average, which could therefore support a population of 30,000 small fishes and 300 large fishes. These densities are far higher than for terrestrial herbivorous mammals or birds for instance (Damuth, 1981; Marquet et al., 1990; Juanes, 1986). These marked differences outline that the smallest area required to support a viable population should greatly differ between taxonomic groups and environmental conditions.

3.10 CONCLUSION

The amount of small and isolated habitat patches is expected to increase with ongoing habitat destruction and fragmentation, and a greater number of ecosystems are likely to suffer modifications in their structure and functioning (Haddad et al., 2015; Newbold et al., 2015). Here we develop a theoretical framework, explaining the scaling of body-size with island area and isolation, which is flexible and can easily be applied to other functional traits. Several studies revealed a scaling of functional diversity with area (Mazel et al., 2014; Whittaker et al., 2014), thus providing expectations of functional and phylogenetic diversity loss following habitat destruction (Keil et al., 2015).

These studies are essentially descriptive and none of them provided process-based hypotheses to explain these observations. There are many alternative hypotheses, usually in line with a mechanistic explanation of the species-area relationship (e.g. heterogeneity area relationship, (Kadmon and Allouche, 2007), but none of them have been rigorously tested. Our framework can facilitate such discriminant tests of hypotheses derived from the theory of island biogeography. Interestingly, our theory not only predicts the scaling of functional diversity with area and isolation, but it also proposes that some mean trait values can also consistently scale with these biogeographical constraints. It is also clear that the multivariate functional composition of food webs is related to network structure (Gravel et al., 2016), thus challenging an extension of this framework to multiple traits at a time.

3.11 ACKNOWLEDGEMENTS

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3.12 SUPPORTING INFORMATION

3.12.1 Model parameters considered in the stochastic simulations

In this section, we report all the parameters used the biogeographical models (Table 7). We further explain the different assumptions we make regarding the scaling of colonization and extinction rates with body-size and provide more details on the parameterization of the regional food web structure used in the ATTIB.

Table 7: Model parameters considered in the TIB, the ATIB and in the stochastic simulations of the ATTIB.

Parameter	Symbol	Values	Description
Regional species pool	R	200	Species richness
	μ	3.45	Average body-size (log)
	σ	1	Standard deviation of body-size (log)
Biogeography	c	[0.01 : 0.99]	Colonization rate (island isolation)
	e	[0.01 : 0.99]	Extinction rate (island area)
Allometric relationships	x_c	5×10^{-3}	Coefficient of equation (3.4)
H_1	x_e	10^{-2}	Coefficient of equation (3.5)
H_2	M_{max}	400	Coefficient of equation (3.6)
Trophic interactions	α_1	0.47	Slope of the regression line
	α_0	0.2	Intercept of the regression
	$\beta_{1,low}$	$\alpha_1 - 0.28$	Slope of the 10% quantile regression
	$\beta_{0,low}$	0.24	Intercept of the 10% quantile regression
	$\beta_{1,high}$	$\alpha_1 + 0.34$	Slope of the 90% quantile regression
	$\beta_{0,high}$	0	Intercept of the 90% quantile regression

3.12.2 Regional species pool

We compare the ability of different distributions (normal, lognormal, log-lognormal, gamma) to fit the body-size distribution of the 991 tropical reef fishes composing our dataset by maximum likelihood (Bayesian and Akaike's Information Criteria). The lognormal distribution with a mean $\mu = 3.45$ and a standard deviation $\sigma = 1$ has the best fit to the data. Consequently, we generate a regional species pool composed of 200 species with body-sizes randomly drawn from this distribution. We also perform supplementary simulations using a right skewed lognormal distribution for the regional species pool, illustrated in Fig. 35.

3.12.3 Allometric relationships (ATIB & ATTIB)

In the ATIB and the ATTIB, the species-specific colonization rate c_i scales positively with body size M_i of species i:

$$c_i = c(1 + log_{10}(c) \times e^{-x_c M_i}) \tag{3.4}$$

where c corresponds to the basal colonization rate of the TIB, related to island isolation. The equation translates the following assumptions: (*i*) colonization rate increases with body-size until an asymptote is reached (inverted exponential curve), (*ii*) the effect of body-size on dispersal rate is high when island isolation is high (i.e. $c \approx 0.1$) and small in islands close to the mainland ($c \approx 1$). We arbitrary set x_c to 5×10^{-3}, leading to the relationship illustrated in Fig. 30 (dashed red lines).

We make three different assumptions regarding the scaling of extinction rate with body-size, leading to three versions of the ATIB and the ATTIB.

- H_0: extinction rate is independent of body-size: $e_i = e$, where e corresponds to the basal extinction rate of the TIB, related to island area.

-H_1: extinction rate increases with body size until an asymptote is reached:

$$e_i = e(1 - 0.2 \times e^{-x_e M_i}) \tag{3.5}$$

such that the effect of body-size on extinction rate is high when island area is small (i.e. $e \approx 1$) and small in large islands ($e \approx 0.1$). We set x_e to 5×10^{-3}, leading to the relationship illustrated in Fig. 30 (wide dashed lines, in black).

- H_2: intermediate body-sized species are less prone to extinction than small and large species (U-shape, small dotted line in Fig. 30):

$$e_i = e(1 - M_i \times \frac{(M_{max} - M_i)}{M_{max}^2}) \tag{3.6}$$

where M_{max} corresponds to maximum body-size in the regional species pool. Again, this equation expresses the assumption that the influence of body-size on extinction rate is high when island area is small (i.e. $e \approx 1$) and small on large islands ($e \approx 0.1$).

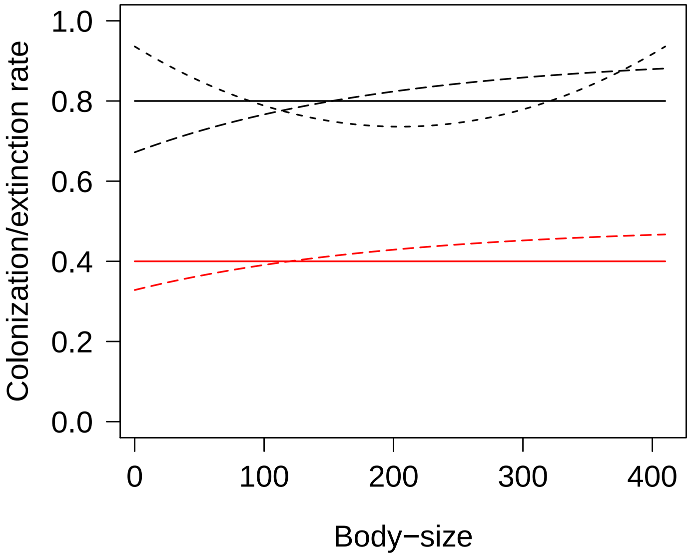

Figure 30: Relationship between body size and extinction rate (in black) or colonization rate (in red). In the TIB, both rates are independent of body-size (full lines). In the $ATIB_{H0}$ and $ATTIB_{H0}$, colonization rate increases with body-size (red dotted line), but not extinction rate. In the $ATIB_{H1}$ and $ATTIB_{H1}$, both colonization and extinction rates increase with body-size (wide dotted lines). Finally, in the $ATIB_{H2}$ and $ATTIB_{H2}$, the relationship between extinction rate and body-size is U-shaped (small dotted line, in black).

3.12.4 Trophic interactions (ATTIB)

We use the method presented in Gravel *et al.* (2013) to parameterize the regional food web based on the niche model of food web structure (Williams *et al.* 2011). The model summarizes the position of a species in a food web with a set of three parameters for each species: the niche position n, the feeding optimum o and the feeding range r (diet breadth). An interaction occurs between two species if the niche position (n_i) of prey species i lies in between the lower ($o_j - r_j$) and upper ($o_j + r_j$) limits of the feeding niche of the predator species j. The parameterization of the model considers that body-size is the main niche axis structuring feeding interactions. Then, the niche position n_i corresponds to the log of body-size of species i. The feeding niche optimum is estimated from the linear regression between predator and prey log body-size: $o = log_{10}(M_{prey}) = \alpha_0 + \alpha_1 \times log_{10}(M_{pred})$ where M_{prey} and M_{pred} are the prey and predator body-size, respectively. Finally, the lower and upper boundaries of the feeding range are determined from the 10% and 90% quantile regressions between $log_{10}(M_{prey})$ and $log_{10}(M_{pred})$, Fig. 31. We implement the allometric niche model with a slope of predator-prey body-size relationship $\alpha_1 = 0.47$, derived from a tropical reef food web reported in Barnes *et al.* (2010), which is close to what we observed on others tropical reefs Fig. 32. The quantile regressions were derived from data on a mediterranean food web (Gravel *et al.* 2013).

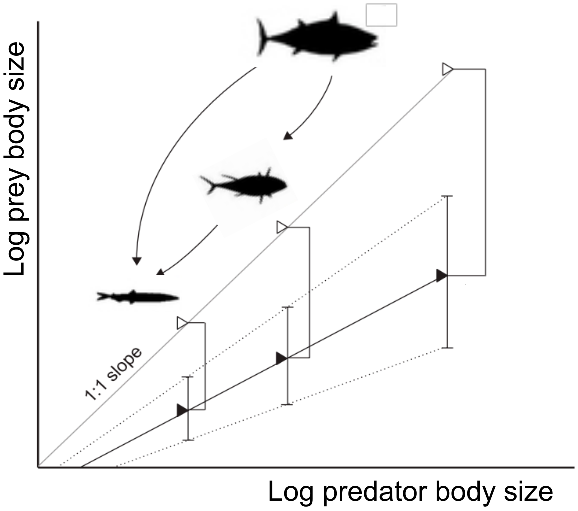

Figure 31: The allometric niche model with log of species body-size as niche axis is applied to infer the feeding relationships between the species of the regional pool (modified from Gravel *et al*. 2013). The white triangles correspond to species niche position (i.e. their body-size). For a given species, the feeding niche optimum (black triangles) is given by the linear relationship between predator and prey size (black line).The boundaries of the feeding range are given by the 10% and 90% quantile regression lines (dotted lines). A predator feeds on all prey species which their niche lies between these boundaries. In this example, the largest species feeds on the two smaller species (the white triangles depicting preys' body-sizes lie between predator's range boundaries)

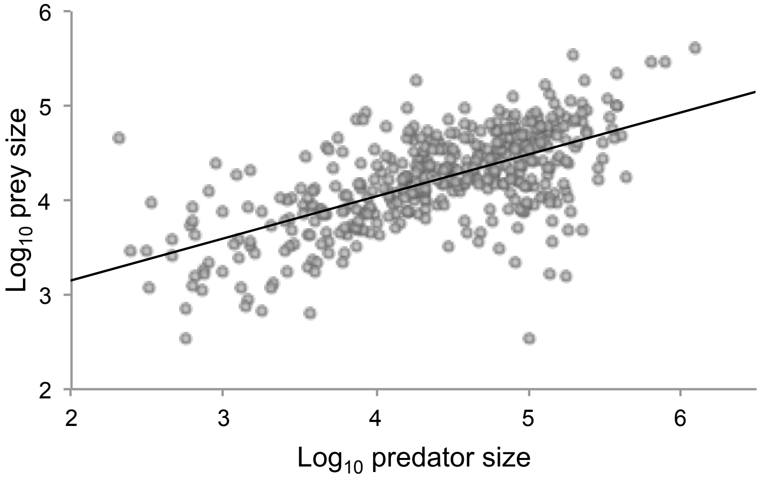

Figure 32: Allometric relationship between predator and prey size ($log_{10}(g)$) observed in 426 transects of $250m^2$, located in tropical reefs of the South Pacific ocean. Equation of the linear regression: $log_{10}(M_{prey}) = 2.49 + 0.44 \times log_{10}(M_{pred})$, $R^2 = 0.4$ (Vouriot 2011).

3.13 Correlation between reef area and reef isolation

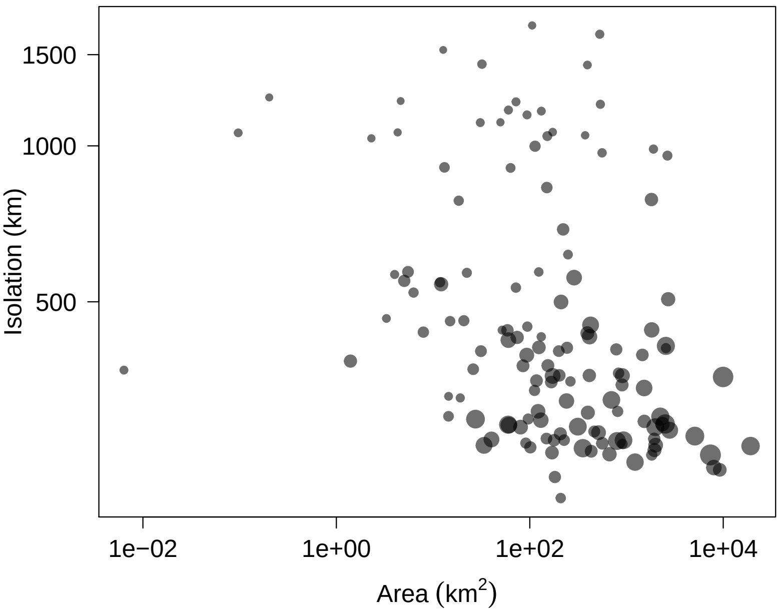

Figure 33: Relationship between reef area (*km^2*) and isolation (*km*) on a logarhitmic scale. Circle size is proportionnal to species richness. Spearman's rank correlation: $r = -0.42$, $P = 3.8 \times 10^{-7}$.

3.14 Mechanism leading to the emergent relationship between body-size and occupancy in the ATTIB

Together, the body-size frequency distribution in the regional species pool (Fig. 34a) and the predator-prey body-size relationship (Table 7) give rise to a relationship between body-size and diet breadth (Fig. 34b). The occurrence probability on an island increases asymptotically with diet breadth (Fig. 34c). This relationship holds only in constrained islands (isolated and of small area). On larger and more connected islands, the probability that a predator had at least one prey already present in the local food web was high and consequently trophic interactions do not limit predator colonization and persistence (Fig. 34c). Therefore, a relationship between species body-size and occupancy only emerged in isolated or small islands (Fig. 34d).

The slope and the range of the predator-prey body-size relationship influences the scaling of trophic rank with body-size as well as the generality, and thus should further impact the body-size occupancy relationship. We therefore compared two regional food webs, one with a slope $\alpha_1 = 0.9$ (in grey) and one with a slope $\alpha_1 = 0.47$ (in black). For the regional food web with a slope $\alpha_1 = 0.9$, predators having less than 75 potential prey corresponded mainly to large species (Fig. 34b), which explained the negative relationship between species body-size and occupancy observed in Fig. 34d (grey line). In the regional food web with a slope $\alpha_1 = 0.47$, species diet breadth increased with body-size and species having less than 75 potential prey corresponded to small species (Fig. 34b). Consequently, occupancy increased with body-size in this case (Fig. 34d).

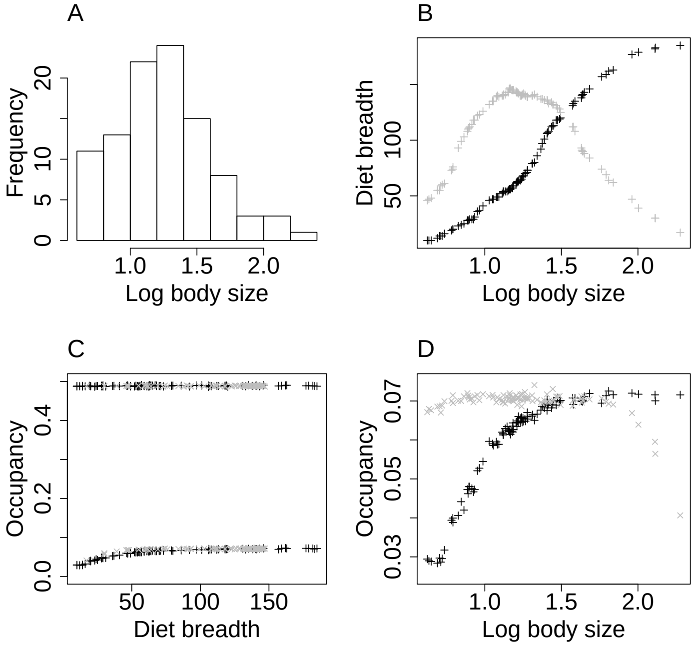

Figure 34: a) Frequency distribution of species body-size in the regional assemblage (log-normal distribution with μ = 3.45 and σ = 1). b) Relationship between log body-size and diet breadth for regional food webs with a slope of predator-prey body-size relationship α_1 = 0.47 (black line) or α_1 = 0.9 (grey line). c) Relationship between occupancy and diet breadth for 2 pairs of c and e, corresponding to low and high biogeographical constraints. d) Relationship between occupancy and log body-size in a species poor habitat patches (high geographical constraints).

3.15 Simulations using a right-skewed log-normal distribution

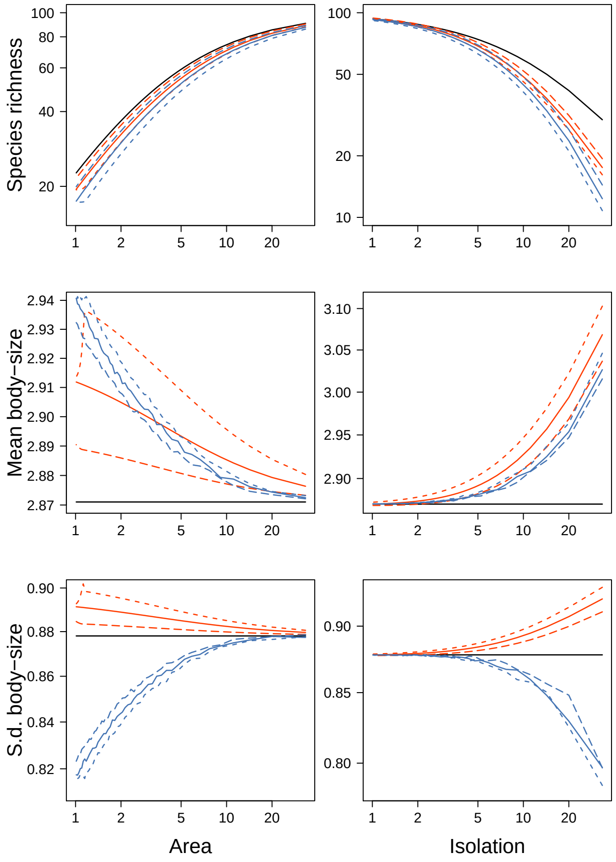

Figure 35: Influence of island area and isolation on species body-size distribution predicted by the TIB (in black) and different versions of the ATIB and the ATTIB. Red lines correspond to the ATIB and blue lines to the ATTIB. Full lines correspond to H_0, wide dotted lines to H_1 and small dotted lines to H_2. Island area corresponds to 1/e where e is species extinction rate and colonization rate is fixed to 0.29. Island isolation corresponds to 1/c and extinction rate is fixed to 0.03. a-b) Relationship between species richness S at equilibrium and habitat area or isolation in local assemblages. c-d) Relationship between average body-size at equilibrium and island area (c) or isolation (d) in local assemblages. e-f) Relationship between standard deviation of body-size at equilibrium and island area (e) or isolation (f) in local assemblages.

CONCLUSION GÉNÉRALE

L'objectif général de cette thèse était d'intégrer différents domaines de l'écologie afin de comprendre les effets combinés de mécanismes opérant à différentes échelles spatiales sur les propriétés des écosystèmes, tels que leur structure et leur stabilité. Dans cette conclusion générale, je synthétise dans un premier temps les contributions apportées par chacun de mes chapitres de thèse puis je discute des limites de l'approche et enfin je propose des perspectives concernant l'intégration des mécanismes écologiques et macroécologiques liés au fonctionnement des écosystèmes via les traits fonctionnels des espèces.

SYNTHÈSE DES RÉSULTATS

Quelles propriétés favorisent la stabilité des écosystèmes ?

Dans le cadre du débat concernant la stabilité des écosystèmes complexes initié il y a plus de quarante ans (McCann, 2000), j'ai étudié la relation entre la complexité des écosystèmes et leur stabilité à partir de réseaux trophiques issus de données empiriques, initialement échantillonnés pour construire des modèles de type Ecopath. La stabilité est définie ici comme la vitesse à laquelle un écosystème amortit une perturbation de la densité des espèces qui y coexistent. La complexité des écosystèmes, théoriquement déstabilisante, augmente à mesure que la richesse spécifique, le nombre ou la variance de la force des interactions entre proies et prédateurs augmentent. Je montre qu'il n'existe pas de relation significative entre complexité et stabilité dans les écosystèmes, corroborant les prédictions de R. May et de l'existence de *"devious strategies"* permettant à des écosystèmes réels complexes de demeurer stables comparativement à des modèles théoriques de complexité équivalente (May, 2001).

Dans une seconde partie, je propose d'expliquer pourquoi le critère de stabilité, établi par R. May et basé sur la théorie des matrices aléatoires, ne s'applique pas dans le cas présent. Un certain nombre d'études suggèrent qu'il existe des éléments stabilisants dans les écosystèmes réels qui ne sont pas présents dans les écosystèmes théoriques (Yodzis, 1981; De Ruiter et al., 1995; McCann and Hastings, 1998; Neutel et al., 2002; Neutel and Thorne, 2014), mais il manquait d'études empiriques à ce sujet. L'important jeu de données utilisé (116 réseaux trophiques empiriques) a permis de mettre en évidence des propriétés spécifiques aux écosystèmes. Premièrement, la topologie des réseaux trophiques est non aléatoire : les espèces les plus généralistes ont tendance à se situer à des niveaux trophiques élevés. D'autre part, pour chaque interaction trophique, il existe une corrélation entre l'effet négatif d'un prédateur sur sa proie et l'effet positif de la proie sur le prédateur. Or la corrélation entre les éléments de la matrice d'interaction est supposée nulle dans les matrices aléatoires. Enfin, les interactions de forte intensité, correspondant à un effet très négatif d'un prédateur sur une population de proies, sont rares et se situent aux bas niveaux trophiques. Pour déterminer l'influence de ces propriétés sur la relation complexité-stabilité, j'ai réalisé des tests de permutations qui modifient la structure des réseaux trophiques empiriques. La disparition de chacune des trois propriétés est très déstabilisante, mais l'absence de relation complexité-stabilité est principalement liée à la distribution non aléatoire des forces d'interactions.

Ces résultats mettent en évidence le rôle fondamental des interactions proies-prédateurs qui contraignent les flux d'énergie entre les espèces et permettent la persistance d'écosystèmes complexes. Cette étude résout le débat complexité-stabilité en démontrant pourquoi la complexité, définie par R. May à partir de la théorie des matrices aléatoires, ne permet pas de prédire la stabilité des écosystèmes réels. La distribution non aléatoire des forces d'interactions biaise en effet l'estimation de la complexité et de nouveaux outils devront être développés pour réussir à prédire la stabilité des écosystèmes réels.

Relier la stabilité des réseaux trophiques aux traits fonctionnels des espèces qui le composent

Dans mon second chapitre, j'ai tenté de relier les propriétés non aléatoires des écosystèmes à des caractéristiques mesurables à l'échelle de l'espèce. À partir de la masse corporelle des espèces, j'ai déterminé la topologie, les besoins énergétiques ainsi que les biomasses à l'équilibre des espèces d'un écosystème. Ces informations m'ont permis de construire des réseaux trophiques théoriques possédant une topologie et une distribution des forces d'interactions réalistes. J'ai ensuite étudié l'effet de la distribution de fréquence de la masse corporelle des espèces d'un assemblage sur la structure et la stabilité d'un écosystème. Afin d'aller plus loin dans la compréhension des mécanismes liés à l'absence de relation entre la complexité et la stabilité (chapitre 1), je me suis focalisée sur l'effet de la masse corporelle sur la connectance, la moyenne et la variance des forces d'interactions, qui sont intégrées au critère de stabilité de R. May et devraient théoriquement influencer la stabilité des écosystèmes. J'étudie à la fois la stabilité asymptotique, qui nous renseigne sur la réponse à long terme d'un système suite à une perturbation (aussi utilisée dans le chapitre 1), ainsi que la réactivité, qui mesure la dynamique transitoire du système avant qu'il ne retourne à l'équilibre. Je montre que les réseaux trophiques construits à partir de la masse corporelle des espèces sont très stables sur le long terme, quel que soit leur niveau de complexité. Ces résultats font échos à ce qui a été observé dans les réseaux trophiques empiriques du chapitre 1, suggérant que la masse corporelle et les relations allométriques utilisées dans ce modèle permettent l'émergence de propriétés non aléatoires stabilisantes. D'autre part, je trouve qu'une distribution de masse corporelle ayant une moyenne et une variance élevées génère des réseaux trophiques caractérisés par un nombre important d'interactions de faible intensité et une faible réactivité : une perturbation ne sera donc pas fortement amplifiée dans ces réseaux.

Effet de la taille et de l'isolement de l'habitat sur la structure en taille des espèces d'un écosystème

Afin de mieux comprendre l'effet de la taille et de l'isolement de l'habitat sur le fonctionnement des écosystèmes, une première étape consistait à intégrer l'écologie fonctionnelle et la théorie de la biogéographie des îles. Dans mon troisième chapitre de thèse, j'ai développé une approche qui prend en compte la variation interspécifique des probabilités de présence des espèces dans les fragments d'un type d'habitat. Un assemblage local correspond alors à un échantillon biaisé du pool régional d'espèces et non à un sous-ensemble aléatoire du pool régional comme le prédit la théorie classique de la biogéographie des îles (TBI). À partir de cette approche, j'ai comparé les prédictions de trois modèles biogéographiques concernant l'effet de la taille et de l'isolement d'un fragment d'habitat sur la moyenne et l'écart type de la masse corporelle des espèces qui le composent. Ces modèles présentent un niveau de complexité croissant dans l'intégration des processus influençant la probabilité de présence d'une espèce. Le premier modèle est la TBI, soit l'hypothèse nulle, où seules les caractéristiques géographiques de l'habitat (taille et isolement) influencent la dynamique spatiale des espèces. Le second modèle correspond à la théorie allométrique de la biogéographie des îles (TABI), où les taux de colonisation et d'extinction sont propres à chaque espèce et varient en fonction de la masse corporelle. Enfin, la théorie allométrique et trophique de la biogéographie des îles (TATBI) prend également en compte les interactions trophiques pour déterminer la probabilité de présence des espèces. Elle prédit que les prédateurs ayant un régime alimentaire très diversifié (espèces généralistes) ont des probabilités de présence plus importantes que les prédateurs se nourrissant d'un nombre restreint de proies. J'ai comparé ces prédictions aux distributions de la masse corporelle au sein des assemblages de poissons récifaux tropicaux. Comme prédit par les trois modèles biogéographiques, la richesse spécifique augmente avec la taille du récif et diminue avec son isolement. L'analyse de la variation de la masse corporelle des poissons dans les écosystèmes coralliens valide les prédictions de la théorie allométrique et trophique de la biogéographie des îles (TATBI) et rejette celles de la TBI. En effet les assemblages locaux de poissons ne correspondent pas à un sous-ensemble aléatoire du pool régional : les récifs petits et isolés possèdent une plus forte proportion d'espèces de grandes tailles comparativement aux récifs grands et très connectés. Les récifs petits et isolés possèdent également moins de piscivores de masses extrêmes, alors il n'y a pas de relation significative entre l'écart type de la masse corporelle des poissons herbivores et la taille ou l'isolement de l'habitat. La TATBI suppose que ces tendances sont liées à la plus grande capacité de dispersion des poissons de grande taille et à la difficulté des piscivores spécialistes à trouver une quantité de proies suffisante dans les récifs pauvres en espèces.

LIMITES ET PERSPECTIVES

Mesurer la stabilité des écosystèmes : décalage entre théorie et réalité

L'étude de la stabilité des écosystèmes a donné naissance à une grande diversité de mesures (voir Ives and Carpenter (2007); Donohue et al. (2013, 2016) pour une revue de littérature), traduisant la diversité des types de perturbations s'exerçant sur les écosystèmes. Les perturbations correspondent à des changements dans l'environnement biotique et abiotique qui altèrent la structure et la dynamique des écosystèmes. Elles peuvent être caractérisées par leur intensité, leur durée et leur fréquence (Donohue et al. 2016). Dans le premier chapitre, je me suis concentrée sur la stabilité asymptotique des écosystèmes, qui mesure la vitesse à laquelle un écosystème retourne à l'équilibre après une perturbation ponctuelle de la densité de ses espèces, pour étudier la relation entre la complexité et la stabilité des écosystèmes. Dans le second chapitre, j'étudie à la fois la stabilité asymptotique, qui nous renseigne sur la réponse à long terme d'un système suite à une perturbation, ainsi que la réactivité, qui mesure la dynamique transitoire du système avant qu'il ne retourne à l'équilibre. L'avantage de ces mesures réside dans le fait qu'elles sont basées sur de solides bases mathématiques et ont des applications interdisciplinaires. Cependant, la stabilité locale et la réactivité sont des mesures théoriques de la stabilité d'un système et sont difficilement mesurables dans le cas de systèmes aussi complexes que les réseaux écologiques. D'autre part, elles mesurent la réponse des écosystèmes à une petite perturbation de la densité des espèces, elles traduisent donc le niveau minimal de stabilité requis pour qu'un écosystème soit stable. Les écosystèmes réels subissent des perturbations de plus grande intensité et de durée plus longue, illustrée par exemple par l'épisode massif de blanchissement qui a touché 60% des coraux de l'archipel des Maldives cette année. Il serait par conséquent pertinent d'appliquer l'approche présentée dans le chapitre 2 à d'autres mesures de stabilité.

Des mesures de stabilité plus globale, pouvant être mesurées soit empiriquement soit à l'aide de modèles théoriques, ont été proposées. La robustesse d'un écosystème mesure par exemple l'impact de la disparition d'espèces sur le nombre d'extinctions secondaires potentielles et correspond à la proportion d'espèces qui doivent disparaitre avant d'observer l'extinction d'au moins 50% de l'ensemble des espèces de l'écosystème (Dunne et al., 2002; Allesina et al., 2009). La persistance des écosystèmes est une mesure proche de la robustesse : elle correspond au nombre d'espèces restantes après la disparition d'une espèce donnée (Stouffer, 2010; Stouffer and Bascompte, 2011; **?**; Gilarranz et al., 2016).

La stabilité des écosystèmes devrait cependant être étudiée sous une perspective plus appliquée et plus en phase avec l'ampleur des perturbations actuellement subies par les écosystèmes. Si l'on veut prédire l'effet des activités humaines sur le fonctionnement des écosystèmes à long terme, il est nécessaire d'étudier les mécanismes liés à leur stabilité, mais il est également fondamental de quantifier de façon précise l'intensité, la fréquence et l'étendue spatiale des perturbations générées par les activités humaines (Donohue et al., 2016). Dans les écosystèmes marins, la pêche industrielle, responsable de la surexploitation de plus de 30% des stocks de poissons mondiaux (FAO, 2012), est une problématique majeure qui affecte l'ensemble des océans (Pauly et al., 2002). La pression de pêche est plus importante sur les espèces de grande taille situées à des niveaux trophiques élevés (Myers and Worm, 2003; Worm et al., 2006; Pauly and Zeller, 2016), entrainant une pression de pêche hétérogène à travers les niveaux trophiques. Ces changements sont susceptibles de modifier la

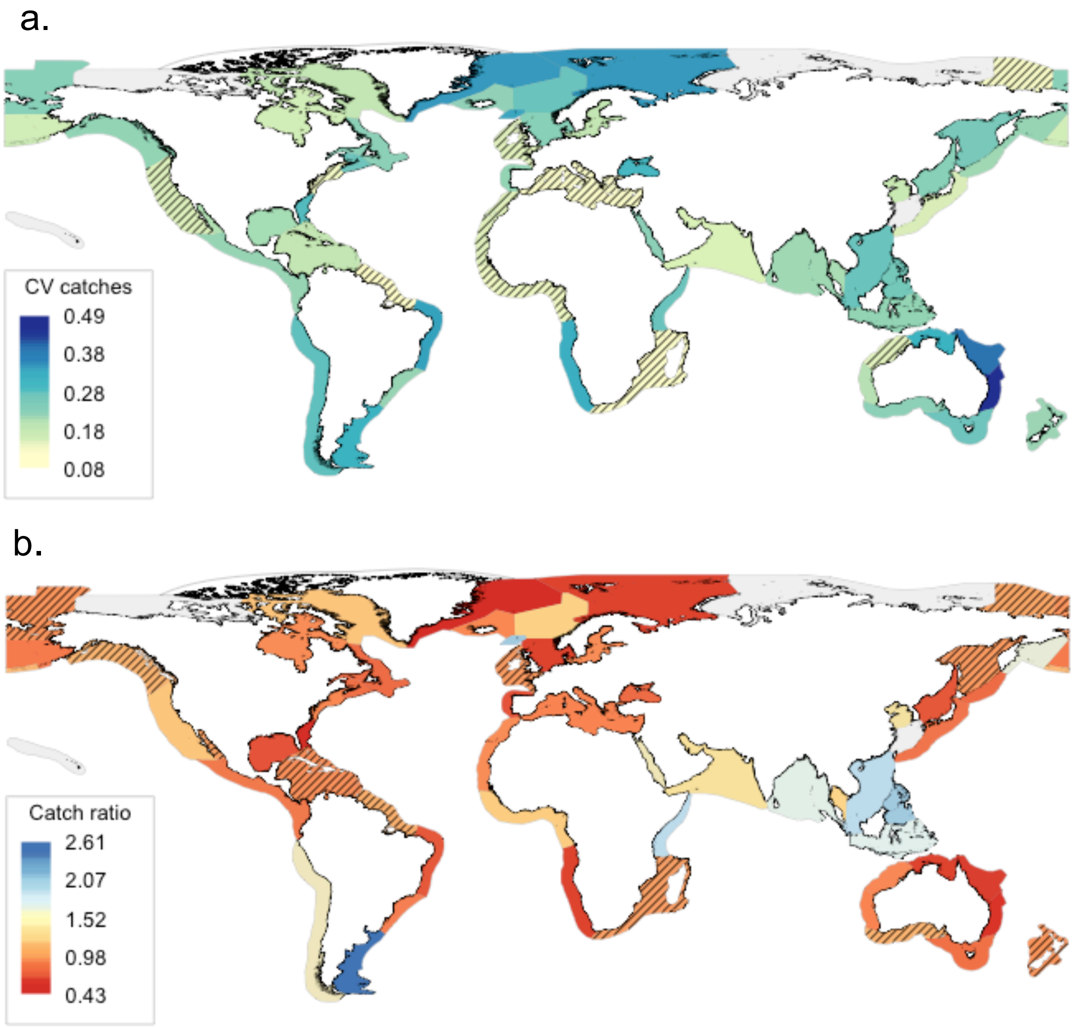

Figure 36: Distribution globale de la variabilité des prises de pêches entre 1980 et 2010, calculée à partir de la base de données Sea Around Us (Pauly and Zeller, 2015). a) Le coefficient de variation (CV) des stocks annuels totaux (%), illustre l'amplitude de la variabilité des prises de pêches. Les zones possédant les pêcheries les plus stables (CV $\leq$ 12.5%) sont hachurées. b) Le ratio entre les prises moyennes de 2005-2010 et celles 1980-1985 informe sur le statut des zones de pêche (en déclin, stable, en expansion). Un ratio inférieur à 1 illustre un déclin des prises de pêche par rapport aux années 80 (en rouge), tandis qu'un ratio supérieur à 1 correspond à une augmentation (en jaune et bleu). Les zones de pêches les plus stables (ratio entre 0.9 et 1.1) sont hachurées.

force des interactions entre les espèces, la dynamique et la stabilité des écosystèmes marins. Or la stabilité et les services rendus par les écosystèmes marins sont très fortement liés et constituent un enjeu sociétal important. D'importantes bases de données ont été construites à l'échelle globale, permettant de quantifier la variation spatiale et temporelle de la pression de pêche à partir de séries temporelles couvrant plusieurs décennies (Figure 36). Ces données permettraient de calibrer des modèles théoriques qui analysent l'effet de perturbations continues sur un écosystème (Bender E.A. et al., 1984; Ives et al., 2003; Montoya et al., 2009). Des outils ont également été développés pour détecter l'existence de signaux avant-coureurs d'un changement abrupt de l'écosystème dans ce type de données (Scheffer et al., 2009) et pourraient être utilisés pour modéliser le niveau d'exploitation à partir duquel la variabilité de la densité des stocks, et donc leur probabilité d'effondrement, s'accroît fortement.

Effet des interactions non trophiques sur la stabilité des écosystèmes

J'ai focalisé mon travail uniquement sur les interactions trophiques alors que de nombreuses études s'intéressent à l'effet des interactions non trophiques, telles que le mutualisme ou la compétition interspécifique, sur la stabilité des écosystèmes. Tout comme les relations proie-prédateur, ces interactions créent des boucles de rétroactions entre les dynamiques des espèces, mais il s'agit de rétroactions positives dans le cas du mutualisme (Thébault and Fontaine, 2010; Kéfi et al., 2012; Neutel and Thorne, 2014; Sauve et al., 2014). Pour éclaircir ce point, on peut prendre l'exemple de deux espèces en interaction, soit A et B. Un changement de la densité de A causera un changement de la densité de B, qui à son tour causera un changement de la densité de A, etc. Si le processus se renforce, c'est-à-dire que B augmente lorsque A augmente et que A augmente également lorsque B augmente, on parle de rétroaction positive, qui aura tendance à amplifier une perturbation. Si au contraire A augmente lorsque B augmente mais que B diminue lorsque A augmente, on obtient une boucle de rétroaction négative, typique des interactions proie-prédateur ou hôte-parasite, qui fera converger la densité des deux espèces vers un équilibre.

La théorie des matrices aléatoires démontre que les rétroactions positives déstabilisent l'état d'équilibre dans lequel se trouve un écosystème (Allesina and Tang, 2012). Les interactions mutualistes ont un effet particulièrement significatif dans les écosystèmes à faible biomasse, où l'énergie disponible est très peu exploitée à cause d'un facteur limitant, comme l'eau en zone désertique par exemple (Kéfi et al., 2007, 2014). Les rétroactions positives générées par les interactions mutualistes permettent d'augmenter localement la production de biomasse et de maintenir un niveau de biomasse stable à large échelle spatiale. La contribution relative de la prédation, du mutualisme et de la compétition aux flux de matière et d'énergie entre les espèces d'un écosystème pourrait donc varier en fonction de la quantité d'énergie exploitable par les espèces. L'étude de cette hypothèse nécessiterait néanmoins de définir une variable quantitative commune pour mesurer l'intensité des différents types d'interaction.

Mécanismes d'organisation des interactions trophiques

Le modèle de niche allométrique (Gravel et al., 2013), utilisé dans les chapitres 2 et 3 pour modéliser la topologie des réseaux trophiques se base sur deux hypothèses qu'il convient de questionner. Premièrement, le modèle de niche ne prend pas en compte les filtres spatiaux et temporels qui influencent la co-occurrence des espèces et donc la probabilité qu'elles interagissent entre elles. En se basant sur les masses corporelles des espèces référencées dans un écosystème, le modèle prédit que toutes les espèces d'une certaine gamme de taille feront partie du régime alimentaire d'un prédateur. Pourtant, un prédateur et ses proies potentielles sont susceptibles de ne jamais se rencontrer si leur mode de vie ne permet pas leur co-occurrence. Un prédateur diurne ne consommera pas les proies potentielles qui ont un mode de vie nocturne par exemple. Concernant la co-occurrence spatiale, la position des espèces dans la colonne d'eau est également un filtre qui va réduire la probabilité qu'un prédateur coexiste avec toutes ses proies potentielles. Cette limitation peut toutefois être facilement dépassée : il suffirait de recouper la matrice d'interactions générée par le modèle de niche allométrique avec une matrice de co-occurrence des espèces, basée sur des traits fonctionnels qualitatifs qui informent sur les périodes et les zones d'activité des espèces en définissant plus finement les habitats.

Deuxièmement, le modèle suppose que la masse corporelle est l'axe principal caractérisant la niche trophique des espèces, négligeant les potentielles autres dimensions de l'espace fonctionnel de la niche trophique. Cette hypothèse est relativement robuste pour les réseaux trophiques aquatiques qui sont fortement structurés par la taille (Barnes et al., 2010; Gravel et al., 2013). En effet, comme le montre l'étude présentée en annexe, les écosystèmes aquatiques étaient déjà structurés en réseaux trophiques durant le Dévonien, il y a plus de 380 millions d'années. Cette période géologique, aussi appelée "l'Âge des Poissons", est caractérisée par une importante radiation évolutive de la plupart des groupes de poissons (développement d'écailles mobiles et de mâchoires, augmentation de la taille corporelle), entrainant un considérable accroissement de la diversité fonctionnelle et du nombre de niveaux trophiques au sein des écosystèmes marins (Friedman and Sallan, 2012). Ces preuves d'interactions trophiques passées (contenus stomacaux fossilisés), structurées par la taille corporelle des poissons, conforte l'aspect réaliste des règles imposées par le modèle de niche allométrique. Ces observations renforcent également la pertinence de l'application de la théorie allométrique et trophique de la biogéographie des îles aux assemblages de poissons tropicaux (chapitre 3).

La relation entre la masse corporelle d'un prédateur et celle de ses proies est plus ténue dans certains réseaux trophiques terrestres en raison de l'existence d'une plus grande diversité de stratégies d'acquisition des ressources qui permet de s'affranchir des contraintes liées à la masse corporelle (production de poison ou de pièges). On pourrait envisager d'implémenter le modèle de niche avec des axes alternatifs qui varient également en fonction du niveau trophique des espèces, tel que le ratio carbone-azote ou la distance phylogénétique par exemple (Naisbit et al., 2012; Fink et al., 2012; Coux et al., 2016). Une analyse intéressante serait de comparer le pouvoir prédictif de modèles de niche implémentés avec la masse corporelle ou le ratio carbone-azote pour différents réseaux trophiques.

Intégrer la dynamique spatiale des espèces au fonctionnement des écosystèmes

Le diagramme qui présente l'articulation des chapitres de thèse souligne le maillon manquant de l'intégration de la biogéographie et du fonctionnement des écosystèmes (Figure 37). Actuellement, seule la topologie des interactions influence les probabilités de colonisation et d'extinction des espèces. L'approche se base sur les règles simples de la théorie trophique de la biogéographie des îles (TTBI), où la présence d'un prédateur est conditionnée par la présence d'au moins une de ses proies. La prochaine étape consistera à ajouter une dimension quantitative aux conditions de présence d'un prédateur, qui seront calculées en fonction de la quantité minimale de ressource requise pour supporter une taille de population viable de prédateurs (Hatton et al., 2015; Brown et al., 2004).

Pour ajouter du réalisme à ce modèle, il faudra également modéliser la probabilité d'extinction des proies en fonction de la pression de prédation qu'elles subissent. Actuellement, seul un contrôle trophique ascendant (bottom-up) est pris en compte dans la TTBI : les proies influencent les probabilités de présence des prédateurs et la généralité du régime alimentaire est la variable centrale de la TTBI. Avec l'ajout d'un contrôle trophique descendant, la vulnérabilité des espèces aura également un impact sur leurs probabilités de présence. Il sera possible d'exprimer, en fonction de la masse corporelle, la pression de prédation maximale pouvant être supportée par chaque espèce et qui entrainera son extinction si elle est atteinte. Grâce à cette intégration, il sera possible d'étudier comment la généralité (nombre de proies) et la vulnérabilité (nombre de prédateurs) des espèces varient en fonction de la taille et de l'isolement l'habitat. En se basant sur la relation allométrique entre la masse et l'abondance des espèces, il serait également possible d'étudier l'effet de la distribution de la masse corporelle sur la productivité d'un fragment d'habitat de taille et d'isolement donné.

Enfin, un autre point de développement intéressant de la théorie allométrique et tro-

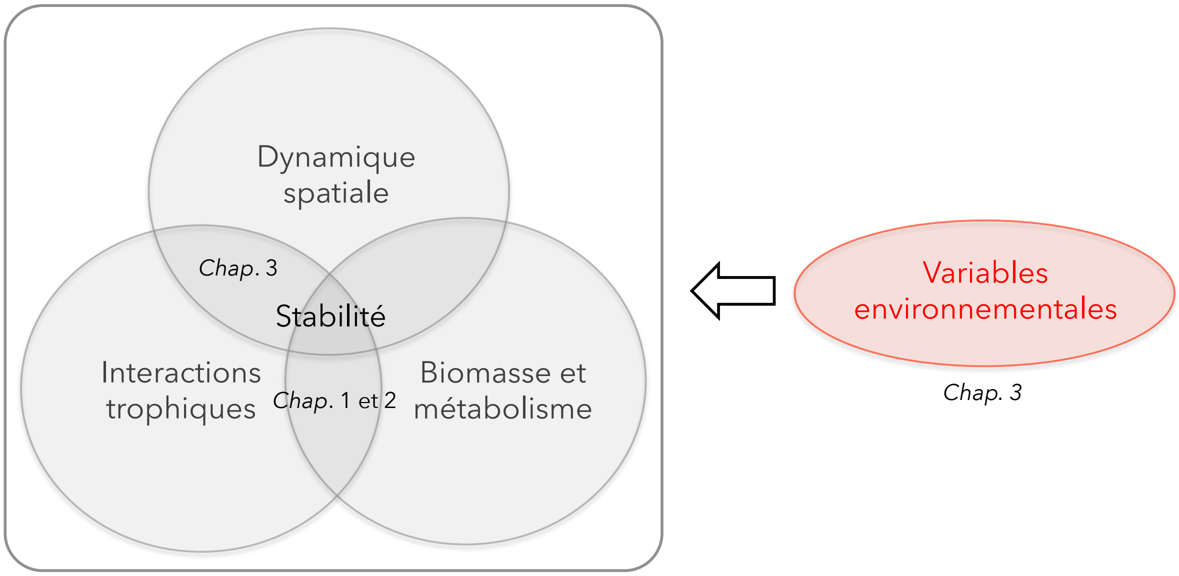

Figure 37: Articulation des chapitres de la thèse. Le chapitre 1 étudie les propriétés stabilisantes des écosystèmes complexes. Le chapitre 2 relie la masse corporelle des espèces à la structure et aux flux de biomasse circulant dans un écosystème, permettant d'étudier sa stabilité à partir des caractéristiques des espèces qui le composent. Enfin, le chapitre 3 intègre la structure des réseaux trophiques et l'effet de la masse corporelle sur les probabilités de présence à la théorie de la biogéographie des îles. La prise en compte des besoins énergétiques des espèces et de la quantité de ressource disponible dans une zone d'habitat constitue la prochaine étape de l'intégration de la biogéographie et du fonctionnement des écosystèmes.

phique de la biogéographie des îles serait son adaptation à l'échelle de l'individu, afin d'étudier l'effet de la taille et de l'isolement d'une île sur la variation intraspécifique de la masse corporelle des espèces. Ce changement d'échelle permettrait d'ajouter un aspect évolutif à cette théorie afin de modéliser l'émergence du nanisme ou du gigantisme insulaire par exemple.

Distribution spatiale des propriétés écosystémiques

Dans cette thèse, j'ai tenté de réunir les connaissances actuelles concernant les liens existants entre le fonctionnement des écosystèmes et les caractéristiques des espèces qui le composent. Une fois rassemblés, mes chapitres de thèse constituent une approche qui permettrait théoriquement de réaliser des cartographies de la stabilité des écosystèmes, prenant en compte la structure de l'habitat ainsi que les probabilités de dispersion et d'extinction des espèces en fonction de leurs traits fonctionnels. Cette approche peut être adaptée à différentes mesures de stabilité ainsi qu'à d'autres propriétés écosystémiques, telle que la productivité. Une carte montrant la distribution spatiale de propriétés écosystémiques pourrait constituer un support intéressant de transmission des connaissances scientifiques à des non-spécialistes, en présentant différents scénarios d'aménagement du territoire et d'exploitation des ressources par exemple.

Les ponts qui relient chacun des chapitres sont toutefois ténus à l'heure actuelle et il sera nécessaire de réaliser des mesures empiriques afin de tester et de calibrer les relations allométriques sur lesquelles repose cette approche. Il serait très pertinent d'étudier la forme de la relation entre la masse corporelle et les taux de colonisation et d'extinction des espèces pour différents taxons et milieux. Les prédictions du chapitre 2 concernant l'effet de la distribution de la masse corporelle sur la variance des forces d'interaction mériteraient également d'être testées empiriquement.

ANNEXE I

COMPARER LA STRUCTURE DES ÉCOSYSTÈMES ACTUELS ET PASSÉS

Early establishment of vertebrate trophic interactions : Food web structure in two Late Devonian fish assemblages with exceptional fossilization

Marion Chevrinais[1,2*], Claire Jacquet[3,4] and Richard Cloutier[1]

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[1] Laboratoire de Paléontologie et Biologie Evolutive, Université du Québec à Rimouski, 300 allée des Ursulines, G5L 3A1, Rimouski, Québec, Canada

[2] Institut des Sciences de l'Evolution, UMR 5554, CNRS, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier cedex 05, France

[3] UMR MARBEC (MARine Biodiversity, Exploitation and Conservation), Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier cedex 05, France

[4] Département de biologie, chimie et géographie, Université du Québec à Rimouski, 300 allée des Ursulines, G5L 3A1, Rimouski, Québec, Canada

[*] E-mail : marion.chevrinais@uqar.ca

ABSTRACT

In past and present ecosystems, trophic interactions determine material and energy transfers among species, regulating population dynamics and community stability. Food web studies in past ecosystems are helpful to assess the persistence of ecosystem structure throughout geological times and to explore the existence of general principles of food web assembly. We determined and compared the trophic structure of two Devonian fish assemblages [(1) the Escuminac assemblage (ca. 380 Ma), Miguasha, eastern Canada and (2) the Lode assemblage (ca. 390 Ma), Straupe, Latvia] with a closer look at the Escuminac assemblage. Both localities are representative of Middle-Upper Devonian aquatic vertebrate assemblages in terms of taxonomic richness (ca. 20 species), phylogenetic diversity (all major groups of lower vertebrates) and palaeoenvironment (palaeoestuaries). Fossil food web structures were assessed using different kinds of direct (*i.e.*, digestive contents and bite marks in fossils) and indirect (*e.g.*, ecomorphological measurements, stratigraphic species co-occurrences) indicators. First, the relationships between predator and prey body size established for the Escuminac fishes are comparable to those of recent aquatic ecosystems, highlighting a consistency of aquatic food web structure across geological times. Second, non-metric dimensional scaling on ecomorphological variables and cluster analyses showed a common pattern of functional groups for both fish assemblages ; top predators, predators, primary and secondary consumers were identified. We conclude that Devonian assemblages were organized in multiple trophic levels and that size-based feeding interactions were established during the early vertebrate history.

Keywords : digestive contents, fossil fish, ecomorphology, palaeoecology.

INTRODUCTION

The trophic structure of recent ecosystems has long been described as controlled either by lower trophic levels (bottom-up control) or by higher trophic levels (top-down control) depending on species interactions. In extant aquatic ecosystems, both bottom-up and top-down controls are recognized (McQueen et al., 1989; Menge, 2000; Arreguin-Sanchez, 2011). Large body size species are represented in upper trophic level, but in relatively low abundance, whereas smaller and more abundant species represent lower trophic levels (Cohen et al., 1993) implying that relationships between predator and prey total lengths can be estimated.

Trophic interactions in taxonomically, environmentally and temporally diverse past ecosystems [*e.g.*, Cambrian (Vannier and Chen, 2005; Dunne et al., 2008; Vannier, 2012), Devonian (Lebedev, 1992; Mark-Kurik, 1995), Permian (Kriwet et al., 2008), Jurassic (Frey and Tischlinger, 2012), (Nesbitt et al., 2006), Cretaceous (Maisey, 1994; Wang et al., 2005), Quaternary (Nenzen et al., 2014)] have been reconstructed based on direct (*e.g.*, digestive contents) and indirect (*e.g.*, species co-occurrences) evidences. Most of these studies rely on qualitative descriptions of assemblages. Little is known about the similarity of species functional traits related to trophic interactions between past and recent ecosystems.

The Devonian period [416 ± 2.8 Ma to 359.2 ± 2.5 Ma (Walker et al., 2012)] is commonly referred to as ‘The Age of Fishes’, owing to the important evolutionary radiation of most major groups of fishes (Friedman and Sallan, 2012). Although it is well established that major phylogenetic events in the history of vertebrates occurred in the Devonian, not much has been documented regarding the ecological structure of Devonian fish assemblages. This study aims to determine if structured trophic interactions among fishes were already established in the Middle-Upper Devonian, and if a redundant structure can be observed between Devonian fish assemblages, given that species diversification allows for the establishment of hierarchical ecosystems (Bambach, 1999, 2002) and that fossil assemblages could be characterized in terms of ecological variables (*e.g.*, number of species in a guild or a functional group) (Louys et al., 2012). In order to investigate the structure of vertebrate assemblages, we studied and compared two classical Middle-Late Devonian fish assemblages : the Escuminac (Miguasha, Quebec, Canada) and Lode (Straupe, Latvia) assemblages. These two assemblages are comparable because of their taxonomic (ca. 20 vertebrate species, poor invertebrate diversity), phylogenetic (presence of representatives of most major groups of early vertebrates), palaeogeographical (coastal to the Rheic ocean in Laurasia) and palaeoenvironmental (palaeoestuaries) similarities (Schultze and Cloutier 1996). First, trophic links among Escuminac species were registered using direct observations of digestive contents in order to make predictions about the trophic structure of the Escuminac palaeoecosystem. In extant aquatic ecosystems, the body size of a predator is positively correlated to the mean body size of its prey and to its range of prey size (Cohen et al., 1993; Woodward et al., 2005; Barnes et al., 2010; Reuman et al., 2014). In order to evaluate the trophic structure of past ecosystems, relationships between predator and prey lengths are compared to the ones observed in extant fish assemblages. Second, the structures of food webs of both Devonian assemblages were compared. Ecomorphospace comparisons of the two Devonian communities allowed us to make predictions concerning trophic similarities of phylogenetically and morphologically closely related species. Finally, three-dimensional networking is performed to visualize food web structures. This comparison will lead to fundamental questions : Are body size and other morphological traits correlated to trophic level in Devonian assemblages as it is in recent assemblages ? Can we expect to observe functional similarities in Upper Devonian palaeoestuaries and to record stable trophic relationships in early vertebrate evolutionary history ?

MATERIAL AND METHODS

Studied fish assemblages

The late Givetian-early Frasnian (ca. 390 Ma) Lode assemblage (Lode clay quarry, Straupe, Latvia), including 16 vertebrate species (Upeniece, 2001), is a Konservat-Lagerstätte (Upeniece, 2011). Plant (*e.g.*, *Archeopteris spp.*, *Svalbardia polymorpha*, *Platyphyllum sp.*) and invertebrate (*e.g.*, eurypterids, conchostracans) species are abundant, supporting a diverse vertebrate assemblage (Upeniece, 2001). The 200-m thick Lode Formation, composed of siltstone, sandstone and clay (Upeniece, 2001), shows a typical estuarine sedimentation (Ponten and Plink-Bjorklund, 2007). Upeniece (2011) reported the presence of swallowed prey based on which a theoretical trophic network has been reconstructed.

The middle Frasnian (ca. 380 Ma) Escuminac assemblage (Miguasha, Quebec, Canada), including 20 vertebrate species, is considered to be a Konservat- and Konzentrat-Lagerstätte in numerous horizons (Cloutier et al., 2011; Cloutier, R 2013). Plant (*e.g.*, *Archeopteris spp.*, *Barinophyton*) and invertebrate (*e.g.*, *Asmusia membranacea*, *Petaloscorpio bureaui*) species have been recorded (Gensel and Barnett-Lawrence, 1996; Jeram, 1996; Cloutier, R 2013). The 119-m thick Escuminac Formation, registering from 59,500 yrs to 2.5 Ma [time span estimates based on different proxies (Cloutier et al., 2011)], shows typical estuarine sedimentation (Cloutier et al., 1996, 2011). Throughout the formation, more than 18,000 specimens of vertebrate species have been found. Predator-prey relationships have been briefly documented (Arsenault, 1982; Janvier, 1996; Cloutier et al., 2011; Cloutier, R 2013) ; new observations allowed us to document numerous ingested prey and to reconstruct the Escuminac food web.

Material

A total of 249 specimens, out of the 10,658 vertebrate specimens of the MHNM collection, and five specimens from various museums have been selected for their digestive contents. Specimens were observed under binoculars (MS9.5 or MZ16A). Selected specimens were visualized in SEM in an attempt to identify remains in the amorphous organic matter found in the digestive track.

Food web of the Escuminac assemblage

The size range of prey for a predator is derived from scatter diagrams between prey estimated total length (eTL) and predator eTL (Scharf et al., 2000; Brose et al., 2006b), each one including all vertebrate species from the Escuminac assemblage (Scharf et al., 2000; Brose et al., 2006b). For each vertebrate species, specific eTL has been taken from the literature. Log_{10}(eTL) has been used to define an optimal scaling. Five scatter diagrams have been used to describe the relationships between prey and predator log_{10}(eTLs) for the 20 species of the Escuminac Formation, each one defined by a lower confidence degree than the subsequent one : (1) ecomorphological theory (Wootton, 1992), (2) simple stratigraphic species co-occurrences, (3) weighted stratigraphic species co-occurrences, and (4) fossilized digestive contents.

Regression 1 shows theoretical interactions between predators log_{10}(eTL) and their corresponding prey log_{10}(eTLs), assuming that a species consumes smaller species (Yodzis and Innes, 1992; Cohen et al., 1993; Wainwright and Richard, 1995; Clifton and Motta, 1998). For both prey and predator species, the maximum body size is used, based on data from Cloutier et al. (2009). Regressions 2 and 3 show theoretical predator-prey interactions considering their stratigraphic co-occurrences. Only predator-prey interactions (represented in the regression 1) for which stratigraphic co-occurrence (*i.e.*, species found in the same stratigraphic horizon) was confirmed were included. Furthermore, the predator-prey interactions of regression 3 were weighted by the number of times a predator and its prey co-occurred in the same stratigraphic horizon. Species occurrences by stratigraphic horizon have been recorded by Cloutier et al. (2011). The two *Diplacanthus* species have been pooled at a generic level because of the low number of specimens and the poor stratigraphic data available on some of these specimens. Furthermore, stratigraphic data are lacking for *Callistiopterus clappi* and *Holoptychius jarviki*.

Regression 4 is performed based on the observed digestive contents for 14 species. The eTL of prey and predators were measured on specimens whenever possible ; when direct measurement was impossible, eTL was calculated based on known proportions from reconstructions. Maximum size of *Asmusia membranacea* was measured on specimens when it was possible ; otherwise we used the average size [*i.e.*, 3 mm (Martens, 1996)].

Ecomorphological comparison of faunal assemblages

Ecomorphological theory assumes that morphological variables are significantly correlated with foraging behaviour (Wootton, 1992). Morphological disparity among the 20 Escuminac and 16 Lode vertebrate species is too important to define a common set of morphometric parameters. Owing to the broad phylogenetic representativeness, numerous structures (*e.g.*, teeth, jaw, fins) are only present in subsets of the 36 taxa. Each taxa is defined from morphological and morphometric parameters (Willis et al., 2005). A non-metric multidimensional scaling (NMDS) was used on six semi-quantitative and seven qualitative variables observable on all taxa (Table 1) in order to attribute a trophic level to a species. For each variable, four classes were recognized, representing a benthophageous to pelagic predator gradient (Table 1).

NMDS quantitative data were recorded from most-recent species reconstructions because of the potential bias owing to taphonomic alteration. In addition, coding for anatomically incomplete species was estimated from closely-related species with similar complete morphology (e.g., *Eusthenopteron kurshi* estimated from *E. foordi*). ETL is used as a proxy of body size (Cohen et al., 1993; Jennings et al., 2001; Emmerson and Raffaelli, 2004; Romanuk et al., 2011). Mouth position, size, shape, dentition, protrusion degree and eye size are indicators of foraging behavior (Clifton and Motta, 1998). For example, big eyes and mouth with teeth are traits related to predator species (Wootton, 1992). Since locomotion is an important factor for predation behaviour, caudal fin shape and repartition of median fins are used as indicative of locomotion mode (Trewin, 1985; Belles-Isles, 1992).

The NMDS performed in Euclidean distances allowed us to associate taxa by their ecomorphological similarities. Two living taxa were included in the analysis in order to polarize the results along a benthophageous (a Rajidae) – pelagic predator (*Albula vulpes*) gradient. A generalised skate (Batoidea, Rajidae), showing specific benthic life characters (*e.g.*, body dorsoventrally flattened, eyes in dorsal position) was used as representative of a benthophageous-type (Schultze, 1999), whereas the bonefish *Albula vulpes* (Actinopterygii, Albuliformes) was used for its predator characteristics (*e.g.*, fusiform body, eyes in lateral position, symmetrical caudal fin). Convex hulls are used to visualize species repartition and superimposition of both Devonian assemblages. An UPGMA cluster analysis using Euclidean distances (Legendre and Legendre, 1979) was performed in order to highlight clusters sharing high ecomorphological similarity. Interpretation of trophic and level classes were inferred from (Dineley, 1999a; Elliott et al., 2002; Upeniece, 2011; Cloutier, R 2013). NMDS and cluster analysis were realized with PAST software (Hammer et al., 2001). Trophic interactions for the Escuminac (observed) and Lode (inferred) assemblages were modelled with Network 3D software to visualize predator-prey interactions.

Table 1: Semi quantitative and qualitative variables defined from reconstructions.

Classes	1	2	3	4
Total length[1]	0-200 mm	200-500 mm	500-1000 mm	> 1000 mm
Body shape	depressiform	«cubic»	ovoid sagittiform	fusiform
Mandibles	absence	presence		
Head length[2]/total length	0-15%	15-30%	30-40%	> 40%
Mouth position	inferior	subterminal	terminal	superior
Eye position	dorsal	anterior	lateral	
Snout length[3] / head length	0-15%	15-30%	30-40%	>40%
Caudal fin shape	heterocercal	hypocercal	symmetrical	
Caudal height/body height[4]	0-30%	30-70%	70-100%	> 100%
Unpaired fin repartition	homogeneous	posterior half	posterior third	
Teeth	absence	small	big	slide
Eye size[5]/head length	0-10%	10-20%	20-30%	> 30%
Mouth gape opening length /head length	0-20%	20-40%	40-60%	> 60%

[1] Body anterior extremity to caudal posterior extremity
[2] Head anterior extremity to opercular bones or cephalic plates posterior extremity
[3] Head anterior extremity to orbit anterior extremity
[4] Maximum height without fins
[5] Horizontal diameter of the orbit

Table 2: Vertebrate digestive contents records and corresponding stratigraphical co-occurrence probabilities (SCOP) between predator and prey species

Predator species	Specimen ID	Prey species	SCOP (%)
Cheirolepis canadensis	MHNM 05-18 MHNM 05-399	*Homalacanthus concinnus*	10
Eusthenopteron foordi	MHNM 06-700 MHNM 06-915	*Bothriolepis canadensis*	9.1
Eusthenopteron foordi	MHNM 06-126	*Homalacanthus concinnus*	2.9
Eusthenopteron foordi	MHNM 06-32B AMNH 5968	*Cheirolepis canadensis*	1.8
Eusthenopteron foordi	MHNM 06-1754	*Scaumenacia curta*	9.5

RESULTS

Food web of the Escuminac assemblage

Digestive contents observed in 255 specimens were used to reconstruct the Escuminac food web. Among the 255 specimens, 78 (31%) showed recognizable digestive contents, and 177 (69%) contained amorphous organic matter. Digestive contents have been recorded for 16 of the 20 vertebrate species.

The digestive contents of anaspids, osteostracans, placoderms, acanthodians and dipnoiforms include solely the conchostracan *Asmusia membranacea*. *Cheirolepis canadensis* and *E. foordi* are the only species with vertebrates in their digestive tract (Table 2). The majority of specimens documents an interaction between two species with the exception of two specimens documenting a three-trophic level interaction. The three represented levels are : primary consumers (*A. membranacea*), secondary consumers (*H. concinnus*) and predators (*C. canadensis*) [MHNM 05-226 (Fig. 38) and 05-399 (Fig. 39C, D)]. *C. canadensis* swallowed *H. concinnus* head first.

Eusthenopteron foordi is the most common species with fish found in the digestive tract. A total of 66 specimens of *E. foordi* showed digestive contents ; prey have been identified in 24 of these specimens (36%). Two specimens of *E. foordi* showed a specimen of *Bothriolepis canadensis* in the anterior part of the digestive tract (Fig. 39A, B) ; in both specimens, the ingested specimens of *Bothriolepis* were relatively medium-sized individuals (eTL = 96 mm and 139 mm) with pectoral fins, cephalic and thoracic plates preserved. In most cases of predation by *E. foordi*, prey [*H. concinnus* (Fig. 40C), *C. canadensis* (Fig. 41A), *S. curta* (Fig. 41B)] were swallowed head first. The predator behaviour of *E. foordi* was present early in ontogeny : a complete juvenile specimen of *E. foordi* (eTL = 58 mm) has ingested a complete juvenile specimen of S. curta (eTL = 36 mm) (Fig. 4B ; I. Béchard, pers. comm.).

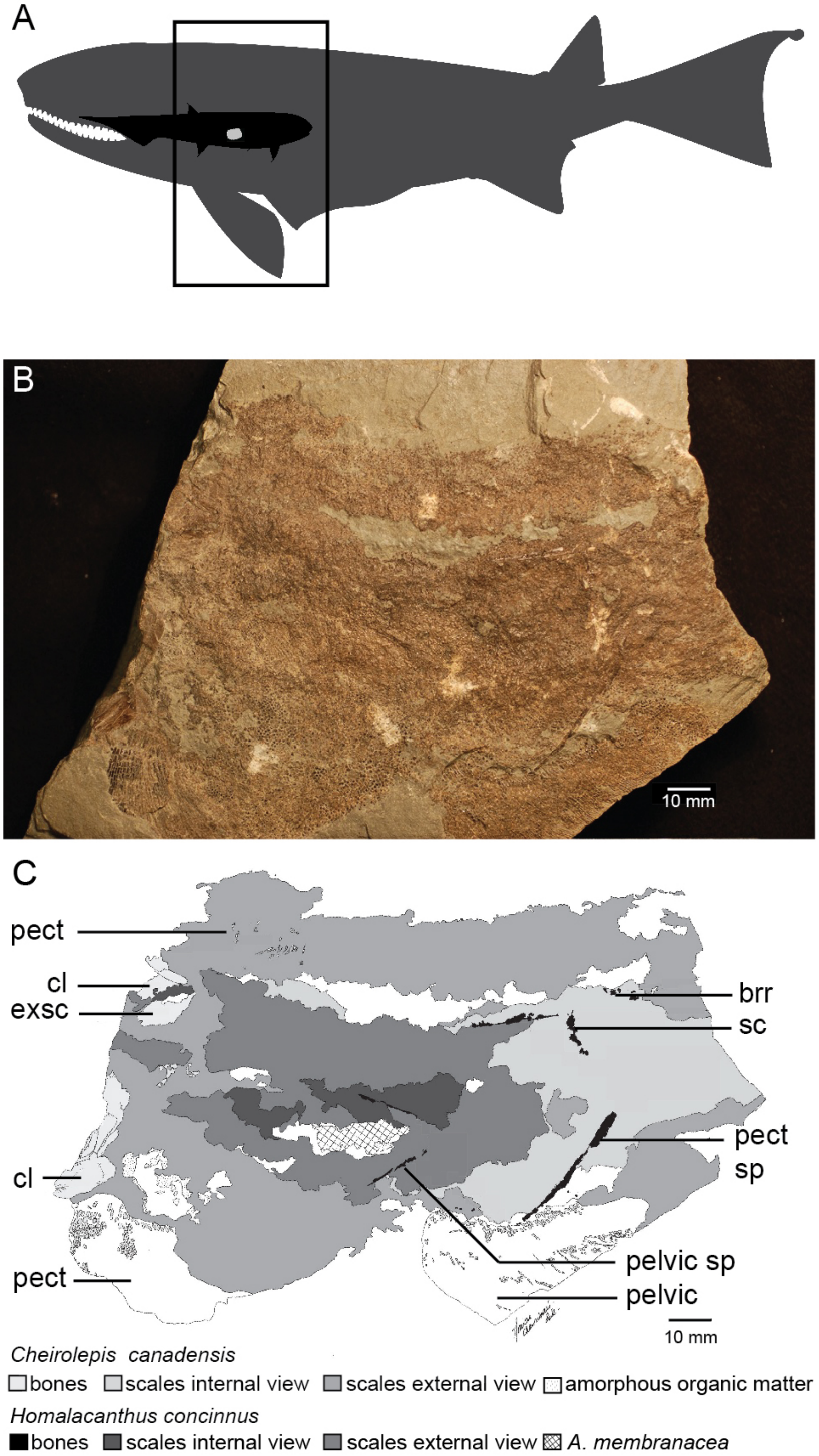

Figure 38: Three-trophic-level specimen. A – Schematic representation of the three-trophic-level specimen. The estimated length of *C. canadensis* is 548.4 mm ; the estimated length of *H. concinnus* is 249.3 mm. The frame indicates the region represented in the fossil B, C. B – Dorso-ventrally preserved specimen MHNM 05-226. C – Drawing of specimen MHNM 05-226.

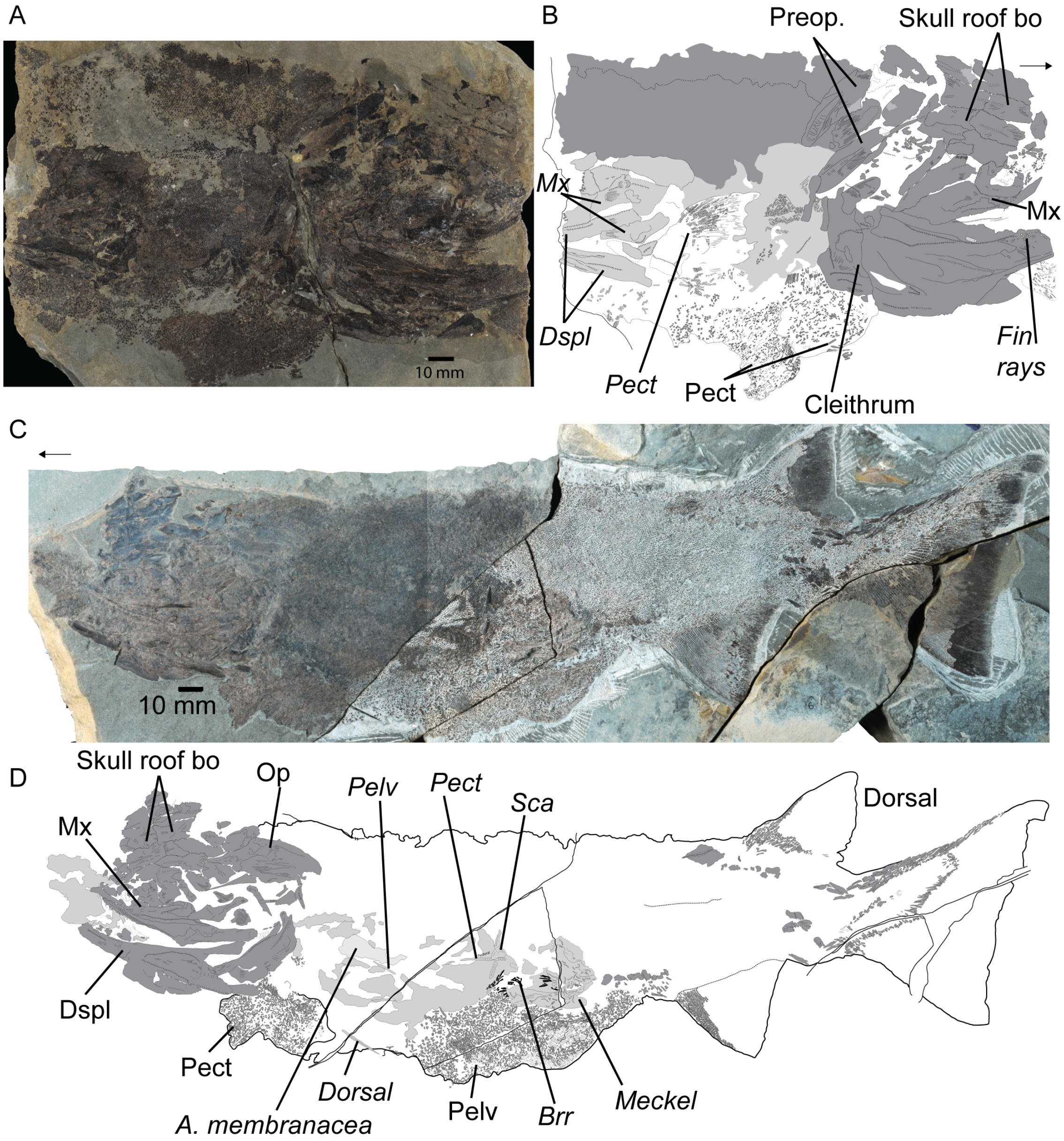

Figure 39: Digestive contents of the *actinopterygian Cheirolepis canadensis*. A – Photography and B – drawing of specimen MNHN 1968.4 showing of a swallowed C. *canadensis* showing skull roof bones (Skull roof bo), preopercular (Preop.), maxillary (Mx), pectoral fins (Pect), cleithrum and dentalospenial of the predator (regular) and of the prey (italics). C – Photography and D – drawing of a swallowed *H. concinnus* with *A. membranacea* in his digestive tract MHNM 05-399 showing skull roof bones (Skull roof bo), maxillary (Mx), opercular (Op), dentalospenial (Dspl), pectoral fins (Pect) and pelvic fins (Pelv), scapulocoracoid (Sca), branchiostegal rays (Brr), Meckel's cartilage (Meckel). Regular text is for the predator skeletal elements, italic text is for the prey skeletal elements. Arrow points anteriorly.

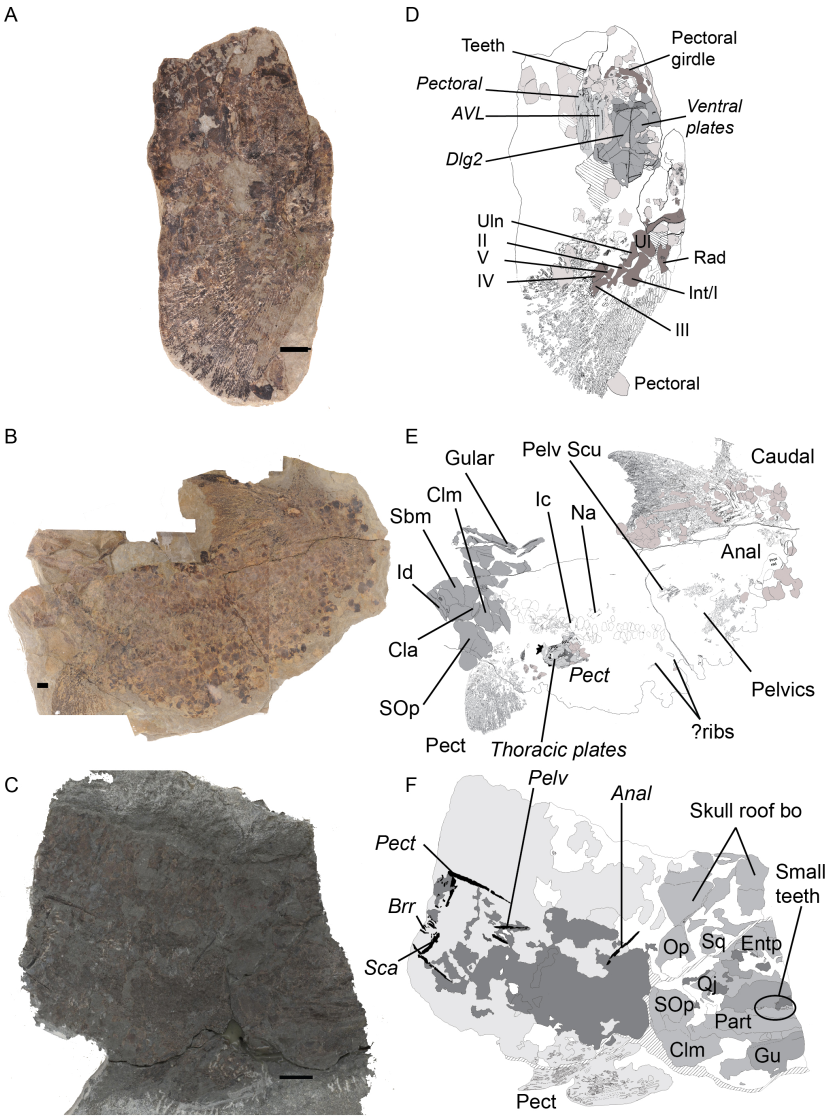

Figure 40: Digestive contents of the osteolepiform *Eusthenopteron foordi*. A – Photography and D – drawing of a swallowed *B. canadensis* MHNM 06-915 showing antero-ventral plate (AVL), radius (Rad), ulna (Ul), ulnare (Uln), pectoral fin bones (I-V). B – Photography and E – drawing of a swallowed *B. canadensis* MHNM 06-700 showingclavicle (Cla), cleithrum (Clm), intercentrum (Ic), Infradentary (Id), neural arch (Na), pelvic scutes (Pelv Scu), sub-mandibular (Sbm) and Sub-opercular (SOp). C – Photography and F – drawing of a swallowed H. concinnus MHNM 06-126 showing branchiostegal rays (Brr), cleithrum (Clm), entopterygoid (Entp), gular (Gu), opercular (Op), pre-articular (Part), pectoral fin spine (Pect), pelvic fin spine (Pelv), quadratojugal (Qj), scapulocoracoid (Sca), squamosal (Sq), subopercular (SOp). Regular text is for the predator skeletal elements, italic text is for the prey skeletal elements. Scale bars equal 10 mm.

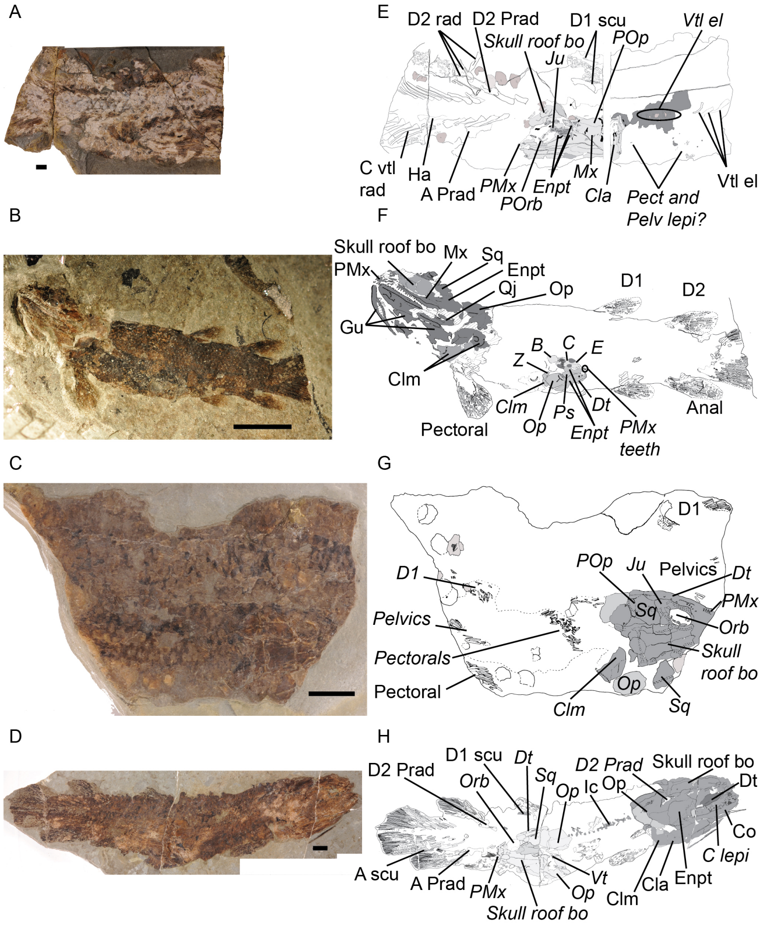

Figure 41: Digestive contents of the osteolepiform Eusthenopteron foordi. A – Photography and E – drawing a swallowed *C. canadensis* MHNM 06-32 showing proximal radial of anal fin (A Prad), clavicle (Cla), caudal neural arch (C Na), caudal ventral radial (C vtl rad), scutes of first dorsal fin (D1 cu), proximal radial of second dorsal fin(D2 Prad), radials of second dorsal fin(D2 rad), entopterygoid (Enpt), haemal arch (Ha), jugal (Ju), maxillary (Mx), possible pectoral and pelvic lepidotrichia (Pect and Pelvic lepi), premaxillary (Pmx), Preopercular (Pop), postorbital (Porb), vertebral element imprints (Vtl el). B – Photography and F – drawing of a swallowed S. curta MHNM 06-1754 showing cleithrum (Clm), first dorsal fin (D1), second dorsal fin (D2), dentary (Dt), entopterygoid (Enpt), gular (Gu), maxillary (Mx), opercular (Op), premaxillary (Pmx), parasphenoid (Ps), quadratojugal (Qj), squamosal (Sq). C – Photography and G – drawing of a swallowed *E. foordi* MHNM 06-502 showing cleithrum (Clm), dentary (Dt), first dorsal fin (D1), jugal (Ju), opercular (Op), orbit (Orb), premaxillary (Pmx), preopercular (Pop), squamosal (Sq). D – Photography and H – drawing of a swallowed *E. foordi* FMNH PF6261 showing anal proximal radial (A Prad), scutes of anal fin (A scu), clavicle (Cla), cleithrum (Clm), caudal lepidotrichia (C lepi), coronoid (Co), dentary (Dt), scutes of first dorsal fin (D1 scu), proximal radial of second dorsal fin (D2 Prad), entopterygoid (Enpt), intercentrum (Ic), opercular (Op), orbit (Orb), premaxillary (Pmx), squamosal (Sq), first vertebral elements (Vt). Regular text is for predator skeletal elements, italic text is for prey skeletal elements. Scale bars equal 10 mm.

The predator *C. canadensis* (MNHN 1968.8.4, Fig. 39A, B) and *E. foordi* (MHNM 06-502, FMNH PF6261, Fig. 41C, D) demonstrate cannibalistic behaviour. Prey size did not exceed 70% of *E. foordi* body size with the exception of the extreme value of 86% in FMNH PF6261. *C. canadensis* consumed prey in a body size range of 45 to 70% of its eTL. In Eusthenopteron specimen FMNH PF6261 (Fig. 41D) and Cheirolepis specimens MNHN 1968.8 and MHNM 05-399 (Fig. 39B), the caudal fin of the prey is still in the oral cavity of the predator ; the swallowing of the prey likely caused the suffocation of the predator.

The three relationships between prey maximum body size and predator maximum body size for the Escuminac assemblage are characterized by similar equations : (1) theoretical (Fig. 42A) : log_{10}(prey eTL) = 0.97 × log_{10}(predator eTL) – 0.51 ($P = 6.1 \times 10^{-10}$; ($R^2 = 0.17$) ; (2) simple co-occurrences (Fig. 42B) : log_{10}(prey eTL) = 1.42 × log_{10} (predator eTL) - 0.13 ($P = 2.78 \times 10^{-5}$; ($R^2 = 0.17$) ; and (3) weighted co- occurrences (Fig. 42C) : log_{10}(prey eTL) = 1.24 × log_{10} (predator eTL) - 1.7 ($P < 2.2 \times 10^{-16}$; $R^2 = 0.15$).

Using digestive contents, regression 4 (Fig. 42D) shows relationship between predator estimated maximum total length and prey estimated maximum total length : log_{10}(prey eTL) = 0.84 × log_{10}(predator eTL) - 1.28 ($P = 4.657 \times 10^{-4}$) ; ($R^2 = 0.15$). This linear regression needed estimated size. In some species, estimated size using morphological proxies, is higher than previously recorded maximum size (Cloutier et al., 2009). *A. membranacea* estimated sizes are often smaller than those estimated by Martens (1996).

Ecomorphological comparison of faunal assemblages

The NMDS shows similar patterns of species distribution in both assemblages (Fig. 43). The ecomorphospace of both assemblages is similar and overlap extensively. A 17% stress index is indicative of a weak deformation of raw values. The NMDS shows trophic network clustering. The UPGMA (Fig. 44) specifies the clustering observed with the NMDS. Trophic clusters have been defined by combining NMDS and UPGMA results. The benthopha-

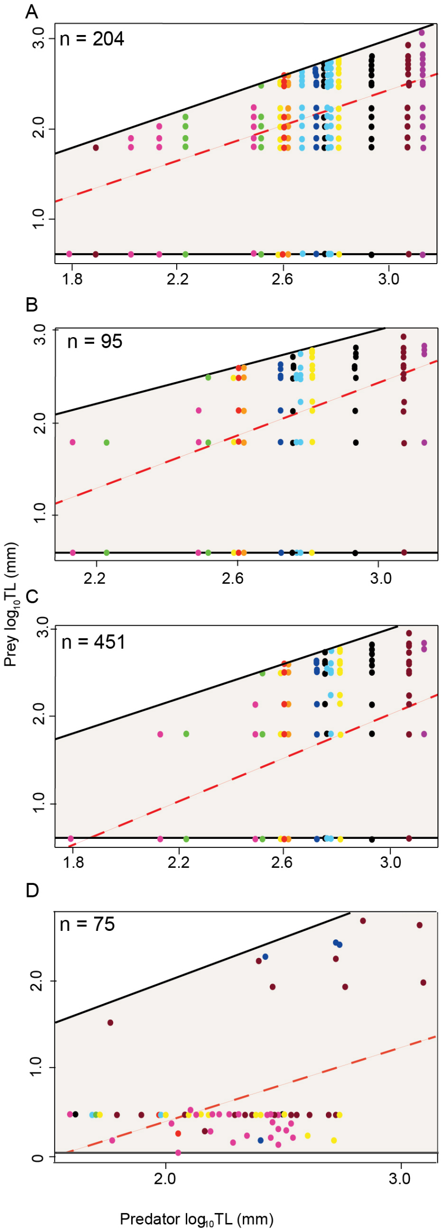

Figure 42: Predator size-prey size scatter diagrams in terms of total length (TL, log_{10}, mm) based on five parameters for the 21 species of the Escuminac assemblage. A – Size-based model including all species. B – Size-based model accounting for simple stratigraphical co-occurrences. C – Size-based model accounting for weighted co-occurrences. D – Observed digestive contents. Regression line is in red. Continuous lines represent minimum and maximum prey sizes, whereas dashed line represents mean prey sizes (linear regression). N is for the number of points on the graph, showing supposed or observed prey-predator interactions. Dots legend : green : *Anaspida*; red : *Osteostraci*; black : *Placodermi*; magenta : *Acanthodii*; blue : *Actinopterygii*; orange : *Actinistia*; yellow : *Dipnoiformes*; cyan : *Porolepiformes*; brown : *Osteolepiformes*; purple : *Elpistostegalia*.

geous cluster (secondary consumers), associated with the Rajidae, gathers placoderms (*i.e.*, *Bothriolepis canadensis*, *Asterolepis ornata*), osteostracans (*i.e.*, *Escuminaspis laticeps*, *Levesquaspis patteni*) and anaspids (*i.e.*, *Psammolepis spp.*). They forage essentially on invertebrate species (*i.e.*, *Asmusia membranacea*, primary consumers). Secondary pelagic consumers include acanthodians (*Homalacanthus concinnus*, *Diplacanthus spp.*, *Triazeugacanthus affinis*, *Lodeacanthus gaujicus*), anaspids (*Euphanerops longaevus*, *Endeiolepis aneri*) and also *Struniussp.*

Two clusters composed by pelagic species correspond to predators and top predators. Predators are gathered around *Albula vulpes*. This cluster assembles piscivores such as "osteolepiforms" (*Eusthenopteron spp.*, *Osteolepididae*), porolepiforms (*Glyptolepis baltica*, *Laccognathus panderi*, *Holoptychius jarviki*, *Holoptychidae indet.*), actinistians (*Miguashaia spp.*), and dipnoiform (*Scaumenacia curta*). An additional predator cluster includes the actinopterygians *Cheirolepis spp.* and the young/juvenile "osteolepiform" *Callistiopterus clappi*. Top predators are the elpistostegalian *Elpistostege watsoni* and *Panderichthys rhombolepis*.

An intermediate cluster, gathered in the NMDS centre, shows *Plourdosteus canadensis* and *Fleurantia denticulata*. UPGMA allowed us to gather *Plourdosteus canadensis* with predator species and *Fleurantia denticulata* with secondary consumers ; these two taxa represent deepest rooted branches for large predators and secondary consumers, respectively.

Phylogenetically related species (*El. watsoni* and *P. rhombolepis* ; *Es. laticeps* and *L. patteni* ; *M. grossi* and *M. bureaui* ; *En. aneri* and *Eup. longaevus* ; *E. foordi* and *E. kurshi*) show high bootstrap values (67 to 96%) (Fig. 44). Lower bootstrap values (40 and 45%) correspond to larger trophic clusters : secondary consumers, predators and benthophageous, respectively.

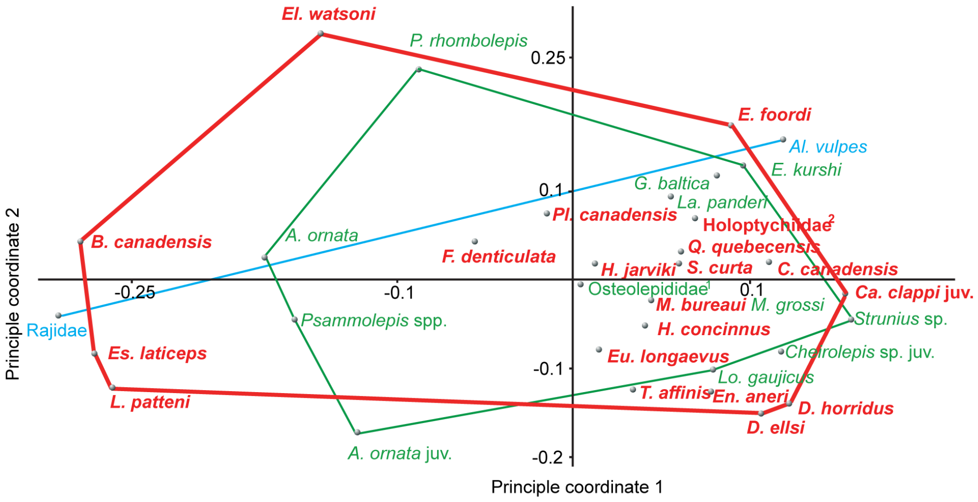

Figure 43: Non-metric multidimensional scaling from morphological and morphometric data scored for the Escuminac and Lode vertebrate species. Lode taxa : green ; Escuminac taxa : bold and red ; polarizing taxa : blue. ^{1}gen. and sp. indet. ; ^{2}indet. Euclidean distances. Coordinate 1 shows benthophageous to pelagic axis whereas coordinate 2 shows size gradient. Stress index : 17%.

Three-dimensional trophic network

Three-dimensional visualization of Lode and Escuminac food webs (Fig.45) shows food web structures with up to four trophic levels. Lode network (Fig. 45A) potentially shows four trophic levels. This ecosystem shows a lack of links between *Miguashaia grossi* ending arm and top predators (*i.e.*, *P. rhombolepis*, *La. panderi*, *G. baltica*) ending arm. However, these taxa most likely foraged on the same species.

Concerning the Escuminac assemblage (Fig. 45B), primary and secondary consumers are well represented, whereas predators are under-represented. More specifically, *E. foordi* shows the highest trophic level followed by *C. canadensis*. The comparison of these two palaeoecosystems, in terms of trophic interactions, suggests new insights on ecological dynamics and interspecies relationships in Upper Devonian geological period.

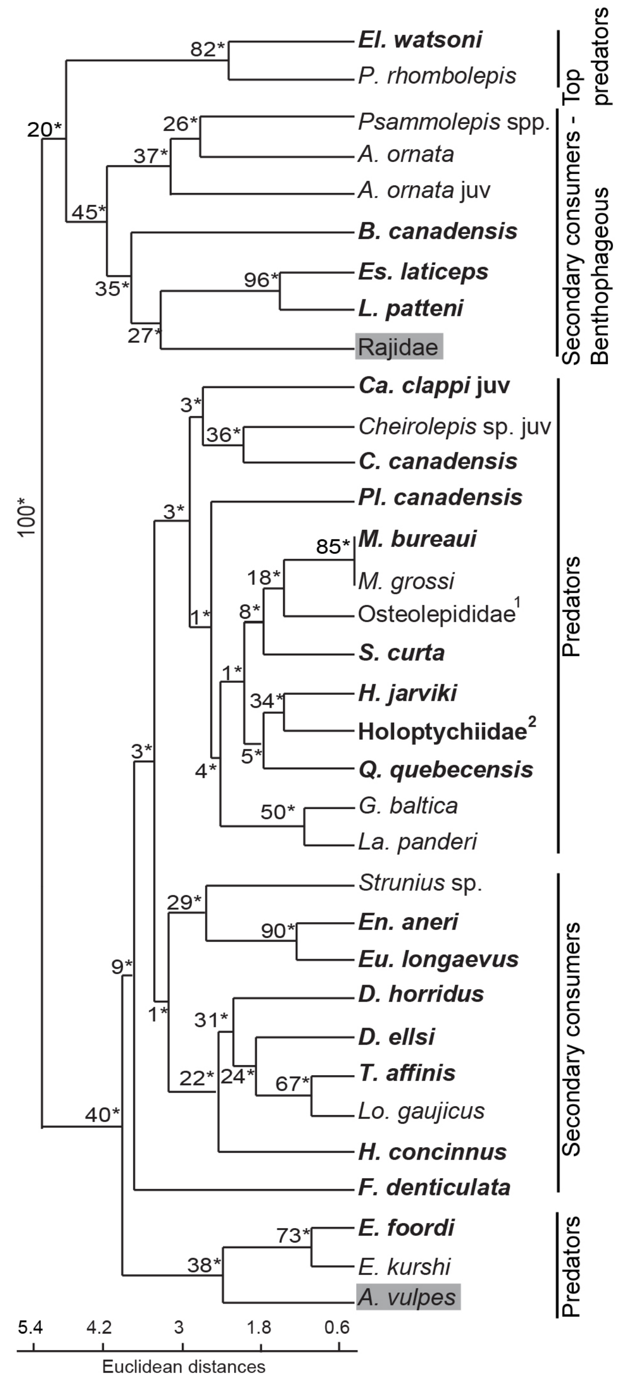

Figure 44: Cluster analysis with morphological and morphometric characters. Lode taxa : regular ; Escuminac taxa : bold ; polarizing taxa : regular with grey font ;* : bootstrap values for 1000 iterations ; 1gen. and sp. indet. ; 2indet. UPGMA method and Euclidean distances. Correlation coefficient : 85%.

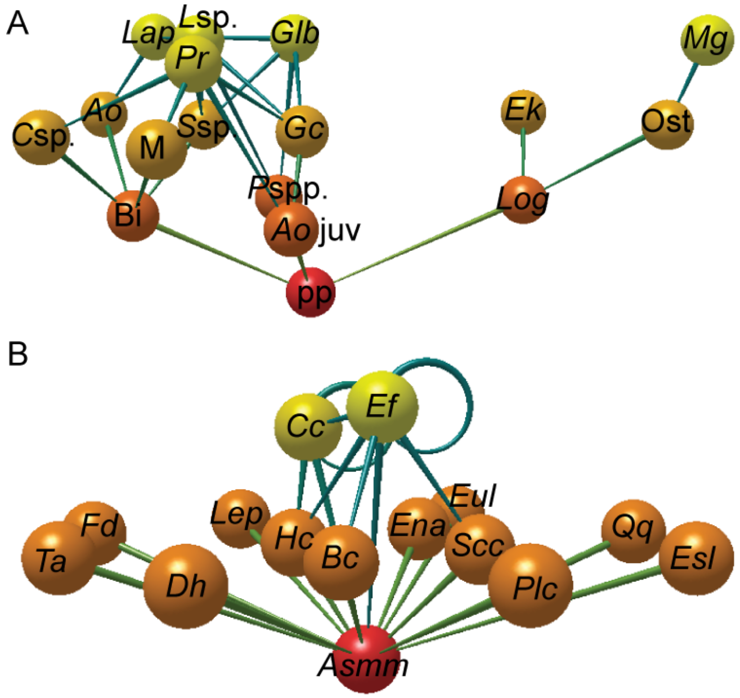

Figure 45: Three-dimensional trophic network representation of the Lode and Escuminac assemblages. A – Representation of the inferred model of the Lode assemblage based on Upeniece (2011). showing *Panderichthys rhombolepis* (*Pr*), *Latvius sp.* (*Lsp*), *Glyptolepis baltica* (*Glb*), *Laccognathuspanderi* (*Lap*),*Miguashaia grossi* (*Mg*), *Strunius sp.* (*Ssp*), *Asterolepis ornata* (*Ao*), *Cheirolepis sp.* (*Csp*), *Merostomata* (*M*), *Grossipterus crassus* (*Gc*), *Eusthenopteron kurshi* (*Ek*), *Osteolepididae indet.* (*Ost*), benthic invertebrates (Bi), *Asterolepis ornata* juvenile (Ao juv),*Psammolepis spp.* (*Pspp*), *Lodeacanthus gaujicus* (*Log*), primary producers (pp). B – Representation of the observed model for the Escuminac assemblage based on data presented in this paper showing *Eusthenopteron foordi* (*Ef*), *Cheirolepis canadensis* (*Cc*), *Levesquaspis patteni* (*Lep*), *Fleurantia denticulata* (Fd), *Triazeugacanthus affinis* (*Ta*), *Bothriolepis canadensis* (*Bc*), *Endeiolepisaneri* (*Ena*), *Euphanerops longaevus* (*Eul*), *Homalacanthusconcinnus*(*Hc*), *Diplacanthus horridus* (*Dh*), *Plourdosteus canadensis* (*Plc*), *Escuminaspis laticeps* (*Esl*),*Quebecius quebecensis* (*Qq*), *Scaumenacia curta* (*Scc*), *Asmusia membranacea* (*Asmm*). Colours represent trophic levels : red, primary consumers/producers ; orange, secondary consumers ; yellow, predators. Loopings are for cannibalistic species.

DISCUSSION

The trophic interactions of the Miguasha Fossil-Fish-Lagerstätte corresponds to one of the oldest vertebrate trophic assemblage showing three trophic level interactions, two cannibalistic species and predation among juveniles. Furthermore, similar food web structures are observed in the two Middle-Late Devonian assemblages (Escuminac and Lode).

Trophic interactions within the Escuminac assemblage

The Escuminac Formation is characterized by the exceptional preservation of a large component of its fauna (Cloutier, 2010). Skeleton transportation was limited or absent (Cloutier, 2010). Thus, we consider the Escuminac taphonomic assemblage as a biological community (Lebedev, 1992), meaning that species found in association came from the same habitats. Furthermore, digestive contents are considered as direct evidence of what the fish were eating at the time of death (Boucot, 1990; Maisey, 1994) and thus corresponding to frozen behaviour (Maisey, 1994). Digestive content analysis allowed us to even highlight three-trophic-level chain. This kind of evidence is rare given the required preservation quality

Although numerous Escuminac specimens were found with identifiable digestive contents, the proportion of predators with recognizable digestive contents remains relatively low compared to the number of specimens with solely amorphous organic matter or devoid of digestive contents. Numerous stomach content analyses of various top predator freshwater and marine fishes show a fairly high proportion of fish with empty stomach [*Esox lucius* : 222 empty out of 409 (54% ; (Alp et al., 2008) ; *Albula vulpes* : 67 empty out of 385 (17% ; (Crabtree et al., 1999) ; *Thunnus maccoyii* : 453 empty out of 1997 (23% ; (Itoh and Sakai, 2016)]. In living species, the proportion of predators with empty stomach could vary as a result of numerous causes such as prey availability, seasonal feeding behaviour, ontogenetic diet shift, fasting during spawning and/or migration and health condition. In addition to these potential causes, the preservation of stomach content in fossil fish could be subjected to different taphonomic conditions such as fermentation from the gut flora or reduced pH of the gut. The amorphous organic matter observed in numerous specimens might either correspond to the infilling of the digestive tract or the soft tissues of the digestive organs themselves. However, preliminary analyses of the amorphous organic matter under scanning electronic microscopy did not provide evidence for the presence of phytoplankton, zooplankton, nor decayed carcases of fishes (R.C., pers. observ.). Particular texture at the surface of the amorphous organic matter of one specimen of $E\ foordi$ (MHNM 06-905) suggests soft tissues preservation (Davidson and Trewin, 2005) and potentially muscles (R.C., pers. observ.).

Several variables, as total length, could be used to qualify trophic level (Wainwright and Richard, 1995; Labropoulou and Eleftheriou, 1997). Ratio between mouth opening length and head length as an approximation (Clifton and Motta, 1998; Upeniece, 2011) has not been used, given degree protrusion occurs with teleost taxa ; so this trait missed in basal gnathostomes (Schaeffer and Rosen, 1961; Alexander, 1967; Motta, 1984; Westneat, 2004). In the Escuminac assemblage, the general scheme of the linear relationship between predator and prey total length shows a triangular structure : prey eTL range and prey eTL mean increase with predator eTL, which is typical of the relationships observed in extant aquatic food webs (Cohen et al., 1993; Scharf et al., 2000).

The bottom part of the Escuminac trophic network is poorly understood owing to the rarity of invertebrates (with the exception of *Asmusia membranacea*) and micro-organisms. Algae are assumed to be aquatic primary producers of the Escuminac assemblage (Cloutier, R 2013). Escuminac aquatic primary consumers are polychaetes, eurypterids (*i.e.*, parastylonulid, *Pterygotus*) and some ichnogenus (*e.g.*, *Planolites*, *Gyrophyllites*) (Jeram, 1996; Maples, 1996). The Escuminac trophic assemblage is particular because it is based on only one aquatic invertebrate species, *A. membranacea*, found throughout the formation (Cloutier et al., 2011). In aquatic ecosystems, benthic invertebrates are responsible of the transformation of organic detritus in dissolved nutrients, using by primary producers (Covich et al., 1999). Since *A. membranacea* has been recorded in all species with identifiable digestive contents, it shows a prevailing role in the ecosystem because the energy of all higher level species runs through it. *A. membranacea* possibly had a bottom-up control on the ecosystem ; however, the prevalence of this species was due either to the true absence of other primary consumers or to a poor fossilization of other invertebrate primary consumers. Recent conchostracans (genus *Cyzicus*) are not constrained to particular habitat ; they are found in benthos as in plankton (Popovic and Gottstein-Matocec, 2006). By analogy with living conchostracans, Escuminac species found with *A. membranacea* are not attributable to a strict habitat.

E. foordi was piscivorous early during ontogeny and remained piscivorous throughout life. *E. foordi* foraged on six different species : *A. membranacea*, *H. concinnus*, *S. curta*, *C. canadensis*, *B. canadensis* and *E. foordi*. The generality and the lack of predator of *E. foordi* allow us to consider this species as a top-predator, having a top-down control on the ecosystem. The prevalence of *E. foordi* and *A. membranacea* shows that the mechanisms of top-down and bottom-up controls were already present in Devonian ecosystems, as observed in the majority of recent aquatic ecosystems (McQueen et al., 1989; Menge, 2000; Arreguin-Sanchez, 2011).

Interpretative palaeoecological synthesis

Estuaries are characterized by fluctuating physico-chemical conditions. Species living in them have to bear a wide range of environmental tolerances, in terms of salinity, turbidity, oxygen concentration and temperature variations (Able and Fahay, 2010; Schultze, 2013). The estuarine ecosystem has long been recognized as an important reproductive and feeding area, especially for fishes, because of its high productivity controlled by fluctuating abiotic (*e.g.*, temperature, turbidity, salinity) and biotic (*e.g.*, prey availability, intra- and interspecific competition) ecological factors (Costanza et al., 1997; Peterson, 2003; Nicolas et al., 2010). An interpretative palaeoecological synthesis is proposed based on trophic level comparison and predation models.

Ecomorphology corresponds to the correlation between morphology and life mode, especially trophic behaviour (Elliott et al., 2002). High trophic levels (*i.e.*, top predators and prey) are limited by energetic constraints, whereas low trophic levels (*i.e.*, primary and secondary consumers) are limited by morphological constraints as mouth opening capacity (Romanuk et al., 2011). Top predators are characterized by an adult piscivory, whereas young/juveniles forage on invertebrate species (Elliott et al., 2002). In extant food webs, intermediate levels are qualified by high fractions. In the Escuminac food web, intermediate levels show high taxonomic richness.

Morpho-anatomical similarities between extant species and extinct species can be interpreted by ecological issues. The position of the median fins is highly correlated with the trophic level (Elliott et al., 2002). Median fins grouped in the most posterior part of the body are characteristic of ”lurk” predation model. For example, the Middle Devonian porolepiform *Glyptolepis sp.* found in Achanarras Fish Bed (Caithness, Scotland) has been compared to the living Esox (Trewin, 1985). Gut content of *Glyptolepis leptopterus* also show that prey were swallowed head first (Ahlberg, 1992). This predation mode had already been suggested for Eusthenopteron by (Arsenault, 1982) and further corroborated by our observations. In our study, actinopterygians, dipnoiforms, porolepiforms and osteolepiforms from Lode and Escuminac Formations showed the highly similar pattern of median fin repartition. Furthermore, in the digestive contents of $E. foordi$ and *C. canadensis*, all prey have been swallowed head first. This predation mode is also described as a typical predation mode for extant piscivorous fishes (Elliott et al., 2002). However, in the studies of extant ecosystems, predators have to surpass a body size threshold before becoming piscivorous (Able and Fahay, 2010).

Intercohort cannibalism (*i.e.*, adults foraging on larvae or juveniles) and intracohort cannibalism (*i.e.*, prey and predator having similar size) is frequent in extant food webs (Elliott et al., 2002). Cannibalism results from abnormal foraging behaviour or abnormal stress response. Cannibalism is justified and viable in a community because it provides several advantages in terms of population dynamics. Cannibalism could be ecologically interpreted as taking part of ecosystem stability by (1) a reduction of organism density in specific cohort (*e.g.*, consumption of larvae and juveniles) (Smith and Reay, 1991), (2) a result of intraspecific competition for resources when populations are characterized by high densities and/or juveniles with limited resources access. *E. foordi* is an ubiquitous species of the Escuminac assemblage (Cloutier et al., 2011) ; this species occurred probably at high density, and in all water column levels because of its benthophageous (*B. canadensis*) or pelagic (*C. canadensis* and *H. concinnus*) prey.

Generalized Devonian estuary conditions

The Escuminac and Lode ecosystems have already been subjected to faunal comparisons owing to their similarities in terms of palaeogeography (Schultze and Cloutier, 1996) and palaeoenvironment (Upeniece, 2011). In our study, food web comparison shows also similar structures. Differences between these two assemblages and their trophic structure are due to minor differences in terms of taxonomical groups.

In contrast to the Escuminac ecosystem, the ectoparasite *Monogenea* has been identified on two Lode fish species (*i.e.*, *Asterolepis ornata* and *Lodeacanthus gaujicus*) (Upeniece, 2011). This case is excluded from the trophic reconstruction because of the non-predation character of parasitism. Digestive contents of Palaeozoic agnathans are poorly known. Janvier (1996) summarized that the digestive contents of agnathans contained large amount of amorphous sediments, suggesting that these organisms were microphageous and suspensivorous. However, in the Escuminac Formation, anaspids and osteostracans ingested *A. membranacea*. With gnathostomes, *e.g.*, placoderms, acanthodians, osteichthyans, large prey started to be find (Janvier, 1996). In the Lode assemblage, the aquatic invertebrate fauna is more diversified (platyhelminthes, eurypterids, conchostracans and Mysidacae) than in the Escuminac assemblage (*A. membranacea* is the only representative of basal level).

Duration of the Escuminac Formation is estimated between 59,500 years (based on sediment time recording) and 2.5 million years (based on conodont and spore biozonation estimations) (Cloutier et al. 2011). Five or six transgression and regression phases are recorded throughout the stratigraphic sequence (Cloutier et al., 2011). These different phases show specific assemblages, which are characteristics of changing environment (*i.e.*, intertidal environment is wider during transgression phases than in regression phases) (Cloutier et al., 2011). Considering these variations in order to infer trophic network and interspecies relationships throughout the formation, three ubiquitous taxa have been highlighted (Cloutier et al., 2011) : *E. foordi*, *S. curta* and *B. canadensis*. These three species occurrences throughout the formation can be explained considering coordinate and evolutionary stasis (Brett, 1996; Ivany et al., 2009). This long duration stasis is only possible if links between species are strong and explained by ecological stability and complexity. According to DiMichele et al. (2004), ecological persistence can be explained by four hypotheses : (1) complex interspecies relationships (*e.g.*, predation), (2) significant overlap of species environmental tolerances, (3) geographic isolation, (4) the "law of large numbers" - the most abundant remain most abundant because they tend to produce more offspring than the less abundant species - . Considering that environmental preferences, at least for one ubiquitous species (*B. canadensis*), are restricted, because it is a benthophageous species (Cloutier et al., 2011), and that species abundance is difficult to define in fossil record, then no hypothesis are merely applicable. *S. curta*, ubiquitous species, appeared not to be benthophageous (deduction by its ecomorphological character) (Figs 43, 44). Moreover, this species occurred throughout the formation, and interacted with several species so it contributed to assemblage stability. Finally, long term stasis owing advanced interspecies relationships could be an explanation to ecological persistence of this assemblage.

The environmental conditions of other Devonian ecosystems showed generalized transitions from freshwater fauna to saltwater fauna between Lower and Upper Devonian (Schultze and Cloutier, 1996; Schultze, 2013). Studying Middle and Upper Devonian of England and Wales (Mill Rocks), Dineley (1999b) also showed this transition from freshwater to saltwater. Furthermore, the Late Devonian Khovanian assemblage (Tula, Russia), described by Lebedev

(1992), encompasses taxonomical groups presents in Lode and Escuminac Formations (*i.e.*, placoderms, dipnoiforms and other sarcopterygians), as a similar palaeoenvironment (*i.e.*, estuarian). Lebedev (1992) made a comparison between the Khovanian and the Devonian *Remigolepis – group* (East Greenland) assemblages which shows no significant differences. This is an evidence for a globalization of estuarine conditions throughout Upper Devonian. Similar taxonomic compositions show similar trophic structures in response to similar environments.

Transition from agnathans to gnathostomes in Devonian assemblages (Anderson et al., 2011) takes part to the diversification of anatomical forms in several taxa. Faunal diversification allowed the emergence of complex food webs (*i.e.*, multiplication of interactions between species and diversification of trophic categories) and then the stability and persistence of species-rich past communities.

Conclusion

Global scheme is established for the food webs of Middle-Upper Devonian estuarine ecosystems, using trophic relationships in two vertebrate assemblages (*i.e.*, Lode and Escuminac) in terms of trophic position and role of taxa. Global scheme is showed between these two assemblages in terms of taxonomic richness, phylogenetic diversity and palaeogeography. The persistence of prey-predator relationships has been observed in the Escuminac assemblage, during several thousand or millions years [depending on approximations used (Cloutier et al., 2011)]. This faunal stability is characteristic to Upper Devonian fauna (Sallan and Coates, 2011). Frasnian/ Fammenian crisis (approx. 375 million years old), punctuated by the Kellwasser event, does not seem to have affected vertebrate fauna (Sallan and Coates, 2011) ; whereas, Devonian/Carboniferous transition, punctuated by the Hangenberg event (approx. 359 million years old), is accountable to faunal turnover, where extant groups of vertebrates (*e.g.*, chondrichthyans, actinopterygians, tetrapods) surpassed early groups of vertebrates (*e.g.*, placoderms, acanthodians, basal sarcopterygians). The Escuminac biota demonstrates that stable assemblages, characterized by diverse trophic relationships among taxa, were already established in the early Upper Devonian ; and shows structural organization in early vertebrate evolutionary history.

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