Écologie, diversité et évolution des moustiques (Diptera Culicidae) de Guyane française : implications dans l'invasion biologique du moustique Aedes aegypti (L.)

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Ecologie, diversité et évolution des moustiques (Diptera: Culicidae) de Guyane française : implications dans l'invasion biologique du moustique *Aedes aegypti* (L.)

Sous la direction d'Alain DEJEAN et de Jean-François CARRIAS

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Ma thématique de recherche s'inscrit dans l'amélioration des connaissances sur la biodiversité en Amazonie et de son rôle dans le phénomène d'invasion biologique, l'un des enjeux majeur de ce XXI^{ème} siècle.

RÉSUMÉ

L'Humanité est en train de transformer les paysages de la Terre à une échelle et à des taux encore inégalés. Les invasions biologiques sont l'une des conséquences de ces perturbations anthropiques et engagent souvent des enjeux socio-économiques importants. Ces invasions peuvent également modifier la structure et le fonctionnement des écosystèmes investis, conduisant parfois à des bouleversements écologiques.

Le moustique *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) a été introduit dans les Amériques depuis le continent africain il y a environ 400 ans. Actuellement, cette espèce est la principale responsable des épidémies de dengue et de chikungunya dans la zone pantropicale et sa large répartition a très probablement joué un rôle important dans l'expansion récente du virus *Zika*. La biologie d'*Ae.* (*Stg.*) *aegypti* est particulièrement bien connue, ce qui n'est pas le cas de son écologie, en particulier de ses interactions avec les communautés résidentes. En adoptant une démarche pluridisciplinaire je me suis intéressé à la contribution relative des facteurs biotiques et abiotiques ainsi que de certains processus évolutifs dans la distribution de cette espèce à différentes échelles en Guyane française.

Dans un premier temps j'ai participé à la révision des connaissances fondamentales sur la diversité des moustiques de Guyane. En alliant la taxonomie classique et moléculaire, cette étape a permis de découvrir plusieurs nouvelles espèces et de mettre en place des outils adaptés à la gestion de ce type de données, notamment pour une utilisation future.

Dans un second temps la structuration spatio-temporelle des communautés résidentes de macro-invertébrés aquatiques a été étudiée en milieu urbain. Cela a permis de mettre en évidence l'existence d'interactions antagonistes et mutualistes avec les taxons des communautés résidentes. En particulier, le moustique autochtone *Limatus durhamii* Theobald 1901 semble empêcher l'établissement durable d'*Ae.* (*Stg.*) *aegypti* dans les milieux faiblement urbanisés *via* un mécanisme d'exclusion compétitive.

Cependant, il apparaît que les interactions avec les communautés résidentes demeurent relativement limitées dans l'espace et dans le temps. À travers l'étude de la spécialisation d'hôtes chez les moustiques associés aux phytotelmes, cette étude suggère que l'histoire évolutive des espèces autochtones pourrait fortement influencer la diversité et la composition des communautés urbaines actuellement en place.

Mots-clés : Amazonie, Biodiversité, Broméliacée à réservoirs, Culicidae, Invasion biologique, Interaction trophique, Moustiques, Phytotelmes, Spécialisation, Urbanisation, Vecteur.

ABSTRACT

Ecology, diversity and evolution of Guianese mosquitoes (Diptera: Culicidae): implications for *Aedes aegypti* (L.) invasiveness

Mankind is transforming the landscapes of the Earth at an unprecedented scale and rate. Biological invasions are one of the consequences of these anthropogenic disturbances and often lead to significant socio-economic challenges. These invasions can also modify the structure and functioning of the invaded ecosystems, sometimes leading to disruptions of ecological processes.

The mosquito species *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) was introduced into the Americas some 400 years ago from the African continent. Currently, this species is the primary agent behind dengue and chikungunya outbreaks in the pan-tropical area and its widespread distribution has likely played an important role in the recent expansion of the *Zika* virus. The biology of *Ae.* (*Stg.*) *aegypti* is particularly well known, which is not the case for its ecology. By adopting a cross-disciplinary approach I attempted to understand the relative contribution of biotic and abiotic factors as well as some evolutionary processes in the distribution of this species at the local and regional scales in French Guiana.

Initially, I was interested in revising the core knowledge concerning the diversity of mosquitoes in French Guiana. By combining traditional and molecular taxonomy, this step allowed my colleagues and I to discover several new species and to create the appropriate tools to manage this type of entomological data.

Secondly, we studied the spatio-temporal structure of resident aquatic macroinvertebrate communities in urban areas. This highlighted the existence of antagonistic and mutualistic interactions. In particular, the native mosquito *Limatus durhamii* Theobald 1901 appears to prevent the sustainable establishment of *Ae.* (*Stg.*) *aegypti* in slightly urbanized environments *via* a mechanism of competitive exclusion.

However, contrary to our expectations, interactions with resident communities remain relatively limited in space and time. By studying the specialization of phytotelm-breeding mosquitoes at regional scale, I conclude that the evolutionary history of native species might strongly influence the diversity and composition of the urban communities that we are currently observing at local scale.

Keywords: Amazonia, Biodiversity, Biological Invasion, Culicidae, Mosquitoes, Phytotelmata, Specialization, Tank bromeliad, Trophic Interaction, Urbanization, Vector.

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I Les invasions biologiques

I.1 Généralités

Les invasions biologiques sont apparues comme un problème majeur au cours du XX^{ème} siècle. De nos jours, ce phénomène est plus que jamais d'actualité et engage souvent des enjeux socio-économiques importants (**Lockwood *et al.* 2013**). Le coût économique au titre de la gestion et des dommages liés aux invasions biologiques s'élèverait à 120 milliards de dollars par an aux Etats Unis et 12,5 milliards d'euros par an pour l'Europe (**Pimentel *et al.* 2005; Kettunen *et al.* 2009**). En plus des impacts économiques, certaines espèces invasives peuvent également causer des bouleversements environnementaux en modifiant la structure et le fonctionnement des écosystèmes investis (**Parker *et al.* 1999**). Certains auteurs vont même jusqu'à considérer les invasions biologiques comme le second facteur responsable de l'érosion de la biodiversité après la destruction des habitats (**Dudgeon *et al.* 2006**).

Les espèces introduites par l'Homme qui s'établissent et s'étendent en dehors de leur région biogéographique d'origine sont définies comme invasives (**Richardson *et al.* 2000**). Le processus d'invasion biologique peut être conceptualisé comme une succession de trois phases : l'introduction, la naturalisation et l'invasion, chacune d'elles constituant une barrière que doit franchir l'espèce pour accéder à la phase suivante (**Richardson *et al.* 2000**). On parlera d'espèces introduites pour les espèces "bloquées" à la première phase et d'espèce naturalisées pour celles "bloquées" à la seconde. Le processus d'invasion biologique est achevé lorsque les trois phases ont été réalisées et on parlera alors d'espèces invasives (**Lockwood *et al.* 2013**). Certains auteurs intègrent également l'impact sur l'écosystème receveur comme une condition nécessaire au concept d'invasion biologique (**Simberloff *et al.* 2013**). En raison des difficultés pour définir les impacts environnementaux et/ou économiques liés aux invasions biologiques et du caractère subjectif de l'impact, cette notion n'apparaitra pas dans notre conception du phénomène d'invasion biologique (**Richardson *et al.* 2000**).

L'étude de la phase d'invasion est particulièrement intéressante car elle représente en quelque sorte un microcosme de l'ensemble des phases se succédant lors du phénomène d'invasion biologique (**Lockwood *et al.* 2013**). La dispersion autogène de l'espèce et son établissement dans un nouvel écosystème peuvent être assimilés à la phase d'introduction puis de naturalisation à une échelle plus réduite. Adopter cette approche présente l'avantage de pouvoir étudier le phénomène d'invasion biologique expérimentalement et d'établir les

critères permettant la dispersion (i.e. l'introduction) et l'établissement (i.e. la naturalisation) de l'espèce dans ce nouvel écosystème. Autrement dit, l'étude de la phase d'invasion peut permettre de mieux comprendre les différents mécanismes en action derrière le phénomène d'invasion biologique dans son ensemble.

Au cours de cette thèse nous nous sommes intéressés à l'invasion biologique du moustique *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) qui est l'une des espèces invasives présentant la plus vaste aire de répartition au monde (**Kraemer *et al.* 2015**). En outre, cette espèce présente une grande importance en santé publique car elle est considérée comme étant la principale responsable des épidémies de dengue et de chikungunya à travers le monde (**Brown *et al.* 2011**). Elle serait également l'un des principaux vecteurs urbains du virus *Zika* avec *Culex* (*Culex*) *quinquefasciatus* Say 1823 (**Chouin-Carneiro *et al.* 2016**).

I.2 Le phénomène d'invasion biologique

L'introduction d'une espèce en dehors de son aire de répartition biogéographique d'origine peut se faire de manière autogène par la dispersion active d'individus, ou bien par la dispersion passive de propagules *via* des mécanismes comme l'anémochorie, la zoochorie ou l'hydrochorie (**Lockwood *et al.* 2013**). Même si elles existent, ces introductions restent rares et surtout sans commune mesure avec celles orchestrées par l'Homme de manière volontaire ou non. Les introductions volontaires d'espèces ont lieu le plus souvent à des fins alimentaires, récréatives ou encore pour servir d'agents de lutte biologique (**Shea & Chesson 2002**). Les introductions involontaires sont quant à elles généralement liées à des espèces présentant une affinité particulière pour l'Homme telles que les espèces domestiques et synanthropiques, ce qui a facilité leur transport.

Une fois introduite, l'espèce doit faire preuve de plasticité écologique pour s'adapter aux nouvelles conditions environnementales et s'établir en réussissant à se reproduire dans ce nouvel écosystème (**Richardson *et al.* 2000**). À cette étape, les organismes présentant plusieurs modes de reproduction sont favorisés. C'est le cas de certaines plantes capables d'assurer à la fois une multiplication végétative et une reproduction sexuée (**Barrett *et al.* 2008**) ou de certains insectes sociaux capables de créer de nouvelles fondations par essaimage ou bien par sous-clonage (**Fournier *et al.* 2005**). Enfin, la dispersion autogène ou exogène de l'espèce en dehors de la zone de naturalisation signera le début de la phase d'invasion. Certains auteurs distinguent deux niveaux d'invasion, le premier où la distribution est limitée aux milieux les plus perturbés et le second où la distribution s'étend jusqu'aux milieux les moins perturbés (**Richardson *et al.* 2000**).

Toutes les espèces introduites ne deviennent pas invasives et un grand nombre d'hypothèses ont été développées pour tenter d'expliquer les raisons de leur "succès" (ou de leur "échec") (**Richardson & Pyšek 2006**). La plupart d'entre elles se rejoignent sur le fait que le succès d'une invasion biologique repose à la fois sur les caractéristiques de l'espèce introduite et sur la réceptivité de l'écosystème receveur (**Catford *et al.* 2009**). Les caractéristiques des espèces invasives ont été pendant longtemps au centre des investigations, cependant l'absence de caractéristiques communes à ces différentes espèces a poussé les chercheurs à considérer plus en détail la réceptivité de l'écosystème receveur (**Goodwin *et al.* 1999**).

I.3 Résistance biotique des écosystèmes à l'invasion

L'introduction d'une espèce en dehors de son aire de répartition biogéographique d'origine va inévitablement conduire à des interactions biotiques avec les espèces des communautés résidentes (**Lockwood *et al.* 2013**). Nous préférerons le terme de communautés résidentes à celui de communautés autochtones en raison des difficultés à identifier l'origine biogéographique de certaines espèces. L'utilisation de cette terminologie implique donc que ces communautés résidentes sont composées d'un mélange d'espèces autochtones et allochtones. Il existe peu d'indices laissant penser que les interactions biologiques puissent réellement empêcher la naturalisation d'une espèce introduite, toutefois elles joueraient un rôle primordial pendant la phase d'invasion (**Levine *et al.* 2004**). La résistance biotique peut être définie comme la capacité de l'écosystème à faire face à l'invasion d'une espèce allochtone. Elle est principalement fonction de la diversité et de l'abondance d'organismes antagonistes tels que des prédateurs, des compétiteurs et des parasites (**Levine *et al.* 2004**). Afin d'évaluer la résistance biotique d'un écosystème il est primordial de comprendre les mécanismes responsables de la composition et de la structuration de ces communautés résidentes.

L'un des paradigmes les plus persistants dans le domaine de la biologie de l'invasion est celui d'une relation négative existant entre la diversité des communautés résidentes et l'invasibilité de l'espèce introduite (**Levine & D'Antonio 1999**). Initialement, cette hypothèse a été proposée par **Elton** (**1958**) dans son livre fondateur *The ecology of invasions by animals and plants*. Elle prédit que les communautés les plus saturées en espèces seront les moins susceptibles d'être investies en raison d'un nombre plus limité de niches écologiques laissées vacantes. Cette hypothèse a été vérifiée à plusieurs reprises, notamment dans les

écosystèmes insulaires ou fortement perturbés (**Tilman 1997; Naeem *et al.* 2000**). Néanmoins, des études ont mis en évidence que dans certains cas les communautés les plus riches en espèces (les plus saturées) sont également les communautés comptant le plus grand nombre d'espèces introduites (**Planty-Tabacchi *et al.* 1996; Levine 2000**). L'hypothèse d'Elton s'intègre dans la théorie de la niche écologique d'Hutchinson, qui stipule que chaque espèce possède une niche fondamentale définie comme un hyper-volume où chaque dimension de l'espace représente une ressource ou une condition de l'environnement. Pour une espèce donnée, nous pouvons postuler que la communauté résidente sera d'autant moins susceptible d'être investie qu'elle possède une ou des espèces ayant une niche fondamentale proche de l'espèce introduite.

Certains résultats, en apparence contradictoires avec la théorie d'Elton, ont fait émerger l'hypothèse de la "niche vide" (**Hierro *et al.* 2005**), qui suppose que, du fait de la faible saturation en individus, les espèces résidentes ne réaliseraient qu'une partie de leur niche fondamentale. Cette hypothèse minimise en quelque sorte l'importance des interactions biologiques dans le phénomène d'invasion, aussi bien pour les espèces introduites que résidentes. Selon cette hypothèse, les espèces introduites n'occuperaient que les niches laissées vacantes par les espèces résidentes (**Shea & Chesson 2002**). La libération de ces niches dans l'espace et/ou le temps est souvent assimilée à des opportunités que certaines espèces introduites seraient capables de saisir en raison de leurs caractéristiques propres (**Johnstone 1986; Holle & Simberloff 2005**). Cette hypothèse implique que l'espèce introduite possède des avantages d'adaptation face aux espèces résidentes pour exploiter ces opportunités.

La dernière hypothèse que l'on peut évoquer a été émise par des paléobiologistes et s'inscrit dans la conception selon laquelle le processus de coévolution aurait créé des communautés coadaptées hautement sophistiquées (**Vermeij 1991**). Cette hypothèse prédit que plus le degré de coadaptation est élevé au sein d'une communauté receveuse, moins cette communauté sera susceptible d'être investie par une espèce introduite (**McKinney 1997**). Le niveau de coadaptation et de coévolution entre espèces au sein d'une communauté est difficile à appréhender et à quantifier. C'est surement pour cette raison qu'à notre connaissance aucune étude n'a tenté de tester cette hypothèse.

I.4 Anthropisation et invasions biologiques

L'Anthropocène est marquée par de profonds remaniements des écosystèmes à l'échelle globale (**Steffen *et al.* 2007**). Le terme d'anthropisation désigne l'ensemble des transformations d'origine humaine et peut revêtir des formes très diverses comme la déforestation, l'agriculture ou l'urbanisation (**McKinney 2002**). Les organismes autochtones sont souvent les premières victimes de ces perturbations, ce qui se traduit le plus souvent par une réduction de la richesse spécifique de ces organismes dans les communautés (**McKinney 2008**). De manière concomitante, les milieux anthropisés sont également susceptibles d'accumuler un plus grand nombre d'événements d'introduction, augmentant ainsi la probabilité de naturalisation et d'invasion (**Talaga *et al.* 2015a**).

Le long d'un gradient environnemental de type naturel-urbain, la capacité à s'adapter des espèces varie selon leur identité. Trois catégories distinctes ont été proposées pour classer les espèces en fonction de leur capacité d'adaptation aux conditions urbaines (**Blair 2001**). Les premières sont qualifiées d'*urban avoiders*, se sont les espèces les plus vulnérables aux perturbations anthropiques que l'on ne retrouvera pas en milieu urbain. Les secondes sont qualifiées d'*urban adapters* et sont constituées d'espèces autochtones et/ou introduites capables de s'adapter à des degrés divers à l'environnement urbain et périurbain. Les troisièmes sont qualifiées d'*urban exploiters* ; composées presque exclusivement d'espèces introduites pré-adaptées à l'environnement urbain et souvent incapables d'en sortir. On parlera d'anachronisme évolutif lorsque les espèces autochtones n'ont pas les capacités de répondre aux perturbations anthropiques et se retrouvent alors mal adaptées au nouvel environnement de l'écosystème dont elles sont pourtant issues (**Robertson & Hutto 2006**).

En prenant comme modèle d'étude l'invasion biologique d'*Ae.* (*Stg.*) *aegypti* en Guyane française, nous avons étudié les effets croisés de l'anthropisation et des interactions biologiques avec les communautés résidentes et plus spécifiquement avec les moustiques autochtones pour tenter de mieux comprendre la distribution actuelle et future de cette espèce invasive.

II Modèles d'étude

II.1 Les moustiques

Généralités

Les moustiques (Diptera : Culicidae) sont des insectes holométaboles comptant 3 549 espèces décrites et distribuées au sein de deux sous-familles, les Anophelinae et les Culicinae

(**Harbach 2015**). Ils font partie de la super famille des Culicoidea incluant également les Corethrellidae, les Dixidae et les Chaoboridae, ces derniers étant considérés comme la lignée ancestrale sœur des Culicidae (**Sæther 2000**). Le plus vieux fossile de moustique connu a été découvert dans de l'ambre birmane datée du Crétacé moyen, il y a environ 95 millions d'années (**Borkent & Grimaldi 2004**). Certains auteurs estiment néanmoins que leur présence sur Terre remonterait à une période plus reculée du Mésozoïque (**Edwards 1923**).

À la fin du XIX^{ème} siècle, les travaux de Patrick Manson en Asie sur la filaire de Bancroft mettent en évidence pour la première fois le rôle de vecteur des moustiques dans un cycle parasitaire (**Chemin 1983**). Sur les conseils de Manson, Ronald Ross mettra en évidence pour la première fois en 1897 ce même rôle pour certains moustiques du genre *Anopheles* dans la transmission du paludisme (**Ross 1899**). Dans la même période à Cuba, Carlos Juan **Finlay** (**1882**) émettra l'hypothèse du rôle vecteur des moustiques dans la transmission du virus de la fièvre jaune. Enfin, **Walter Reed** et ses collaborateurs (**1900**) démontreront le rôle d'*Ae.* (*Stg.*) *aegypti* dans la transmission de ce virus. Dès lors, la capacité de certains moustiques à transmettre des pathogènes chez l'Homme leur a valu une attention toute particulière portée sur tous les aspects de leur biologie, écologie et taxonomie (**Clements 1992**, **1999**, **2011**). À l'heure actuelle, les moustiques sont considérés comme la famille d'arthropodes la plus importante du point de vue de la santé humaine (**Budiansky 2002**).

Le cycle de vie

Les moustiques possèdent un cycle de vie complexe impliquant un basculement ontogénique entre une phase immature aquatique et une phase adulte terrestre (**Wilbur 1980**). Au cours de leur vie ils sont successivement soumis aux contraintes de deux compartiments (aquatique puis terrestre) emboités et interdépendants au sein d'un système complexe.

La phase aquatique est dédiée à la croissance et c'est au cours de cette période que le moustique constituera l'essentiel de sa biomasse (**Clements 1992**). Les modes d'acquisition de la nourriture durant cette phase sont donc particulièrement importants. Typiquement, les larves de moustique s'alimentent en filtrant les particules organiques fines et autres microorganismes (bactéries, protistes, micro-métazoaires) présents dans son milieu. Certaines espèces ont toutefois acquis des modes de nutrition alternatifs ou complémentaires, et on trouve des espèces dont les larves sont racleuses, broyeuses et/ou prédatrices. Si les conditions du milieu sont favorables, la larve passera alors successivement par quatre stades larvaires

distincts, chacun précédé par une mue. Au dernier stade larvaire, l'individu finira par se nymphoser et après quelques jours réalisera sa mue imaginale laissant émerger un moustique adulte.

La phase terrestre est dédiée à la reproduction et à la dispersion (**Clements 1992**). Les moustiques sont représentés par des individus des deux sexes et, chez la plupart des espèces, l'ovogénèse est rendue possible par la prise d'un repas de sang obtenu par la piqûre d'un hôte vertébré. C'est lors de ces repas que la passerelle est faite entre l'hôte vertébré et le moustique, ouvrant la voie à la transmission de pathogènes viraux (e.g. chikungunya, dengue, West Nil), sporozoaires (e.g. différents paludismes), nématozoaires (e.g. filariose de Bancroft), ou encore bactériens (e.g. Rickettsies). Par la suite, les femelles déposeront leurs œufs en groupe ou individuellement dans ou à proximité d'un point d'eau. Une fois en contact avec l'eau les œufs viables finiront par éclore, libérant des larves de premier stade dans l'habitat aquatique.

Les conditions biotiques et abiotiques qui règnent dans le compartiment aquatique vont influencer directement le développement larvaire et indirectement le devenir des adultes en modifiant certains traits d'histoire de vie tels que la longévité, la masse et la fécondité. À leur tour, les conditions biotiques et abiotiques qui règnent dans le compartiment terrestre vont directement influencer la survie et la reproduction des adultes et indirectement la présence et l'abondance des immatures dans le compartiment aquatique.

Au cours de cette thèse, nous nous sommes essentiellement intéressés aux réponses du compartiment aquatique. Cependant, compte tenu du fait que ce compartiment est emboité dans le compartiment terrestre, nous avons considéré le plus souvent l'influence relative de chacun d'entre eux.

Les moustiques des réservoirs

Les moustiques ont réussi à coloniser tous les types de collection d'eau sur Terre, du plus grand lac, au plus petit phytotelme (**Clements 1992**). Plusieurs classifications plus ou moins fines des différents types d'habitats aquatiques ont d'ailleurs déjà été proposées (**Shannon 1931; Bates 1949; Laird 1988**). Nous suivrons ici la classification de **Shannon (1931)** et nous nous contenterons de distinguer deux grands groupes d'espèces. D'une part, celles se développant dans des habitats aquatiques formés par des dépressions du sol (e.g. lacs, mares, rivières), et d'autre part celles se développant dans des habitats aquatiques formés

par des réservoirs d'origine naturelle ou artificielle (e.g. phytotelmes, cavités rocheuses, réservoirs artificiels). Ce deuxième type d'habitat aquatique est connu sous le terme anglo-saxon de *container habitat* (**Bates 1949**). Compte tenu des préférences écologiques d'*Ae.* (*Stg.*) *aegypti* pour les réservoirs d'origine naturelle ou artificielle (**Dégallier *et al.* 1988; Chadee *et al.* 1998**), nous nous sommes naturellement intéressés aux seules espèces se développant dans ce type d'habitat aquatique (**Appendix 1**). En Guyane française, les moustiques des réservoirs sont représentés par 108 espèces, soit près de la moitié des espèces connues sur le territoire (**Appendix 2**). Il est à noter que même si elles existent, les espèces capables de passer d'un type d'habitat à l'autre sont assez rares (e.g. *Cx.* (*Cux.*) *quinquefasciatus*).

Les moustiques invasifs

Les taxons de la famille des Culicidae ont su s'adapter et coloniser l'ensemble des grands biomes terrestres (**Harbach 2015**). Paradoxalement, les espèces naturalisées et/ou invasives sont globalement assez rares. Selon **Juliano et Lounibos** (**2005**), parmi les 3 549 espèces décrites à l'échelle mondiale, les espèces invasives seraient au nombre de 9 et les espèces naturalisées au nombre de 22, soit respectivement 0,25 % et 0,62 % des espèces actuellement décrites. Une proportion significative de ces espèces partage deux caractéristiques communes : la capacité de se développer dans des environnements anthropisés et la capacité de former des œufs fortement résistants à la dessiccation (**Juliano & Lounibos 2005**). Cependant, malgré le nombre limité d'espèces invasives, la forte capacité vectorielle de certaines d'entre elles (e.g. *Ae.* (*Stg.*) *aegypti*, *Aedes* (*Stegomyia*) *albopictus* (Skuse 1894), *Anopheles* (*Cellia*) *gambiae* Giles 1902) s'est avérée particulièrement problématique pour les populations humaines (**Lounibos 2002**).

II.2 Le moustique : *Aedes* (*Stegomyia*) *aegypti*

Généralités

Aedes (*Stg.*) *aegypti* appartient à la tribu des Aedini, qui représente, avec plus de 1 200 espèces décrites, la plus riche des 11 tribus constituant les Culicinae (**Wilkerson *et al.* 2015**). Bien qu'il soit connu comme le *yellow fever mosquito*, cette appellation tend à disparaitre en raison de la mise au point d'un vaccin par l'Institut Pasteur de Dakar dès 1932. Cette espèce est par ailleurs responsable de la transmission de nombreuses maladies émergentes (**Gubler 1998**) ; elle représente donc un problème majeur pour la santé publique dans les pays et les territoires investis (**Kraemer *et al.* 2015**).

Note taxonomique

Entre 2004 et 2009, des travaux menés sur la systématique des Aedini (Diptera : Culicidae) ont entrainé de nombreux changements taxonomiques au sein de cette tribu (**Reinert *et al.* 2004, 2006, 2008, 2009**). La plupart des modifications sont passées inaperçues des non-taxonomistes, ce qui n'a pas été le cas pour les espèces d'importance médicale, comme *Ae.* (*Stg.*) *aegypti* qui répondait dès lors au nom de *Stegomyia* (*Stegomyia*) *aegypti* (**Polaszek 2006**). L'élévation de nombreux sous-genres au rang de genres n'a pas fait l'unanimité, à tel point que certaines revues comme *Journal of Medical Entomology* (**Edman 2005**), *The American Journal of Tropical Medicine and Hygiene* (**Weaver 2005**), ou encore *Vector-Borne and Zoonotic Diseases* (**Higgs 2005**) recommandèrent de conserver la nomenclature traditionnelle. Très récemment, **Wilkerson et ses collaborateurs** (**2015**) ont formellement exhorté un retour à la structure générique traditionnelle des Aedini d'avant l'année 2000, en contestant l'élévation massive des 74 sous-genres au rang de genres. Parmi les principales raisons invoquées la faible robustesse des nœuds soutenant certains clades ainsi que l'absence d'analyses basées sur des caractères moléculaires soutenant leurs résultats. À l'heure actuelle, il est évident que la taxonomie des Aedini fait encore débat. Cependant, ces préoccupations vont bien au-delà de nos objectifs et le choix de l'une ou l'autre des deux nomenclatures n'aurait qu'un impact très négligeable sur le développement de cette thèse. Néanmoins, par souci de clarté et pour faciliter la continuité avec les autres études conduites en Guyane nous avons pris le parti de suivre la classification conservatrice proposée par **Wilkerson *et al.*** (**2015**). C'est pourquoi l'espèce qui nous intéresse ici sera désignée sous la forme : *Aedes* (*Stegomyia*) *aegypti*, et abrégée *Ae.* (*Stg.*) *aegypti* conformément aux recommandations de **Reinert** (**2009**).

Les origines : "Dis-moi d'où tu viens, je te dirai qui tu es"

Les origines d'*Ae.* (*Stg.*) *aegypti* (Linnaeus 1762) sont à rechercher dans les régions d'Afrique subsaharienne. Encore aujourd'hui on trouve une sous-espèce connue sous le nom d'*Ae.* (*Stg.*) *aegypti formosus* (Walker 1848) habitant les forêts tropicales d'Afrique de l'Est. Dans cet écosystème les larves se développent dans des réservoirs naturels tels que des trous d'arbres ou des cavités rocheuses et les femelles ne piqueraient que rarement l'Homme (**Lounibos 1981**). Cette sous-espèce se retrouve également à Madagascar et sur deux îles proches : La Réunion et Europa. Une étude conduite sur des marqueurs microsatellites de

plusieurs populations à travers le monde semble supporter l'hypothèse selon laquelle *Ae.* (*Stg.*) *aegypti formosus* constituerait la lignée ancestrale à toutes les populations distribuées hors d'Afrique (**Brown *et al.* 2011**). L'apparition de la sous-espèce nominale est obscure mais est vraisemblablement le résultat d'une dispersion de populations selvatiques hors des forêts d'Afrique de l'Est en direction de l'Afrique du Nord. L'assèchement du Sahara aurait ensuite pu participer à l'isolement de ces populations, favorisant ainsi leur évolution indépendante (**Powell & Tabachnick 2013**). C'est également à ce moment-là que l'espèce a probablement été contrainte d'utiliser les réserves d'eau d'origine humaine pour la première fois, conduisant ainsi à sa domestication (**Failloux *et al.* 2002**). Les activités d'échanges internationaux ont par la suite permis l'introduction de cette sous-espèce domestique dans l'ensemble du bassin méditerranéen, en Afrique de l'Ouest et de l'Est, puis dans le reste du monde (**Brown *et al.* 2014**). À l'heure actuelle la sous-espèce nominale *Ae.* (*Stg.*) *aegypti aegypti* serait présente dans l'ensemble des pays du monde situés entre le tropique du Cancer et le tropique du Capricorne (**Fig. I.1**).

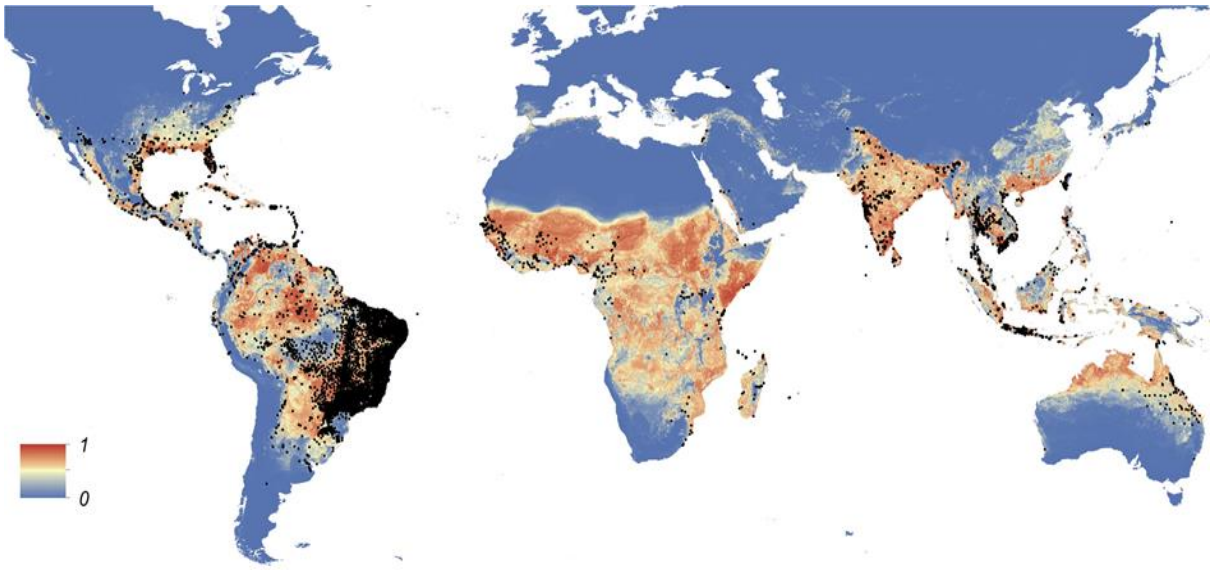

Figure I.1 Distribution actuelle d'*Aedes* (*Stegomyia*) *aegypti* dans le monde modifiée selon **Kraemer *et al.*** (**2015**). La présence avérée d'*Ae.* (*Stg.*) *aegypti* est représentée par des points noirs et la probabilité de présence est représentée par un gradient allant de 0 à 1.

Ces deux sous-espèces ont établi différentes stratégies démographiques et comportementales liées aux différentes forces de sélection auxquelles elles ont été confrontées (**Crovello & Hacker 1972**). Dans le prochain paragraphe nous exposerons quelques-unes des caractéristiques de la sous-espèce *aegypti* qui nous intéresse ici.

Caractéristiques de l'espèce

L'expansion mondiale d'*Ae.* (*Stg.*) *aegypti* n'est évidemment pas étrangère aux caractéristiques propres à l'espèce (**Christophers 1960**). Dans ce paragraphe nous passerons en revue certaines des caractéristiques susceptibles d'expliquer sa forte capacité invasive.

Aedes (*Stg.*) *aegypti* est une espèce de moustique diurne et multivoltine. Chaque femelle peut pondre autour de 300 œufs au cours de sa vie qui durera environ deux semaines dans la nature. Les œufs sont pondus au-dessus de la surface de l'eau sur un support humide et écloront lorsqu'ils seront immergés. Ces œufs ont un chorion protecteur leur permettant de résister à de longues périodes de dessiccation pouvant aller de quelques mois à un an en fonction des conditions environnementales. Cette première caractéristique majeure est partagée avec *Ae.* (*Stg.*) *aegypti formosus* et peut être considérée comme un vestige de l'adaptation à des écosystèmes présentant des périodes de sécheresse marquées. Cette caractéristique a joué un rôle primordial pour la dissémination de cette espèce à travers le monde. De plus, les adultes possèdent eux-mêmes d'excellentes dispositions pour lutter contre la sécheresse. En effet, les pics d'activité de cette espèce se situent aux heures du jour les plus fraîches et les plus humides, à savoir au lever et à la tombée du jour. Enfin, les écailles claires qui ornent le corps des adultes (**Fig. I.2c**) peuvent également être interprétées comme une adaptation visant à limiter l'échauffement.

La seconde caractéristique majeure d'*Ae.* (*Stg.*) *aegypti* est sa forte spécialisation dans les habitats aquatiques artificiels créés volontairement ou non par les activités humaines (**Christophers 1960**). De plus, sa plasticité écologique est telle que, dans certaines conditions, cette espèce peu coloniser des réservoirs naturels comme les cavités rocheuses et une grande variété de phytotelmes (**Chadee *et al.* 1998**). Ce comportement rappelle l'écologie de la forme selvatique d'Afrique et a été interprété par certains auteurs comme un retour à l'état sauvage (i.e. féralisation) de l'espèce (**Parker *et al.* 1983; Fouque & Carinci 1996**). La colonisation des habitats aquatiques naturels est particulièrement intéressante car c'est dans cette situation qu'*Ae.* (*Stg.*) *aegypti* est susceptible d'entretenir des interactions biologiques plus importantes en raison des communautés souvent associées à ce type d'habitat.

La caractéristique la plus marquante d'*Ae.* (*Stg.*) *aegypti* est sans aucun doute la préférence des femelles envers l'Homme lors de leurs repas de sang (**Harrington *et al.* 2001**). Cette caractéristique est souvent résumée sous le simple terme 'anthropophile', elle n'en est pas moins la plus délicate à mettre en évidence (**Ponlawat & Harrington 2005**). En effet, de

nombreuses observations font état de femelles se gorgeant du sang d'animaux domestiques tels que les chiens et les chats. De plus, l'inconvénient des tests de spécificité est que lorsqu'ils sont réalisés sur le terrain, l'origine des repas de sang est directement dépendante de la disponibilité en hôtes. À l'inverse, lorsqu'ils sont réalisés en laboratoire, se pose alors la question de la représentativité des souches utilisées.

III La Guyane

III.1 Démographie, géographie et climat

La Guyane est un département d'outre-mer (DOM) français situé dans la région biogéographique Néotropicale en Amérique du sud entre les latitudes de 2°5'24"N et de 5°50'60"N ; et les longitudes de 54°36'36"O et de 51°31'48"O. Avec sa superficie de 83 534 km² elle constitue le plus vaste département français et sa situation continentale fait figure d'exception parmi les DOM. Au premier janvier 2015, la population guyanaise comprenait 254 541 habitants, principalement distribués le long de la bande côtière dans les trois principales agglomérations : Cayenne, Kourou et Saint-Laurent-du-Maroni (**INSEE 2015; Fig. I.2a**). La dynamique démographique est caractérisée par un fort taux de croissance annuel moyen estimé à 2,9 % pour la période 2006-2011 (**INSEE 2015**). Cette caractéristique implique une pression immobilière croissante et une extension toujours plus importante des milieux anthropisées au détriment des milieux naturels.

D'un point de vu géologique, la Guyane fait partie d'une formation ancienne connue sous le nom de plateau des Guyanes (ou bouclier des Guyanes). Ce dernier s'étend d'Ouest en Est sur le Guyana, le Suriname et la Guyane, ainsi que sur une partie de la Colombie, du Venezuela et du Brésil. Ce socle granitique formé lors du Précambrien est l'un des plus anciens massifs encore visibles sur la planète. À l'exception de la bande côtière atlantique couverte de mangroves, de savanes marécageuses, puis de savanes plus sèches, l'ensemble du territoire guyanais est occupé par la forêt dense équatoriale (**Guitet *et al.* 2015**).

D'un point de vu climatique, la Guyane jouit d'un climat équatorial humide caractérisé par d'abondantes précipitations (en moyenne 3 000 mm par an) et des températures chaudes et relativement stables au cours de l'année (**Peel *et al.* 2007**). Les températures moyennes oscillent entre un minimum de 22°C et un maximum de 32°C. Une baisse marquée des précipitations intervient entre mi-juillet et mi-novembre ('saison sèche') et une saison sèche plus courte et plus irrégulière intervient autour du mois de mars ('petite saison sèche').

III.2 Diversité culicidienne et hypothèses biogéographiques

La Guyane abriterait l'une des plus grandes diversités de moustiques au monde relativement à sa superficie (**Foley *et al.* 2007, 2008**). Si l'on se place à l'échelle de l'évolution, la diversité que l'on observe aujourd'hui pourrait être décomposée selon l'équation suivante :

Diversité = spéciation - extinction + immigration (**Jablonski *et al.* 2006**)

Dans ce cadre, une augmentation du taux de spéciation et/ou d'immigration, et/ou une baisse du taux d'extinction a pu conduire à la forte diversité que l'on observe aujourd'hui. Nous pouvons évoquer plusieurs hypothèses biogéographiques explicatives.

L'hypothèse des refuges

La première hypothèse est celle de l'existence en Guyane d'anciens refuges forestiers. En effet, au cours du Pléistocène, les cycles de Milankovitch ont créé une alternance de périodes glaciaires et interglaciaires sur Terre. Lors des périodes interglaciaires, le climat plus chaud et plus sec aurait conduit à un retrait substantiel des forêts tropicales humides en Amazonie et à la formation de forêts humides refuges séparées par des formations végétales plus sèches de type savane (**Haffer & Prance 2001**). Ce phénomène aurait permis à la fois de limiter le taux d'extinction des espèces forestières et d'augmenter la spéciation allopatrique par vicariance. L'existence de refuges forestiers en Guyane a été corroborée par plusieurs études botaniques et herpétologiques et a donc pu participer à la forte diversité de moustiques que l'on observe à l'heure actuelle (**Dégallier 1982**). Les principaux indices qui trahissent d'anciens refuges forestiers sont la présence de populations relictuelles et d'un fort taux d'endémisme (**Rull 2005**).

L'hypothèse géographique

Après la dernière glaciation la forêt amazonienne a progressivement repris ses droits pour former l'imposant massif forestier que nous connaissons aujourd'hui (**Haffer & Prance 2001**). À partir de ce moment-là, la reformation d'une unité forestière en Amazonie à sûrement permis à certaines espèces d'étendre leur aire de répartition. Selon **Dégallier** (**1982**), de par sa position géographique médiane au sein de la région Néotropicale, la Guyane constituerait une zone de rencontre privilégiée entre les ensembles culicidiens d'Amérique Centrale et d'Amérique du Sud. Cette hypothèse est confortée par la présence d'un mélange

des deux ensembles en Guyane (**Appendix 2**). Le premier est constitué d'espèces d'Amérique Centrale et du Nord de l'Amérique du Sud dont la Guyane constitue la limite Sud de l'aire de répartition. Le second est constitué d'espèces d'Amérique du Sud dont la Guyane constitue la limite Nord de l'aire de répartition.

L'effet muséum

La dernière raison de la grande diversité de moustiques repose probablement sur les écarts d'effort d'échantillonnage entre la Guyane et les pays les plus proches. En effet, durant la première moitié du XX^{ème} siècle, le territoire guyanais a été le siège de nombreuses prospections entomologiques (**Senevet 1937; Senevet & Abonnenc 1938, 1939a, 1939b, 1939c, 1939d, 1940, 1941, 1942, 1946; Senevet *et al.* 1942**). Le niveau d'investigation a visiblement été inférieur chez les pays voisins pour lesquels les seuls travaux sur la diversité des Culicidae sont ceux d'**Aiken et Rowland** (**1906**) et d'**Aiken** (**1907, 1909, 1911**) au Guyana, ainsi que ceux de **Bonne et Bonne-Wepster** (**1920, 1925**), de **Bruijing** (**1959**) et de **Panday** (**1975a, 1975b**) au Suriname. Dans ces conditions il est difficile d'affirmer que la diversité attribuée à la seule Guyane n'est pas partagée, du moins en grande partie, avec ses voisins les plus proches (y compris l'Amapa brésilienne). On peut également noter que le second pays en tête en termes de diversité culicidienne n'est autre que le Panama, pays qui a également fait l'objet d'investigations particulièrement intenses favorisées par les activités liées au canal de Panama (**Busck 1908**). En bref, la question n'est donc pas tant d'admettre l'existence de ce biais que d'en apprécier l'ampleur.

III.3 *Aedes* (*Stegomyia*) *aegypti* en Guyane

"*Dans la suite, il ne put se décider à se rendre au camp de Kourou, tant il redoutait la contagion dont ce lieu était considéré comme le foyer… Augmenter la population du camp, c'était augmenter l'épidémie dont on avait déjà signalé les symptômes ; d'un autre côté, la contagion régnait sur plusieurs bâtiments du convoi…*"

Anonyme 1842

L'épidémie historique de fièvre jaune qui décima l'expédition du Kourou entre 1763 et 1765, sans en apporter la preuve, a fait soupçonner la présence d'*Ae.* (*Stg.*) *aegypti* en Guyane (**Anonyme 1842**). En effet, il est difficile d'imaginer qu'une autre espèce puisse avoir été responsable d'une épidémie sur un camp et surtout au sein même des vaisseaux de l'époque (**Floch & Fauran 1954**).

Un peu d'Histoire

L'introduction d'*Ae.* (*Stg.*) *aegypti* dans les Amériques est liée au trafic maritime avec l'Afrique qui a été accentué par la traite négrière atlantique (**Powell & Tabachnick 2013**). En Guyane, il faudra attendre l'expertise de **Neveu-Lemaire** (**1902**) pour que l'espèce *Ae.* (*Stg.*) *aegypti*, alors désignée sous le nom de *Stegomyia fasciata* (Fabricius 1805), soit formellement identifiée à partir de trois spécimens collectés à Cayenne en avril 1901. Pendant les années 30, Senevet rapportera la présence de cette espèce dans l'ensemble des villes et villages visités du territoire (**Senevet 1937**). À la suite des travaux de Walter Reed et de ses collaborateurs sur le rôle vecteur d'*Ae.* (*Stg.*) *aegypti*, la *Pan-American Health Organization* adopta en 1947 une résolution visant à mettre en place un vaste plan d'éradication du vecteur dans les Amériques (**PAHO 1947**). Dès 1949, l'Institut Pasteur de la Guyane mènera le premier plan de lutte anti-vectorielle sur le territoire guyanais (**Floch 1950**). Ce sont les débuts de l'utilisation des insecticides organochlorés avec un plan de lutte basé sur des pulvérisations intra-domiciliaires de DDT (dichlorodiphényltrichloroéthane). Ce plan est une réussite et **Floch** rapporte officiellement en **1950** qu'*Ae.* (*Stg.*) *aegypti* a été éradiqué du sol guyanais. En 1959, il est fait mention d'une souche résistante au DDT présente sur la côte depuis Saint-Laurent-du-Maroni jusqu'à Cayenne (**Fontan & Fauran 1960**). Bien que l'utilisation de la dieldrine a semble-t-il permis d'éliminer ces nouveaux foyers, cet événement signera la réimplantation durable du vecteur quelques années plus tard (**Fouque & Carinci 1996**). Actuellement, compte tenu des multiples résistances aux insecticides développées par les populations d'*Ae.* (*Stg.*) *aegypti* dans le monde, et notamment en Guyane (**Dusfour *et al.* 2011, 2015**), l'éradication chimique du vecteur qui semblait encore possible au début des années 60, n'est plus qu'un lointain souvenir (**Fontan & Fauran 1960**).

Situation actuelle

Aujourd'hui, *Ae.* (*Stg.*) *aegypti* est plus que jamais implanté sur le territoire guyanais. Comme dans le reste du monde, la distribution de cette espèce est étroitement liée aux milieux urbains et périurbains. La densité de bâtiments s'est d'ailleurs révélée comme un bon prédicteur de la présence et de l'abondance d'*Ae.* (*Stg.*) *aegypti* (**Kamgang *et al.* 2010**). Ainsi, une carte de la distribution probable de l'espèce sur le territoire guyanais, basée sur ce prédicteur, est proposée **Figure I.2a, b**. La situation que décrivait **Senevet** en **1937** semble inchangée ; *Ae.* (*Stg.*) *aegypti* est sans aucun doute l'espèce de moustique la plus courante et la plus abondante dans les villes et villages de Guyane.

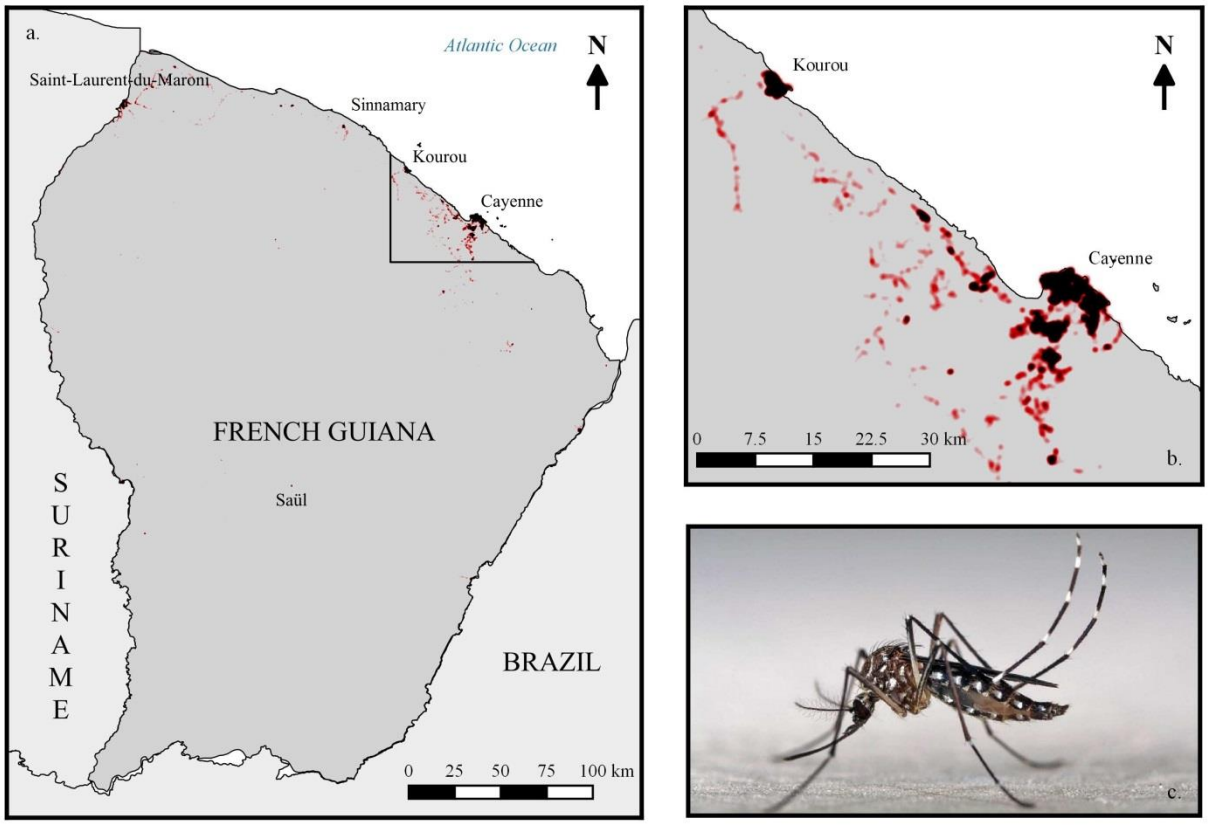

Figure I.2 Distribution probable d'*Aedes* (*Stegomyia*) *aegypti* en Guyane (a.), sur le secteur Cayenne-Kourou (b.), et photographie d'une femelle *Ae.* (*Stg.*) *aegypti* au repos (c.). Les cartes ont été réalisées en se basant sur la densité de bâtiments (BDORTHO® de l'IGN) et sur une capacité de dispersion autogène de 500 mètres (**Harrigton *et al.* 2005**). Crédit photo : **Marcos Teixeira de Freitas**.

Rôle vecteur en Guyane

Une synthèse rapide des travaux publiés au début des années 80 sur les arbovirus (i.e. acronyme d'*arthropod-borne virus*) signalés en Guyane (**Dégallier 1982; Chippaux *et al.* 1983**), couplée à l'arrivée récente sur le territoire des virus *Mayora* (MAYV) en 1998 (**Talarmin *et al.* 1998**), *Chikungunya* (CHIKV) à la fin de l'année 2013 (**ARS 2015**), et *Zika* (ZIKV) à la fin de l'année 2015 fait s'élever à 32 le nombre connu d'arbovirus pathogènes véhiculés par les moustiques en Guyane (**Tableau I.1**). Pour la santé publique, le chikungunya, la dengue et le zika restent les maladies arbovirales les plus importantes en Guyane, causant plusieurs milliers de cas chaque année (**INVS 2015**).

La plupart de ces arbovirus ont été isolés à partir de prélèvements réalisés en dehors des milieux urbains. Cependant, parmi ceux connus pour provoquer des arboviroses chez l'Homme, près des deux tiers (20/33) peuvent se multiplier et/ou être transmis par *Ae.* (*Stg.*) *aegypti* (**Dégallier *et al.* 1988**). En raison de l'abondance de cette espèce en milieu urbain, l'éventualité pour ces arbovirus de passer d'un cycle selvatique à urbain est bien réel.

L'émergence en milieu urbain du virus *Mayaro* au Brésil en est un bon exemple (**Figueiredo 2007**) avec l'implication de l'Homme comme réservoir (**Tesh *et al.* 1999**) et d'*Ae.* (*Stg.*) *aegypti* comme vecteur (**Long *et al.* 2011**).

Tableau I.1 Liste des arbovirus transmis par les moustiques en Guyane réalisée à partir de **Dégallier** (**1982**) et **Chippaux *et al.*** (**1983**). Les virus sont classés alphabétiquement par famille puis par genre. La nomenclature suit les recommandations de l'*International Committee on Taxonomy of Viruses* (**ICTV 2015**) et les abréviations suivent l'*International Catalog of Arboviruses* (**ICA 2015**). La dernière colonne indique les virus se multipliant dans et/ou transmis par *Aedes* (*Stegomyia*) *aegypti* selon **Dégallier *et al.*** (**1988**).

Famille	**Genre**	**Virus**	**Abréviation**	***Ae.* (*Stg.*) *aegypti***
Bunyaviridae	*Bunyavirus*	*Anopheles A*	ANAV	
		Bitimi	BIMV	
		Caraparu	CARV	X
		Catu	CATUV	X
		Guama	GMAV	X
		Guaroa	GROV	X
		Inini	INIV	
		Maguari	MAGV	
		Murutucu	MURV	X
		Oriboca	ORIV	X
		Simbu	SIMV	X
		Tacaiuma	TCMV	X
		Wyeomyia	WYOV	
	Phlebovirus	*Itaporanga*	ITPV	
Poxviridae	Indéterminé	*Cotia*	COTV	
Togaviridae	*Alphavirus*	*Aura*	AURAV	
		Cabassou	CABV	
		Chikungunya	CHIKV	X
		Mayaro	MAYV	X
		Mucambo	MUCV	X
		Pixuna	PIXV	
		Tonate	TONV	
		Una	UNAV	
	Flavivirus	*Dengue*	DENV-1	X
			DENV-2	X
			DENV-3	X
			DENV-4	X
		Ilheus	ILHV	X
		St. Louis Encephalitis	SLEV	X
		Yellow Fever	YFV	X
		Zika	ZIKAV	X
Indéterminé	Indéterminé	*Rochambeau*	RBUV	

IV Plan de thèse

Selon **Lockwood *et al.* (2013)**, l'invasion biologique d'*Ae.* (*Stg.*) *aegypti* en Guyane peut être considérée comme achevée. Les deux premières phases d'introduction et de naturalisation sont bel et bien révolues (**Fontan & Fauran 1960**) et l'impact sanitaire de cette invasion biologique peut être évalué en suivant l'évolution des épidémies de chikungunya, de dengue et de zika dans le département (**INVS 2015; ARS 2015**). Malgré tous les moyens mis en œuvre pour lutter contre ce vecteur, sa distribution sur le territoire guyanais est en constante évolution, notamment en direction des milieux les moins urbanisés.

Comme dans le reste de la zone pantropicale, la résistance biotique des écosystèmes guyanais a été insuffisante pour empêcher la naturalisation d'*Ae.* (*Stg.*) *aegypti* au sein des villes et des villages de cette région. Mais quels rôles jouent les interactions biologiques avec les communautés résidentes dans cette invasion ?

Compte tenu de la forte biodiversité présente en Guyane, ce territoire représente à n'en pas douter le lieu idéal pour étudier les interactions biologiques que peut entretenir *Ae.* (*Stg.*) *aegypti* avec les communautés résidentes et plus particulièrement avec les moustiques autochtones. De plus, les invasions biologiques sous les tropiques ont été assez peu étudiées, ce qui peut nous conduire à nous interroger sur la représentativité de certains mécanismes mis en évidence sous des latitudes plus hautes (**Fridley *et al.* 2007**). Enfin, une meilleure compréhension du phénomène d'invasion biologique a le potentiel de fournir des perspectives uniques dans les domaines de l'écologie, en particulier pour ce qui est du rôle des interactions biologiques et de la co-évolution dans la structuration des communautés (**Hierro *et al.* 2005**).

Cette thèse est articulée autour de deux grandes parties, chacune divisée en quatre chapitres.

Dans la première partie nous nous sommes intéressés à la diversité des moustiques en Guyane à l'échelle régionale, et plus particulièrement à l'histoire évolutive des moustiques associés aux plantes à réservoir dans le but de comprendre comment l'histoire évolutive peut influencer les processus écologiques se déroulant à l'heure actuelle.

Dans la seconde partie, afin de mieux comprendre la distribution d'*Ae.* (*Stg.*) *aegypti* dans cette région du monde, nous nous sommes intéressés aux différents processus écologiques structurant la diversité des communautés de macro-invertébrés aquatiques des réservoirs naturels et artificiels le long de gradients d'urbanisation à l'échelle locale.

Partie I. Diversité et évolution des moustiques de Guyane

Chapitre 1: Updated checklist of the mosquitoes (Diptera: Culicidae) of French Guiana (Talaga *et al.* 2015*, Journal of Medical Entomology,* 52**, 770–782)**

Les moustiques sont représentés par plus de 3 500 espèces décrites à travers le monde (**Harbach 2015**) et la Guyane serait l'une des régions en regroupant le plus grand nombre relativement à sa superficie (**Foley *et al.* 2007**). Mais d'où proviennent ces chiffres et que sait-on réellement sur cette diversité ? Afin d'appréhender correctement les interactions biologiques qu'entretient *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) avec la faune culicidienne autochtone, il nous a semblé judicieux de faire un état des lieux des connaissances sur cette diversité encore mal connue.

Pour cela, nous avons dans un premier temps rassemblé l'intégralité des travaux publiés sur la taxonomie des moustiques de Guyane. Cette première étape a permis de regrouper de nombreux travaux publiés jusqu'en 1980, date à laquelle les recherches sur la diversité des moustiques de Guyane ont pratiquement cessées (**Dégallier & Claustre 1980**). Dans un second temps ces données ont été confrontées avec les révisions taxonomiques publiées depuis 1980, ce qui a conduit au retrait de 32 espèces précédemment reportées de Guyane et à l'ajout de 12 nouvelles espèces. Enfin, cette révision a également été l'occasion d'intégrer 12 autres nouvelles espèces pour la Guyane issues de nos propres prospections entomologiques conduites sur le territoire entre 2013 et 2015.

Cette recherche nous amène à reconnaitre l'existence de 235 espèces de moustiques pour la Guyane inégalement réparties au sein de 2 sous-familles et de 8 tribus. Parmi toutes ces espèces, seules *Ae.* (*Stg.*) *aegypti* et *Culex* (*Culex*) *quinquefasciatus* Say 1823 sont considérées comme allochtones et invasives (**Juliano & Lounibos 2005**). Cette révision nous servira de référence tout au long de cette thèse, aussi bien en matière de nomenclature que de classification.

Chapitre 2: A DNA reference library of French Guiana mosquitoes for barcoding (Talaga *et al.*, en préparation)

Compte tenu de la forte diversité taxonomique sous les tropiques, la 'bonne' délimitation des espèces est souvent problématique et peut même constituer un frein important à la réalisation de certaines études (**De Queiroz 2007**). C'est par exemple le cas en écologie des communautés où l'espèce constitue bien souvent l'unité d'étude fondamentale, ou encore en entomologie médicale où elle peut compromettre les conclusions de certains

suivis. Ceci est particulièrement vrai chez les moustiques dont l'identification morphologique, quand elle est possible, est souvent réservée à une poignée de taxonomistes dans le monde.

Ces dernières décennies, la démocratisation des méthodes d'identification moléculaire a vu l'émergence d'une initiative visant à associer un 'barcode' à l'ensemble du monde vivant via le séquençage de fragments courts d'ADN (**Hebert *et al.* 2003a**). Pour le règne animal, c'est le gène mitochondrial codant pour la sous-unité I de la cytochrome *c* oxydase (COI) qui a été adopté. Chez les Culicidae, cette technique de barcoding a été utilisée avec succès dans plusieurs régions tempérées et tropicales du globe (e.g. **Cywinska *et al.* 2006; Kumar *et al.* 2007; Engdahl *et al.* 2014**). Néanmoins, assez peu d'études se sont encore penchées sur les moustiques Néotropicaux (mais voir **Linton *et al.* 2013; Laurito *et al.* 2014; Rozo-Lopez & Mengual 2015**).

Nous avons entrepris le séquençage d'un fragment de 658 paires de bases du gène COI chez 76 espèces de moustiques identifiées morphologiquement. Ce travail nous a tout d'abord permis de confirmer l'exactitude de nos délimitations/identifications morphologiques, mais également d'identifier des complexes d'espèces probables.

Chapitre 3: Online database for mosquito (Diptera: Culicidae) occurrence records in French Guiana (Talaga *et al.* 2015*, ZooKeys*, 532**, 107–115)**

La gestion et la diffusion de l'information constituent un problème majeur dans le monde scientifique. En effet les études sur de larges étendues géographiques ne sont souvent possibles que par la somme des efforts de nombreuses équipes pendant de nombreuses années. Dans cette optique, afin de valoriser et de partager nos données avec le plus grand nombre, nous avons décidé de publier une base de données centralisant l'ensemble des informations de collectes et de séquençages réalisées au cours de cette thèse.

À l'heure actuelle cette base de données regroupe plus de 1 200 spécimens en collection, incluant des adultes montés en collection (mâle et femelles) et des immatures stockés en alcool 96 %. Ces spécimens sont issus de nombreuses localités de Guyane depuis la côte jusqu'à la limite Sud avec le Brésil. Afin de donner de la visibilité à ces données, elles ont été mises en ligne sur les plateformes du *Global Biodiversity Information Facility* (GBIF ; http://www.gbif.org/), du *Barcode of Life Data Systems* (BOLD ; http://www.boldsystems.org/), ainsi que sur le portail SIG web Guyanensis (http://guyanensis.ups-tlse.fr/).

À court terme cette base de données aura pour but de regrouper l'ensemble des données déjà existantes dans d'autres centres et instituts de recherche, et mènera, sans aucun doute, à

de nouvelles collaborations scientifiques. À plus long terme, cette base de données assurera la continuité avec les recherches menées sur la diversité, l'écologie et l'évolution des moustiques en Guyane.

Chapitre 4: Convergent evolution of intraguild predation in phytotelm-breeding mosquitoes (Talaga *et al.*, soumis à *Evolutionary Ecology*)

La forte diversité taxonomique et génétique des moustiques de Guyane doit nous amener à nous interroger sur les processus ayant causé cette diversification. Dans ce chapitre nous nous sommes intéressés à l'histoire évolutive des espèces de moustiques associées aux plantes à réservoir (ou phytotelmes) en Guyane.

En utilisant les données de collectes présentées dans le chapitre précédent nous avons mis en évidence que ces moustiques étaient associés à leur plante hôte avec des niveaux de spécialisation équivalents à ceux existant chez des associations de types mutualistes. De plus, nos résultats indiquent également la présence invariable de prédation intraguilde chez les espèces associées avec les phytotelmes de petite taille.

À travers cet exemple nous suggérons que la coadaptation des moustiques avec leur habitat aquatique joue un rôle important dans les processus écologiques se déroulant à l'heure actuelle. En l'occurrence, dans le cas des invasions biologiques nous pouvons supposer que cette coadaptation peut avoir au moins deux répercussions majeures. La première est que, compte tenu de cette forte spécialisation pour leur habitat aquatique, les organismes autochtones seraient mieux adaptés et par conséquent limiteraient le risque d'établissement d'espèces introduites, par définition non adaptées. À l'inverse, cette forte spécialisation rendrait ces organismes autochtones moins susceptibles de s'adapter eux-mêmes à des perturbations rapides comme celles liées à l'anthropisation des milieux.

Partie II. Ecologie des communautés résidentes en milieu urbain

Chapitre 5: Urbanization decreases taxonomic and functional diversity in Neotropical bromeliad invertebrates (Talaga *et al.*, soumis à *Urban Ecosystems*)

Dans ce chapitre nous avons analysé les effets potentiels de l'urbanisation sur la diversité taxonomique et fonctionnelle. Pour répondre à cette question nous avons choisi comme modèle d'étude les communautés d'organismes aquatiques hébergées par les broméliacées à réservoirs. Ces dernières ont la particularité d'être présentes dans des environnements anthropisés, d'être naturellement répliquées et d'héberger des communautés relativement diverses.

Pour cette étude nous avons échantillonné 26 broméliacées épiphytes de la région de Sinnamary, soit 13 individus dans la ville et 13 autres dans une zone rurale située 2 km plus loin. L'étude des communautés de macro-invertébrés aquatiques a montré que l'urbanisation réduisait à la fois leur diversité taxonomique et leur diversité fonctionnelle. En outre, plus de la moitié des communautés échantillonnées au sein du milieu urbain contenaient des larves d'*Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762), le principal vecteur de la dengue et du chikungunya dans la région. Les broméliacées à réservoirs ne représentent pas l'habitat aquatique typique de ce vecteur, toutefois ces résultats posent la question du rôle de ce phytotelme dans la dynamique d'*Ae.* (*Stg.*) *aegypti* dans la région, et plus généralement de l'influence de la diversité dans l'établissement d'une espèce invasive.

Chapitre 6: Environmental drivers of community diversity in a Neotropical urban landscape - a multi-scale analysis (Talaga *et al.*, soumis à *Landscape Ecology*)

Dans le chapitre précédent nous avons mis en évidence que les broméliacées à réservoirs pouvaient potentiellement jouer un rôle dans la dynamique d'*Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) en milieu urbain. Dans ce chapitre nous avons estimé la contribution relative des caractéristiques (biotiques et abiotiques) de l'habitat aquatique et de l'hétérogénéité urbaine dans la présence de ce vecteur. Afin d'éliminer le filtre que pourrait constituer l'environnement rural sur *Ae.* (*Stg.*) *aegypti* nous nous sommes cette fois-ci placés dans la ville de Sinnamary.

Pour quantifier l'hétérogénéité urbaine, une carte d'occupation des sols distinguant les bâtiments, les routes, le sol et la végétation a été créée à partir d'une orthophoto haute résolution. Toutes les broméliacées à réservoirs ont ensuite été géoréférencées afin d'évaluer la distribution spatiale de ce méta-habitat aquatique dans la ville. En mars 2013, au cours de la

petite saison sèche, 32 broméliacées ont été échantillonnées afin de couvrir la plus vaste étendue possible dans la ville.

L'étude des communautés de macro-invertébrés aquatiques montre que les caractéristiques de la matrice terrestre environnant les plantes expliquent une part importante de la variation dans les communautés. De plus, dans un rayon de 10 mètres autour de la broméliacée échantillonnée, la matrice terrestre explique plus de variance dans les communautés que les seules caractéristiques de l'habitat aquatique. Seulement trois individus d'*Ae.* (*Stg.*) *aegypti* ont été échantillonnés lors de cette étude. Ce résultat inattendu laisse supposer que l'établissement d'*Ae.* (*Stg.*) *aegypti* dans cet habitat aquatique fluctue probablement annuellement et minimise le rôle de ces réservoirs naturels dans la production d'*Ae.* (*Stg.*) *aegypti*.

Chapitre 7: Impacts of biotic and abiotic factors on immature populations of *Aedes* (*Stegomyia*) *aegypti* (L.) along an urbanization gradient (Talaga *et al.*, en préparation)

Dans cette étude nous avons estimé la part relative des interactions biologiques avec les communautés résidentes et des facteurs abiotiques dans la distribution d'*Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762). L'étude a été réalisée à la fois sur des réservoirs naturels et artificiels, ces derniers étant utilisés typiquement par ce vecteur. L'influence de l'anthropisation sur la distribution d'*Ae.* (*Stg.*) *aegypti* a également été prise en compte en considérant trois sites avec un degré croissant d'urbanisation. Enfin, pour avoir une bonne représentation de l'ensemble des conditions climatiques possibles, les communautés de macro-invertébrés aquatiques ont été suivies pendant un an. Au total, 54 communautés ont été échantillonnées toutes les deux semaines entre 2013 et 2014 dans la ville de Kourou.

Les résultats de cette étude montrent que l'urbanisation influence la diversité selon les prédictions de la perturbation intermédiaire (**Connell 1978**). Contrairement à l'hypothèse diversité-invasibilité l'abondance d'*Ae.* (*Stg.*) *aegypti* est la plus forte dans les sites les plus diversifiés. Nos résultats indiquent également que le degré d'urbanisation influence la contribution relative des interactions trophiques. Les interactions avec des espèces controphiques ne partageant pas le même mode d'acquisition de la nourriture semblent influencer positivement l'abondance d'*Ae.* (*Stg.*) *aegypti*. Ceci suggère un mécanisme de facilitation et pourrait expliquer la plus forte abondance d'*Ae.* (*Stg.*) *aegypti* dans le site présentant les communautés les plus diverses. À l'inverse, l'interaction avec d'autres espèces de Culicidae semble réduire l'abondance d'*Ae.* (*Stg.*) *aegypti* dans le site présentant le plus faible niveau d'urbanisation. *Limatus durhamii* Theobald 1901 étant le moustique dominant

dans ce site, cette espèce autochtone empêche très certainement l'établissement durable d'*Ae.* (*Stg.*) *aegypti* par un mécanisme d'exclusion compétitive.

Chapitre 8: Larval interference with a native Neotropical mosquito species increases *Aedes* (*Stegomyia*) *aegypti*'s fitness (Talaga *et al.*, soumis à *Journal of Medical Entomology*)

La compétition interspécifique avec les espèces résidentes est considérée comme l'un des processus clé lors du phénomène d'invasion biologique car elle peut, dans certains cas, limiter l'invasion (**Lockwood *et al.* 2013**). Sur la base de nos observations en conditions naturelles, nous avons testé l'hypothèse selon laquelle l'interférence larvaire avec *Limatus durhamii* Theobald 1901 influencerait négativement la fitness d'*Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762).

Pour tester cela nous avons mis en place un protocole expérimental composé d'un traitement sans compétition (contrôle), d'un traitement intraspécifique (deux larves conspécifiques) et d'un traitement interspécifique (deux larves hétérospécifiques). Les différents traitements ont été placés dans une chambre climatique reproduisant les conditions de température et de photopériode typique de la Guyane. Enfin, les larves ont été nourries à volonté afin d'éviter les effets de la compétition par exploitation.

Le temps de développement larvaire et la masse sèche des adultes, deux traits d'histoire de vie reliés à la fitness individuelle, ont été mesurés pour chaque espèce et comparés entre les différents traitements. Nos résultats indiquent que l'interférence larvaire a un effet sur la masse sèche à l'émergence, mais pas sur le temps de développement. Cependant, contrairement à nos prédictions, la masse sèche augmente chez *Ae.* (*Stg.*) *aegypti* en cas de traitement interspécifique, suggérant une amélioration de la fitness individuelle. Un résultat similaire a été obtenu chez les femelles *Li. durhamii*, indiquant que cette espèce est aussi capable de faire preuve de plasticité phénotypique en condition d'interférence larvaire. Ces résultats suggèrent que la compétition par interférence n'est probablement pas le processus responsable de l'exclusion compétitive d'*Ae.* (*Stg.*) *aegypti* observée dans l'étude présentée dans le chapitre précédent.

Partie I

Chapitre 1: Updated Checklist of the Mosquitoes (Diptera: Culicidae) of French Guiana (Talaga *et al.* 2015, *Journal of Medical Entomology,* 52, 770–782)

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Abstract: The incredible mosquito species diversity in the Neotropics can provoke major confusion during vector control programs when precise identification is needed. This is especially true in French Guiana where studies on mosquito diversity practically ceased 35 years ago. In order to fill this gap, we propose here an updated and comprehensive checklist of the mosquitoes of French Guiana reflecting the latest changes in classification and geographical distribution and the recognition of current or erroneous synonymies. This work was undertaken in order to help ongoing and future research on mosquitoes in a broad range of disciplines such as ecology, biogeography and medical entomology. Thirty-two valid species cited in older lists have been removed, and 24 species have been added including 12 species (comprising two new genera and three new subgenera) reported from French Guiana for the first time. New records are from collections conducted on various phytotelmata in French Guiana and include the following species: *Onirion* sp. cf. **Harbach & Peyton** (**2000**), *Sabethes* (*Peytonulus*) *hadrognathus* Harbach, *Sa.* (*Pey.*) *paradoxus* Harbach, *Sa.* (*Pey.*) *soperi* Lane & Cerqueira, *Sa.* (*Sabethinus*) *idiogenes* Harbach, *Sa.* (*Sabethes*) *quasicyaneus* Peryassú, *Runchomyia* (*Ctenogoeldia*) *magna* (Theobald), *Wyeomyia* (*Caenomyiella*) sp. cf. **Harbach & Peyton** (**1990**), *Wy.* (*Dendromyia*) *ypsipola* Dyar, *Wy.* (*Hystatomyia*) *lamellata* (Bonne-Wepster & Bonne), *Wy.* (*Miamyia*) *oblita* (Lutz), and *Toxorhynchites* (*Lynchiella*)

guadeloupensis (Dyar & Knab). At this time, the mosquitoes of French Guiana are represented by 235 species distributed across 22 genera, nine tribes and two subfamilies.

Keywords: Culicid, Neotropics, South America, Species checklist, Vector.

INTRODUCTION

Arthropod diversity is massive on a global scale (**Zhang 2011**) and spatial patterns show that there are peaks of diversity throughout the Tropics (**Novotny *et al.* 2006; Foley *et al.* 2007; Basset *et al.* 2012**). Mosquitoes (Diptera: Culicidae) are no exception to that rule with an estimated 1,030 valid species recognized from the Neotropical region alone (**WRBU 2015**), representing nearly one-third of the 3,549 species described world-wide at this time (**Harbach 2015**). Many mosquito species are vectors of pathogens for vertebrates, including humans, creating major health issues in some part of the world (**Dégallier 1982**).

French Guiana is a small overseas French territory situated at the eastern limit of the Guiana Shield (a mountainous tableland region extending, from west to east, across Colombia, Venezuela, Guyana, Suriname and French Guiana) and bordered to the south by northern Brazil. French Guiana is mainly covered by primary rainforest and its inhabitants are mostly distributed along the coast. Mosquito-borne diseases are frequent in French Guiana, including malaria mainly in inland areas of the territory, dengue and chikungunya in urban areas, plus many lesser known crypto-arboviroses in sylvan and/or rural environments (**Chippaux *et al.* 1983; ARS 2015**).

In a changing world, anthropization leads inevitably to greater interaction between humans and vectors, increasing the risks of new and emerging diseases. Identifying vector species is thus crucial to organizing effective mosquito prevention and/or control programs. In French Guiana, taxonomic work on culicid diversity was very prolific before World War II and led to the first record of the presence of many species (**Senevet 1937; Senevet & Abonnenc 1938, 1939a, 1939b, 1939c, 1939d, 1940, 1941, 1942, 1946; Senevet *et al.* 1942**), including 40 species originally described from French Guiana (see **Appendix 2**). Despite the socio-economic issues, studies on mosquito diversity in this area virtually stopped in 1980 with the last publication updating the list of mosquitoes present in French Guiana with new records and many notes on their bionomics (**Dégallier & Claustre 1980**). Since then, a number of taxonomic revisions focusing on a particular species or on groups of species has been published, leading to changes in classification and geographic distribution and the

recognition of current or erroneous synonymies. In order to continue the valuable work of our predecessors, we propose in the present paper a new, updated checklist of the mosquitoes of French Guiana reflecting the latest changes in terms of classification, geographical distribution and synonymy. This work was undertaken in order to help ongoing and future research on mosquitoes in a broad range of disciplines such as ecology, biogeography and medical entomology.

An exhaustive census of all species reported from French Guiana was conducted using existing published data and internal unpublished reports from the Pasteur Institute of French Guiana. Species are listed alphabetically and ranked by subfamily, tribe, genus and subgenus. Species considered to be present in French Guiana are numbered while doubtful species records and misidentifications and/or misinterpretations are indicated but not numbered. New species records since 1980 are underlined and the 12 species reported from French Guiana for the first time are highlighted with an asterisk. The "Notes" section includes explanations about the exclusion and the inclusion of species, and useful remarks on the site of the recorded presence of voucher specimens when necessary. The validity of species and subspecies is based on "A Catalog of the Mosquitoes of the World (Diptera: Culicidae)" (**Knight & Stone 1977**) and its supplements (**Knight 1978; Ward 1984, 1992; Gaffigan & Ward 1985**), and the "Systematic Catalog of Culicidae" (**WRBU 2015**). Considering that there is no consensus concerning the internal classification of the tribe Aedini proposed by **Reinert *et al.*** (**2008**), we have decided to use the traditional classification for the Aedini. An infra-subgeneric classification based on the compiled data of **Harbach** (**2015**) was used for the *Anopheles* and *Nyssorhynchus* subgenera of *Anopheles* and for the *Anoedioporpa*, *Carrollia*, *Culex* and *Melanoconion* subgenera of *Culex*. The abbreviations used for genera and subgenera are based on recommendations by **Reinert** (**2009**).

As a result of this revision, 32 valid species cited in older lists have been removed, and 24 species have been added including 12 species (comprising two new genera and three new subgenera) reported from French Guiana for the first time. New records are reported from a collection campaign of various plant-held waters conducted between 2013 and 2015 in French Guiana and include the following species: *Onirion* sp. cf. **Harbach & Peyton** (**2000**), *Sabethes* (*Peytonulus*) *hadrognathus* Harbach, *Sa.* (*Pey.*) *paradoxus* Harbach, *Sa.* (*Pey.*) *soperi* Lane & Cerqueira, *Sa.* (*Sabethinus*) *idiogenes* Harbach, *Sa.* (*Sabethes*) *quasicyaneus* Peryassú, *Runchomyia* (*Ctenogoeldia*) *magna* (Theobald), *Wyeomyia* (*Caenomyiella*) sp. cf. **Harbach & Peyton** (**1990**), *Wy.* (*Dendromyia*) *ypsipola* Dyar, *Wy.* (*Hystatomyia*) *lamellata* (Bonne-Wepster & Bonne), *Wy.* (*Miamyia*) *oblita* (Lutz), and *Toxorhynchites* (*Lynchiella*)

guadeloupensis (Dyar & Knab). Voucher specimens from the 2013-2015 collections are deposited in the collections of the Pasteur Institute of French Guiana (IPGF) and at the UMR-Ecofog, respectively, in Cayenne and Kourou, French Guiana. At this time, the mosquitoes of French Guiana are represented by 235 species distributed across 22 genera, nine tribes and two subfamilies. Most of the species have a geographical range across Central and South America (127 species), while 70 out of the 235 species are restricted to South America (**Appendix 2**). The rest are divided into species restricted to the Guiana Shield (15 species) and species believed to be endemic to French Guiana (23 species) (**Appendix 2**). **Foley *et al.*** (**2008**) stated that French Guiana has one of the highest relative species densities of mosquitoes anywhere in the world. Our findings reinforce this view of French Guiana as a hotspot of mosquito diversity.

We are aware that the present checklist is likely to evolve with the addition of new species records or due to changes in the classification of some taxa. In order to permit frequent and rapid updates, the present list will be also published online in the Global Biodiversity Information Facilities (GBIF; http://www.gbif.org/) as a taxonomic checklist.

THE MOSQUITOES OF FRENCH GUIANA

Species considered to be present in French Guiana are numbered while doubtful species records and misidentifications and/or misinterpretations are indicated but not numbered. New species records since 1980 are underlined and the 12 species reported from French Guiana for the first time are highlighted with an asterisk.

FAMILY CULICIDAE
SUBFAMILY ANOPHELINAE

Genus *Anopheles* Meigen

Subgenus *Anopheles* Meigen

Laticorn Section

Arribalzagia Series

- *An.* (*Ano.*) *apicimacula* Dyar & Knab 1906 (see Note 1)
1- *An.* (*Ano.*) *costai* da Fonseca & da Silva Ramos 1939 (see Note 2)
2- *An.* (*Ano.*) *forattinii* Wilkerson & Sallum 1999 (see Note 2)
3- *An.* (*Ano.*) *intermedius* (Peryassú 1908) (see Note 1)
4- *An.* (*Ano.*) *maculipes* (Theobald 1903)
- *An.* (*Ano.*) *mediopunctatus* Lutz 1903 (see Note 2)
5- *An.* (*Ano.*) *minor* da Costa Lima 1929
6- *An.* (*Ano.*) *peryassui* Dyar & Knab 1908

Angusticorn Section

Anopheles Series
Pseudopunctipennis Group
7- *An.* (*Ano.*) *eiseni* Coquillett 1902
- *An.* (*Ano.*) *pseudopunctipennis* Theobald 1901 (see Note 3)
Subgenus *Kerteszia* Theobald
- *An.* (*Ker.*) *bambusicolus* Komp 1937 (see Note 4)
- *An.* (*Ker.*) *bellator* Dyar & Knab 1906 (see Note 4)
- *An.* (*Ker.*) *boliviensis* (Theobald 1905) (see Note 4)
- *An.* (*Ker.*) *cruzii* Dyar & Knab 1908 (see Note 4)
- *An.* (*Ker.*) *homunculus* Dyar & Knab 1908 (see Note 4)
8- *An.* (*Ker.*) *neivai* Howard Dyar & Knab 1913
Subgenus *Lophopodomyia* Antunes
9- *An.* (*Lph.*) *squamifemur* Antunes 1937
Subgenus *Nyssorhynchus* Blanchard
Albimanus Section
Oswaldoi Group
Oswaldoi Subgroup
10- *An.* (*Nys.*) *aquasalis* Curry 1932
- *An.* (*Nys.*) *evansae* (Brethés 1926) (see Note 5)
11- *An.* (*Nys.*) *ininii* Senevet & Abonnenc 1938
Oswaldoi Complex
12- *An.* (*Nys.*) *oswaldoi* s.l. (Peryassú 1922)
13- *An.* (*Nys.*) *sanctielii* Senevet & Abonnenc 1938
Nuneztovari Complex
14- *An.* (*Nys.*) *nuneztovari* s.l. Gabaldón 1940
Strodei Complex
- *An.* (*Nys.*) *strodei* Root 1926 (see Note 5)
Triannulatus Subgroup
15- *An.* (*Nys.*) *triannulatus* s.l. (Neiva and Pinto 1922)
Argyritarsis Section
Albitarsis Series
Albitarsis Group
Albitarsis Complex
16- *An.* (*Nys.*) *marajoara* Galvão & Damasceno 1942 (see Note 6)
Braziliensis Group
17- *An.* (*Nys.*) *braziliensis* (Chagas 1907) (see Note 7)
Argyritarsis Group
- *An.* (*Nys.*) *argyritarsis* Robineau-Desvoidy 1827 (see Note 7)
Darlingi Group
18- *An.* (*Nys.*) *darlingi* Root 1926
Subgenus *Stethomyia* Theobald
19- *An.* (*Ste.*) *acanthotorynus* Komp 1937
20- *An.* (*Ste.*) *canorii* Floch & Abonnenc 1945
21- *An.* (*Ste.*) *kompi* Edwards 1930
22- *An.* (*Ste.*) *nimbus* (Theobald 1902)

Genus *Chagasia* Cruz
23- *Ch. bathana* (Dyar 1928) (see Note 8)
24- *Ch. bonneae* Root 1927

SUBFAMILY CULICINAE

TRIBE AEDEOMYIINI

Genus *Aedeomyia* Theobald

Subgenus *Aedeomyia* Theobald

25- *Ad.* (*Ady.*) *squamipennis* (Lynch Arribálzaga 1878)

TRIBE AEDINI

Genus *Aedes* Meigen

Subgenus *Georgecraigius* Reinert, Harbach & Kitching

26- *Ae.* (*Gec.*) *fluviatilis* (Lutz 1904)

Subgenus *Howardina* Theobald

27- *Ae.* (*How.*) *arborealis* Bonne-Wepster & Bonne 1920
28- *Ae.* (*How.*) *fulvithorax* (Lutz 1904)
- *Ae.* (*How.*) *septemstriatus* Dyar & Knab 1907 (see Note 10)

Subgenus *Ochlerotatus* Lynch Arribálzaga

- *Ae.* (*Och.*) *crinifer* (Theobald 1903) (see Note 9)
29- *Ae.* (*Och.*) *eucephalaeus* Dyar 1918
30- *Ae.* (*Och.*) *fulvus* (Wiedemann 1828)
31- *Ae.* (*Och.*) *hastatus* Dyar 1922
32- *Ae.* (*Och.*) *hortator* Dyar & Knab 1907
33- *Ae.* (*Och.*) *martineti* Senevet 1937
34- *Ae.* (*Och.*) *nubilus* Theobald 1903
35- *Ae.* (*Och.*) *oligopistus* Dyar 1918
36- *Ae.* (*Och.*) *perventor* Cerqueira & Costa 1946
37- *Ae.* (*Och.*) *scapularis* (Rondani 1848)
38- *Ae.* (*Och.*) *serratus* (Theobald 1901)
39- *Ae.* (*Och.*) *taeniorhynchus* (Wiedemann 1821)

Subgenus *Protomacleaya* Theobald

40- *Ae.* (*Pro.*) *argyrothorax* Bonne-Wepster & Bonne 1920
41- *Ae.* (*Pro.*) *braziliensis* Gordon & Evans 1922
42- *Ae.* (*Pro.*) *terrens* (Walker 1856)

Subgenus *Stegomyia* Theobald

43- *Ae.* (*Stg.*) *aegypti* (Linnaeus 1762)

Genus *Haemagogus* Williston

Subgenus *Conopostegus* Dyar

44- *Hg.* (*Con.*) *leucocelaenus* (Dyar & Shannon 1924)

Subgenus *Haemagogus* Williston

45- *Hg.* (*Hag.*) *albomaculatus* Theobald 1903
- *Hg.* (*Hag.*) *equinus* Theobald 1903 (see Note 11)
46- *Hg.* (*Hag.*) *janthinomys* Dyar 1921 (see Note 12)
- *Hg.* (*Hag.*) *spegazzinii* Brethés 1912 (see Note 12)

Genus *Psorophora* Robineau-Desvoidy

Subgenus *Grabhamia* Theobald

47- *Ps.* (*Gra.*) *cingulata* (Leicester 1908)

Subgenus *Janthinosoma* Lynch Arribálzaga

48- *Ps.* (*Jan.*) *albipes* (Theobald 1907) (see Note 13)

49- *Ps.* (*Jan.*) *ferox* (von Humboldt 1819)
50- *Ps.* (*Jan.*) *lutzii* (Theobald 1901) (see Note 13)

Subgenus *Psorophora* Robineau-Desvoidy

- *Ps.* (*Pso.*) *ciliata* (Fabricius 1794) (see Note 14)
51- *Ps.* (*Pso.*) *cilipes* (Fabricius 1805)
52- *Ps.* (*Pso.*) *lineata* (von Humboldt 1819)

TRIBE CULICINI

Genus *Culex* Linnaeus

Subgenus *Aedinus* Lutz

53- *Cx.* (*Ads.*) *accelerans* Root 1927
54- *Cx.* (*Ads.*) *amazonensis* (Lutz 1905)
55- *Cx.* (*Ads.*) *clastrieri* Casal & Garcia 1968
56- *Cx.* (*Ads.*) *guyanensis* Clastrier 1970

Subgenus *Anoedioporpa* Dyar

Conservator Group
57- *Cx.* (*And.*) *belemensis* Duret & Damasceno 1955
58- *Cx.* (*And.*) *damascenoi* Duret 1969
59- *Cx.* (*And.*) *originator* Gordon & Evans 1922

Subgenus *Carrollia* Lutz

Bihaicolus Group
60- *Cx.* (*Car.*) *infoliatus* Bonne-Wepster & Bonne 1920
Iridescens Group
Urichii Subgroup
61- *Cx.* (*Car.*) *urichii* (Coquillett 1906)
Iridescens Subgroup
62- *Cx.* (*Car.*) *antunesi* Lane & Whitman 1943
63- *Cx.* (*Car.*) *bonnei* Dyar 1921 (see Note 15)
64- *Cx.* (*Car.*) *insigniforceps* Clastrier & Claustre 1978
- *Cx.* (*Car.*) *iridescens* (Lutz 1905) (see Note 15)

Subgenus *Culex* Linnaeus

Coronator Group
65- *Cx.* (*Cux.*) *coronator* Dyar & Knab 1906
Pipiens Group
Apicinus Subgroup
66- *Cx.* (*Cux.*) *bonneae* Dyar & Knab 1919
67- *Cx.* (*Cux.*) *mollis* Dyar & Knab 1906
68- *Cx.* (*Cux.*) *nigripalpus* Theobald 1901
Pipiens Subgroup
69- *Cx.* (*Cux.*) *quinquefasciatus* Say 1823
Tarsalis Subgroup
70- *Cx.* (*Cux.*) *brevispinosus* Bonne-Wepster & Bonne 1920 (see Note 16)
71- *Cx.* (*Cux.*) *declarator* Dyar & Knab 1906
- *Cx.* (*Cux.*) *janitor* Theobald 1903 (see Note 17)
72- *Cx.* (*Cux.*) *surinamensis* Bruijning 1959
Uncertain infrasubgeneric placement
73- *Cx.* (*Cux.*) *pseudojanthinosoma* Senevet & Abonnenc 1946 (see Note 18)

Subgenus *Melanoconion* Theobald

Melanoconion Section
Atratus Group
74- *Cx.* (*Mel.*) *commevynensis* Bonne-Wepster & Bonne 1920
75- *Cx.* (*Mel.*) *dunni* Dyar 1918
76- *Cx.* (*Mel.*) *ensiformis* Bonne-Wepster & Bonne 1920
77- *Cx.* (*Mel.*) *trigeminatus* Clastrier 1970
78- *Cx.* (*Mel.*) *zeteki* Dyar 1918
Bastagarius Group
Bastagarius Subgroup
79- *Cx.* (*Mel.*) *bastagarius* Dyar & Knab 1906
80- *Cx.* (*Mel.*) *comatus* Senevet & Abonnenc 1939
81- *Cx.* (*Mel.*) *coppenamensis* Bonne-Wepster & Bonne 1920
82- *Cx.* (*Mel.*) *creole* Anduze 1949
83- *Cx.* (*Mel.*) *tournieri* Senevet & Abonnenc 1939
Iolambdis Subgroup
84- *Cx.* (*Mel.*) *corentynensis* Dyar 1920
85- *Cx.* (*Mel.*) *dolichophyllus* Clastrier 1970
Distinguendus Group
Distinguendus Subgroup
86- *Cx.* (*Mel.*) *alcocki* Bonne-Wepster & Bonne 1920
87- *Cx.* (*Mel.*) *comminutor* Dyar 1920
88- *Cx.* (*Mel.*) *distinguendus* Dyar 1928
89- *Cx.* (*Mel.*) *maxinocca* Dyar 1920
90- *Cx.* (*Mel.*) *patientiae* Floch & Fauran 1955
91- *Cx.* (*Mel.*) *productus* Senevet & Abonnenc 1939
Putumayensis Subgroup
92- *Cx.* (*Mel.*) *phlabistus* Dyar 1920
93- *Cx.* (*Mel.*) *putumayensis* Matheson 1934
Rorotaensis Subgroup
94- *Cx.* (*Mel.*) *rorotaensis* Floch & Abonnenc 1946
Conspirator Group
95- *Cx.* (*Mel.*) *dyius* Root 1927
96- *Cx.* (*Mel.*) *elevator* Dyar & Knab 1906
Educator Group
97- *Cx.* (*Mel.*) *cristovaoi* Duret 1968
- *Cx.* (*Mel.*) *educator* Dyar & Knab 1906 (see Note 19)
98- *Cx.* (*Mel.*) *inadmirabilis* Dyar 1928
99- *Cx.* (*Mel.*) *theobaldi* (Lutz, 1904)
100- *Cx.* (*Mel.*) *vaxus* Dyar 1920 (see Note 19)
Erraticus Group
Clarki Subgroup
- *Cx.* (*Mel.*) *clarki* Evans 1924 (see Note 20)
Erraticus Subgroup
101- *Cx.* (*Mel.*) *erraticus* (Dyar & Knab 1906)
Evansae Group
102- *Cx.* (*Mel.*) *batesi* Rozeboom & Komp 1948
103- *Cx.* (*Mel.*) *evansae* Root 1927
Inhibitator Group
Egcymon Subgroup
104- *Cx.* (*Mel.*) *caudatus* Clastrier 1970

105- *Cx.* (*Mel.*) *serratimarge* Root 1927
Inhibitator Subgroup
106- *Cx.* (*Mel.*) *abonnenci* Clastrier 1970
107- *Cx.* (*Mel.*) *albinensis* Bonne-Wepster & Bonne 1920
108- *Cx.* (*Mel.*) *contei* Duret 1968
109- *Cx.* (*Mel.*) *flabellifer* Komp 1936
110- *Cx.* (*Mel.*) *inhibitator* Dyar & Knab 1906
111- *Cx.* (*Mel.*) *phlogistus* Dyar 1920
112- *Cx.* (*Mel.*) *plectoporpe* Root 1927
113- *Cx.* (*Mel.*) *vidali* Floch & Fauran 1954
Intrincatus Group
Eastor Subgroup
114- *Cx.* (*Mel.*) *eastor* Dyar 1920
Idottus Subgroup
115- *Cx.* (*Mel.*) *idottus* Dyar 1920
Intrincatus Subgroup
116- *Cx.* (*Mel.*) *equinoxialis* Floch & Abonnenc 1945
117- *Cx.* (*Mel.*) *intrincatus* Brethés 1916
118- *Cx.* (*Mel.*) *rabanicola* Floch & Abonnenc 1946
119- *Cx.* (*Mel.*) *trisetosus* Fauran 1961
120- *Cx.* (*Mel.*) *ybarmis* Dyar 1920
Pilosus Group
Caudelli Subgroup
121- *Cx.* (*Mel.*) *alogistus* Dyar 1918
122- *Cx.* (*Mel.*) *caudelli* (Dyar & Knab 1906)
123- *Cx.* (*Mel.*) *foliafer* Komp & Rozeboom 1951
124- *Cx.* (*Mel.*) *lacertosus* Komp & Rozeboom 1951
125- *Cx.* (*Mel.*) *palaciosi* Duret 1968
Pilosus Subgroup
126- *Cx.* (*Mel.*) *innovator* Evans 1924
127- *Cx.* (*Mel.*) *pilosus* Lee 1946
128- *Cx.* (*Mel.*) *unicornis* Root 1928
Saramaccensis Group
129- *Cx.* (*Mel.*) *saramaccensis* Bonne-Wepster & Bonne 1920
Spissipes Section
Crybda Group
Pedroi Subgroup
130- *Cx.* (*Mel.*) *adamesi* Sirivanakarn & Galindo 1980 (see Note 21)
131- *Cx.* (*Mel.*) *epanastasis* Dyar 1922 (see Note 22)
132- *Cx.* (*Mel.*) *pedroi* Sirivanakarn & Belkin 1980 (see Note 22)
Faurani Group
133- *Cx.* (*Mel.*) *faurani* Duret 1968 (see Note 22)
Jubifer Group
- *Cx.* (*Mel.*) *jubifer* Komp & Brown 1935 (see Note 23)
- *Cx.* (*Mel.*) *simulator* Dyar & Knab 1906 (see Note 23)
Spissipes Group
134- *Cx.* (*Mel.*) *spissipes* (Theobald 1903) (see Note 22)
Taeniopus Group
135- *Cx.* (*Mel.*) *taeniopus* Dyar & Knab 1907 (see Note 22)
Vomerifer Group

136- *Cx.* (*Mel.*) *portesi* Senevet & Abonnenc 1941
137- *Cx.* (*Mel.*) *vomerifer* Komp 1932

Subgenus *Microculex* Theobald
138- *Cx.* (*Mcx.*) *chryselatus* Dyar & Knab 1919
139- *Cx.* (*Mcx.*) *imitator* Theobald 1903
140- *Cx.* (*Mcx.*) *pleuristriatus* Theobald 1903
141- *Cx.* (*Mcx.*) *reginae* Floch & Fauran 1955
142- *Cx.* (*Mcx.*) *stonei* Lane & Whitman 1943

Subgenus *Phenacomyia* Harbach & Peyton
143- *Cx.* (*Phc.*) *corniger* Theobald 1903

Subgenus *Tinolestes* Coquillett
144- *Cx.* (*Tin.*) *breviculus* Senevet & Abonnenc 1939
145- *Cx.* (*Tin.*) *cauchensis* Floch & Abonnenc 1945

Uncertain subgenus
146- *Cx. flochi* Duret 1969
147- *Cx. nigrimacula* Lane & Whitman 1943
148- *Cx. ocellatus* Theobald 1903
149- *Cx. punctiscapularis* Floch & Abonnenc 1946

Nomen dubium
- *Cx. americanus* Neveu-Lemaire 1902 (see Note 24)
- *Cx. nigrescens* (Theobald 1907) (see Note 24)

Genus *Deinocerites* Theobald
- *De. cancer* Theobald 1901 (see Note 25)
150- *De. magnus* (Theobald 1901)

Genus *Lutzia* Theobald

Subgenus *Lutzia* Theobald
151- *Lt.* (*Lut.*) *allostigma* Howard, Dyar & Knab 1915

TRIBE MANSONIINI

Genus *Coquillettidia* Dyar

Subgenus *Rhynchotaenia* Brethés
152- *Cq.* (*Rhy.*) *albicosta* (Peryassú 1908)
153- *Cq.* (*Rhy.*) *arribalzagae* (Theobald 1903)
154- *Cq.* (*Rhy.*) *fasciolata* (Lynch Arribálzaga 1891) (see Note 26)
155- *Cq.* (*Rhy.*) *lynchi* (Shannon 1931)
156- *Cq.* (*Rhy.*) *venezuelensis* (Theobald 1912)

Genus *Mansonia* Blanchard

Subgenus *Mansonia* Blanchard
157- *Ma.* (*Man.*) *humeralis* Dyar & Knab 1916
- *Ma.* (*Man.*) *flaveola* (Coquillett 1906) (see Note 27)
158- *Ma.* (*Man.*) *pseudotitillans* (Theobald 1901)
159- *Ma.* (*Man.*) *titillans* (Walker 1848)

TRIBE ORTHOPODOMYIINI

Genus *Orthopodomyia* Theobald
160- *Or. fascipes* (Coquillett 1906)

TRIBE SABETHINI

Genus *Johnbelkinia* Zavortink
- *Jb. leucopus* (Dyar & Knab 1906) (see Note 28)
161- *Jb. longipes* (Fabricius 1805)
162- *Jb. ulopus* (Dyar & Knab 1906) (see Note 28)

Genus *Limatus* Theobald
163- *Li. asulleptus* (Theobald 1903)
164- *Li. durhamii* Theobald 1901
165- *Li. flavisetosus* de Oliveira Castro 1935
166- *Li. martiali* Senevet & Abonnenc 1939
167- *Li. pseudomethysticus* (Bonne-Wepster & Bonne 1920)

Genus *_Onirion_ Harbach & Peyton
168- *_Onirion_ sp. cf. **Harbach & Peyton** (**2000**) (see Note 29)

Genus *_Runchomyia_ Theobald
Subgenus *_Ctenogoeldia_ Edwards
169- *_Ru. (Cte.) magna_ (Theobald 1905) (see Note 30)

Genus *Sabethes* Robineau-Desvoidy
Subgenus *Peytonulus* Harbach
- *Sa.* (*Pey.*) *aurescens* (Lutz 1905) (see Note 31)
- *Sa.* (*Pey.*) *identicus* Dyar & Knab 1907 (see Note 31)
170- *_Sa. (Pey.) hadrognathus_ Harbach 1995 (see Note 32)
171- *_Sa. (Pey.) paradoxus_ Harbach 2002 (see Note 32)
172- *_Sa. (Pey.) soperi_ Lane & Cerqueira 1942 (see Note 32)
173- *Sa.* (*Pey.*) *undosus* (Coquillett 1906)
Subgenus *Sabethes* Robineau-Desvoidy
174- *Sa.* (*Sab.*) *albiprivus* Theobald 1903
175- *Sa.* (*Sab.*) *belisarioi* Neiva 1908
176- *Sa.* (*Sab.*) *bipartipes* Dyar & Knab 1906
177- *Sa.* (*Sab.*) *cyaneus* (Fabricius 1805)
178- *Sa.* (*Sab.*) *purpureus* (Theobald 1901)
179- *_Sa. (Sab.) quasicyaneus_ Peryassú 1922 (see Note 33)
180- *Sa.* (*Sab.*) *tarsopus* Dyar & Knab 1908
Subgenus *Sabethinus* Lutz
181- *_Sa. (Sbn.) idiogenes_ Harbach 1994 (see Note 34)
182- *Sa.* (*Sbn.*) *intermedius* (Lutz 1904)
Subgenus *Sabethoides* Theobald
183- *Sa.* (*Sbo.*) *chloropterus* (von Humboldt 1819)

Genus *Shannoniana* Lane & Cerqueira
184- *Sh. fluviatilis* (Theobald 1903)
185- *Sh. schedocyclia* (Dyar & Knab 1908)

Genus *Trichoprosopon* Theobald
186- *Tr. compressum* Lutz 1905
187- *Tr. digitatum* (Rondani 1848)
188- *Tr. pallidiventer* (Lutz 1905)
189- *Tr. soaresi* Lane & Cerqueira 1942

Genus *Wyeomyia* Theobald
Subgenus **Caenomyiella* Harbach & Peyton
190- *Wy. (Cae.)* sp. cf. **Harbach & Peyton (1990)** (see Note 35)
Subgenus *Cruzmyia* Lane & Cerqueira
191- *Wy.* (*Cru.*) *forattinii* Clastrier 1974
Subgenus *Decamyia* Dyar
192- *Wy.* (*Dec.*) *pseudopecten* Dyar & Knab 1906
193- *Wy.* (*Dec.*) *ulocoma* (Theobald 1903)
Subgenus *Dendromyia* Theobald
194- *Wy.* (*Den.*) *complosa* (Dyar 1928)
195- *Wy.* (*Den.*) *luteoventralis* Theobald 1901
196- *Wy.* (*Den.*) *testei* Senevet & Abonnenc 1939
197- *Wy.* (*Den.*) *trifurcata* Clastrier 1973
198- *Wy. (Den.) ypsipola* Dyar 1922 (see Note 36)
Subgenus *Dodecamyia* Dyar
199- *Wy.* (*Dod.*) *aphobema* Dyar 1918
Subgenus **Hystatomyia* Dyar
200- *Wy. (Hys.) lamellata* (Bonne-Wepster & Bonne 1920) (see Note 37)
Subgenus **Miamyia* Dyar
201- *Wy. (Miamyia) oblita* (Lutz 1904) (see Note 38)
Subgenus *Phoniomyia* Theobald
202- *Wy.* (*Pho.*) *splendida* Bonne-Wepster & Bonne 1919
Subgenus *Prosopolepis* Lutz
- *Wy.* (*Prl.*) *confusa* (Lutz 1905) (see Note 39)
Subgenus *Spilonympha* Motta & Lourenço-de-Oliveira
203- *Wy.* (*Spi.*) *bourrouli* (Lutz 1905)
- *Wy.* (*Spi.*) *mystes* Dyar 1924 (see Note 40)
Subgenus *Triamyia* Dyar
204- *Wy.* (*Triamyia*) *aporonoma* Dyar & Knab 1906
Subgenus *Wyeomyia* Theobald
205- *Wy.* (*Wyo.*) *arthrostigma* (Lutz 1905)
206- *Wy.* (*Wyo.*) *pertinans* (Williston 1896)
207- *Wy.* (*Wyo.*) *pseudorobusta* Pajot & Fauran 1975
208- *Wy.* (*Wyo.*) *robusta* Senevet & Abonnenc 1939
Uncertain subgenus
209- *Wy. albosquamata* Bonne-Wepster & Bonne 1919
210- *Wy. argenteorostris* (Bonne-Wepster & Bonne 1920)
211- *Wy. chalcocephala* Dyar & Knab 1906 (see Note 41)
212- *Wy. clasoleuca* Dyar & Knab 1908
213- *Wy. compta* Senevet & Abonnenc 1939
214- *Wy. ininicola* Fauran & Pajot 1974
215- *Wy. melanocephala* Dyar & Knab 1906
216- *Wy. nigricephala* Clastrier & Claustre 1978
217- *Wy. occulta* Bonne-Wepster & Bonne 1919

218- *Wy. rorotai* Senevet Chabelard & Abonnenc 1942 (see Note 41)
219- *Wy. surinamensis* Bruijning 1959 (see Note 42)

TRIBE TOXORHYNCHITINI

Genus *Toxorhynchites* Theobald
Subgenus *Ankylorhynchus* Lutz
220- *Tx.* (*Ank.*) *trichopygus* (Wiedemann 1828)
Subgenus *Lynchiella* Lahille
221- *Tx. (Lyn.) guadeloupensis* (Dyar & Knab 1906) (see Note 43)
222- *Tx.* (*Lyn.*) *haemorrhoidalis haemorrhoidalis* (Fabricius 1787)
223- *Tx.* (*Lyn.*) *haemorrhoidalis superbus* (Dyar & Knab 1906)
- *Tx.* (*Lyn.*) *theobaldi* (Dyar & Knab 1906) (see Note 44)
224- *Tx. (Lyn.) moctezuma* (Dyar & Knab 1906) (see Note 44)

TRIBE URANOTAENIINI

Genus *Uranotaenia* Lynch Arribálzaga
Subgenus *Uranotaenia* Lynch Arribálzaga
225- *Ur.* (*Ura.*) *apicalis* Theobald 1903
226- *Ur.* (*Ura.*) *calosomata* Dyar & Knab 1907
227- *Ur.* (*Ura.*) *geometrica* Theobald 1901
228- *Ur.* (*Ura.*) *hystera* Dyar & Knab 1913
229- *Ur.* (*Ura.*) *leucoptera* (Theobald 1907)
230- *Ur.* (*Ura.*) *lowii* Theobald 1901
231- *Ur.* (*Ura.*) *mathesoni* Lane 1943
232- *Ur.* (*Ura.*) *nataliae* Lynch Arribálzaga 1891
233- *Ur.* (*Ura.*) *pallidoventer* (Theobald 1907)
234- *Ur.* (*Ura.*) *pulcherrima* Lynch Arribálzaga 1891
235- *Ur.* (*Ura.*) *socialis* Theobald 1901

NOTES

1. *Anopheles* (*Ano.*) *apicimacula* is mentioned by **Dyar** (**1928**) as occurring in the Guianas and reported as widespread in Suriname (**Bonne & Bonne-Wepster 1925**). **Dégallier and Claustre** (**1980**) are the first to report the presence of females in the localities of Guisanbourg, Kaw and Saül in French Guiana. Nonetheless, the authors argue that *An.* (*Ano.*) *apicimacula* females are indistinguishable from *An.* (*Ano.*) *intermedius* females and admit that these records need verification. Since then, morphological characters that permit the females of both species to be distinguished have been made available (**Dusfour *et al.* 2012a**). The recent reexamination of females (IPGF-1762, 1763, 1764, in part) has only permitted the confirmation of the presence of *An.* (*Ano.*) *intermedius.* The presence of *An.* (*Ano.*) *apicimacula* in French Guiana still needs to be confirmed; thus, it is not included here.

2. The recent revision of *An.* (*Ano.*) *mediopunctatus* s.l. has revealed that the nominal species has been largely confused throughout South America with the closely related *An.* (*Ano.*) *costai* (**Sallum *et al.* 1999**) and *An.* (*Ano.*) *forattinii* (**Wilkerson & Sallum 1999**). The geographical range of *An.* (*Ano.*) *mediopunctatus* is currently restricted to the coastal parts of the States of Rio de Janeiro and São Paulo, Brazil. Records of the presence of *An.* (*Ano.*) *mediopunctatus* should be interpreted as misidentifications and/or misinterpretations (not included). However, records of the presence of *An.* (*Ano.*) *costai* and *An.* (*Ano.*) *forattinii* have been confirmed from males captured in French Guiana (**Sallum *et al.* 1999; Wilkerson & Sallum 1999**); thus, they are included in the present list.

3. *Anopheles* (*Ano.*) *pseudopunctipennis* is known as widespread throughout much of the American Continent (**Lane 1953**), and the presence of this species is cited in French Guiana by the **WRBU** (**2015**). Nonetheless, there are neither existing materials nor confirmed records of the presence of this species in French Guiana. Furthermore, northeastern South America seems to have been spared this malaria vector, which is confirmed by the recent revision of that particular species (**Rueda *et al.* 2004**); thus, it is not included here.

4. As reported by **Fauran and Pajot** (**1974**), the presence of *An.* (*Ker.*) *bambusicolus*, *An.* (*Ker.*) *bellator*, *An.* (*Ker.*) *boliviensis*, *An.* (*Ker.*) *cruzii*, and *An.* (*Ker.*) *homunculus* was only noted in the Guianas by **Levi-Castillo** (**1949**). A revision of the subgenus *Kerteszia* by **Zavortink** (**1973**) confirmed the exclusion of all of these species, with the exception of *An.* (*Ker.*) *bellator* whose theoretical distribution includes French Guiana. However, there are neither existing materials nor confirmed records of the presence of these species in French Guiana; none of the species cited above are, therefore, included here.

5. *Anopheles* (*Nys.*) *strodei* was reported by **Senevet and Abonnenc** in **1938** and was subsequently considered synonymous with *An.* (*Nys.*) *evansae* (**Stone *et al.* 1959**) before being removed from synonymy by **Faran** in **1980**. There is no additional record after that by **Senevet and Abonnenc** of the presence of *An.* (*Nys.*) *strodei* or *An.* (*Nys.*) *evansae* in French Guiana. Furthermore, the identification made by these authors was questioned by **Fauran** (**1961**) as regards to the published illustration of the male genitalia that does not match the original description. A recent examination of only the male genitalia of these species (IPGF-09/SAU-014) in the collection at the Pasteur Institute of French Guiana confirms this supposition; these particular genitalia belong to the *An.* (*Nys.*) *triannulatus* s.l. species

complex. The presence of both *An.* (*Nys.*) *strodei* and *An.* (*Nys.*) *evansae* is doubtful and needs to be confirmed. Therefore, neither of these two species is included here.

6. The occurrence of *An.* (*Nys.*) *marajoara* from the Albitarsis group was recently confirmed in French Guiana using morphological identification and DNA barcoding (**Dusfour *et al.* 2012b**). This species is, therefore, included in the present list.

7. The presence of *An.* (*Nys.*) *argyritarsis* in French Guiana was cited by early authors (**Neveu-Lemaire 1902**) as *An. argyrotarsis* by **Laveran** (**1903**) and as *Cellia argyrotarsis* by **Thézé** (**1916**) and **Léger** (**1918**). **Floch and Abonnenc** (**1947a**) questioned records attributed to that species and considered them to be misidentifications of *An.* (*Nys.*) *pessoai*, the latter synonymous with *An.* (*Nys.*) *braziliensis* (**Lane 1953**). At this time, there is no confirmed record of *An.* (*Nys.*) *argyritarsis* in French Guiana. Therefore, the species is not included here.

8. The presence of *Ch. bathana* in French Guiana was cited for the first time by **Fauran and Pajot** (**1974**). They report the presence of this species near a small creek on the Oyapock River near the Petit-Massera rapids. This is the only citation and record of an unspecified number of adults of that species in French Guiana. Here, we point out the doubtfulness of this record based on the fact that, although **Harbach and Howard** (**2009**) include this species in French Guiana in a recent revision of the *Chagasia* genus, they do so without any additional examination of material from this area which is far to the east of their own, recent confirmed records. However, because collection specimens were not available to us, we decided not to make a decision regarding this species; therefore, we have kept it in the present list.

9. The presence of *Ae.* (*Och.*) *crinifer* was indicated by a unique adult individual from Cayenne, French Guiana (**Floch & Abonnenc 1944**). A revision of the Scapularis group of *Ochlerotatus* restricts this species to the Parana River system in Brazil, Paraguay and northeastern Argentina (**Arnell 1976**). Its presence in French Guiana should be interpreted as a misidentification and, thus, the species is not included here.

10. In French Guiana, the presence of *Ae.* (*How.*) *septemstriatus* was reported by **Floch and Abonnenc** (**1942a**) in the Rorota, Remire-Montjoly, French Guiana. A revision of the subgenus *Howardina* of the genus *Aedes* by **Berlin** (**1969**) concludes that the distribution of this species is restricted to Colombia, Costa Rica, Nicaragua and Panama. The only female

specimen available to us and tagged as *Ae.* (*How.*) *septemstriatus* (IPGF-09/SG052) has proven to be *Ae.* (*How.*) *arborealis*. Records indicating the presence of *Ae.* (*How.*) *septemstriatus* in French Guiana should be interpreted as misidentifications and, thus, the species is not included in the present list.

11. **Stone, Knight and Starcke** (**1959**) questioned the presence of *Hg.* (*Hag.*) *equinus* in the Guianas. Confirmed records exist for Guyana (**Arnell 1973**), but there is no record of this species in French Guiana. Even if *Hg.* (*Hag.*) *equinus* is widely distributed (**Arnell 1973**), nothing indicates that this species occurs in French Guiana. Therefore, the species is not included here.

12. Records of the presence of *Hg.* (*Hag.*) *spegazzinii* in French Guiana (**Fauran 1961**) are a result of the former synonymy with *Hg.* (*Hag.*) *janthinomys* (**Cerqueira 1943**). In addition, the latest revision of the genus *Haemagogus* shows that the distribution of this species is almost entirely restricted to the lower Amazon (**Arnell 1973**). For these reasons, *Hg.* (*Hag.*) *spegazzinii* is not included in the present list.

13. Certainly because of the former synonymy with *Ps.* (*Jan.*) *lutzii*, there are no clear citations in the early literature of the presence of *Ps.* (*Jan.*) *albipes* in French Guiana. The collection campaign of the project "Mosquitoes of Middle America" conducted in French Guiana (**Heinemann & Belkin 1978**) reports that a *Psorophora* species was captured at the base of the Montagne Tigre, Cayenne, which could be attributed to *Ps.* (*Jan.*) *albipes*. We cannot rely on this citation because of the uncertainty of the identification. However, a recent examination of several females (IPGF-07/GST119, 120, 08/COF045, in part) sampled from six sites and stored in the collection at the Pasteur Institute of French Guiana confirms the presence of this species in French Guiana; thus, *Ps.* (*Jan.*) *albipes* is included in the present list.

14. **Lane** (**1953**) indicated the presence of *Ps.* (*Pso.*) *ciliata* from southern Canada to Argentina. Nevertheless, to the best of our knowledge, there is no record whatsoever of this species in French Guiana. Therefore, the species is not included in the present list.

15. The *Cx.* (*Car.*) *iridescens* reported by **Senevet and Abonnenc** (**1939a**) were without a doubt confused with *Cx.* (*Car.*) *bonnei.* As **Fauran** (**1961**) pointed out, *Cx.* (*Car.*) *iridescens*

is restricted to sites typically associated with the Parana River system southward from the State of Espirito Santo to the State of Parana in Brazil (**Valencia 1973**). The latter species is therefore not included in the present list.

16. *Culex* (*Cux.*) *brevispinosus* was first recorded in Maripasoula during the collection campaign of the project "Mosquitoes of Middle America" conducted in French Guiana (**Heinemann & Belkin 1978**). The presence of this species was originally reported in Suriname (**Bonne & Bonne-Wepster 1920**) and is, thus, included in the present list.

17. *Culex* (*Cux.*) *janitor* was first recorded by **Floch and Abonnenc** (**1942a**, **1942b**, **1947b**). As **Fauran** (**1961**) believed, the revision of the Culicids of Jamaica restricts this species to Hispaniola, Jamaica and Puerto Rico (**Belkin *et al.* 1970**). These records, based on captured females, should be attributed to another closely related species. Thus, *Cx.* (*Cux.*) *janitor* is not included in this list.

18. The presence of *Cx.* (*Cux.*) *pseudojanthinosoma* in French Guiana was first reported by **Senevet and Abonnenc** (**1946**) on the basis of three females and associated larval and pupal skins. Unfortunately, there are no existing data on the type of site or even indications on the type of water collection used for that species. Nonetheless, this species is considered valid (**Belkin 1968**) and is, thus, included in the present list.

19. The presence of *Cx.* (*Mel.*) *educator* was reported by **Fauran** (**1961**) in Tonate and the Rorota, Remire-Montjoly, French Guiana. This species was considered a senior synonym of *Cx.* (*Mel.*) *vaxus* (**Dyar 1923**) until the latter species was resurrected (**Forattini & Sallum 1993**). The redescription of both species has permitted records of the presence of *Cx.* (*Mel.*) *vaxus* to be confirmed in French Guiana (**Forattini & Sallum 1993**). The presence of *Cx.* (*Mel.*) *educator* in French Guiana still needs confirmation and, thus, is not included here; however, *Cx.* (*Mel.*) *vaxus* has been added to the present list.

20. The presence of *Cx.* (*Mel.*) *clarki* was reported in French Guiana by **Floch and Abonnenc** (**1947b**). This species was consequently synonymized with *Cx. nigrescens* (**Rozeboom & Komp 1950**, but see Note 24) and resurrected 13 years later (**Casal 1963**). Currently, confirmed records of *Cx.* (*Mel.*) *clarki* are restricted to Argentina, Brazil, Paraguay,

Uruguay and Venezuela (**Pecor *et al.* 1992; Rossi & Martinez 2003**). This species is, therefore, not included here.

21. *Culex* (*Mel.*) *adamesi* was newly described by **Sirivanakarn and Galindo** (**1980**) on the basis of 84 specimens, including two individuals from French Guiana captured during the campaign of the project "Mosquitoes of Middle America" (**Heinemann & Belkin 1978**). These two specimens represent the only records of that species in French Guiana; nevertheless, *Cx.* (*Mel.*) *adamesi* is included in the present list of mosquitoes in French Guiana.

22. A valuable study of the Spissipes Section of *Culex* (*Melanoconion*) enabled the redefinition of related species and the clarification of synonyms (**Sallum & Forattini 1996**). In short, a reexamination of materials from French Guiana has permitted both the confirmation of the presence of *Cx.* (*Mel.*) *taeniopus* and the addition of new records for *Cx.* (*Mel.*) *epanastasis*, *Cx.* (*Mel.*) *faurani*, *Cx.* (*Mel.*) *pedroi* and *Cx.* (*Mel.*) *spissipes* (**Sallum & Forattini 1996**). All the previously cited species have thus been added to the present list.

23. *Culex* (*Mel.*) *jubifer* was only mentioned by **Fauran and Pajot** (**1974**) as being present in Camopi, French Guiana, without any other indication. It appears that this species is restricted to Central America and seems to have been largely confused with *Cx.* (*Mel.*) *simulator* (**Sallum & Forattini 1996**). Mention of the presence of *Cx.* (*Mel.*) *jubifer* in French Guiana should be attributed to *Cx.* (*Mel.*) *simulator*; nevertheless, considering the paucity of the record and especially the absence of confirmed records, neither of these species is included.

24. Typical examples of the male genitalia of *Cx. americanus* and *Cx. nigrescens* have to be considered respectively as non-existent and lost (**Belkin *et al.* 1971; Sirivanakarn 1982**). As a result, both species are considered *nomen dubium*. Even if records of the presence of these species exist in French Guiana (e.g. **Floch 1944**), because of their status, these records could not be verified and thus cannot be considered reliable. These two species are therefore not included.

25. The presence of *De. cancer* is mentioned in Kourou, French Guiana by **Floch and Abonnenc** (**1947c**). The revision of the genus *Deinocerites* revealed that the geographical

range of this species is limited to the south by the Bocas del Toro province in Panama (**Adames 1971**). The record of the presence of this species in French Guiana should be interpreted as the result of misidentifications and, as such, the species is not included in the list.

26. *Coquillettidia* (*Rhy.*) *fasciolata* is a species recorded for the first time in the collections of the project "Mosquitoes of Middle America" (**Heinemann & Belkin 1978**). Thus, it has been added to the present list as belonging to the culicid fauna of French Guiana.

27. The presence of *Ma.* (*Man.*) *flaveola* was reported in French Guiana in Cayenne and in the region of Saut-Tigre (**Floch & Abonnenc 1942b, 1947c**). Because its distribution range seems restricted to Jamaica and Puerto Rico (**Belkin *et al.* 1970**), reports of this species in French Guiana should be considered misinterpretations. Therefore, the species is not included here.

28. The presence of *Jb. leucopus* in French Guiana was recorded by **Floch and Abonnenc** (**1942b**). In the preliminary reclassification of the genus *Trichoprosopon* s.l., **Zavortink** (**1979**) restricts the presence of this species to Costa Rica, Nicaragua and Panama. Reports of this species in French Guiana should be interpreted as misidentifications of *Jb. ulopus*, a species which has actually been confirmed to be present in French Guiana (**Zavortink 1979**). *Johnbelkinia leucopus* is therefore not included in the present list.

29. Samples of larvae of the genus *Onirion* were obtained from broken and perforated bamboo (*Bambusa vulgaris* and *Guadua* sp.) at two localities: in the regions of Montsinéry (Ecofog-MB10351, 0618, 0637) and Saül (Ecofog-MB10731-0733, in part), French Guiana. This is the first time that species of the genus *Onirion* have been reported in French Guiana. Collected fourth instar larvae were identified as *On. brucei* (**Del Ponte & Cerqueira 1938**) based on criteria proposed by **Harbach and Peyton** (**2000**). However, because the authors admit that the larvae cannot without a doubt be attributed to the seven recognized species and because of the great geographical distance with other records (**Harbach & Peyton 2000**), we decided to withhold judgement on the specific identification until we are able to study males.

30. The presence of *Ru.* (*Cte.*) *magna* was reported in Suriname by **Bonne and Bonne-Wepster** (**1925**). We report here the presence of this species in French Guiana from larval

collection conducted on the leaf axils of *Ischnosiphon* sp (Marantaceae) in the regions of Montsinéry and Saül. These records, based on the examination of several fourth instar larvae (Montsinéry, Ecofog-MB10591-0593, in part; and Saül, Ecofog-MB10781-0783, in part) and link-reared females (Ecofog-MB10557, 0800), represent the first report of the presence of this genus in French Guiana.

31. *Sabethes* (*Pey.*) *aurescens* is mentioned by **Senevet *et al.*** (**1942**) from an unknown Guianese location. In his "Annotated Catalog of the Mosquitoes of French Guiana" (**1961**), **Fauran** reiterated the relative uncertainty surrounding the identification of that species based on a single female and, finally, noted that the primary description matched closely with the depiction of *Sa.* (*Pey.*) *identicus*. The report of the presence of that mysterious *Peytonulus* is intriguing, but definitely needs verification (but see Note 31); thus, neither of the two species are included here.

32. *Sabethes* (*Pey.*) *hadrognathus* (Ecofog-MB10794, 0798), *Sa.* (*Pey.*) *paradoxus* (Ecofog-MB10793, 0797) and *Sa.* (*Pey.*) *soperi* (Ecofog-MB10795, 0799) larvae were collected from perforated bamboo internodes (*Guadua latifolia*) found in the region of Saül, French Guiana. Given the unique features presented by immature individuals of these species, the specimens were identified as fourth instar larvae based on original descriptions (respectively, **Lane & Cerqueira 1942; Harbach 1995a; Harbach & Howard 2002**). The presence of these three species in French Guiana is reported for the first time.

33. We report here for the first time the presence of *Sa.* (*Sab.*) *quasicyaneus* in French Guiana. This record is based on the examination of three females captured on human bait at the three following sites: Kourou (IPGF-10/KOU-1071), Macouria (IPGF-09/MAC-4482) and Saint Georges (IPGF-09/SG-2545), French Guiana.

34. *Sabethes* (*Sbn.*) *idiogenes* larvae were collected from perforated *Guadua* sp. internodes growing along riverbanks at La Trinité, Saint-Elie, French Guiana. Identification was based on several link-reared male specimens (Ecofog-ST10269, 0270, 0271, in part). *Sabethes* (*Sbn.*) *idiogenes*, only known from the type locality in southeastern Peru (**Harbach 1994**), is reported in French Guiana for the first time.

35. The subgenus *Caenomyiella* of the genus *Wyeomyia* was proposed by **Harbach and Peyton** (**1990**) after the redescription of *Wy.* (*Cae.*) *fernandezyepezi* (Cova Garcia, Sutil Oramas & Pulido F. 1974) formerly known as *Sabethes fernandezyepezi*, and of a distinct species temporarily identified as *Wy.* (*Cae.*) species 69. This subgenus is known from Panama, Colombia, and Venezuela where the locality of La Raya constitutes the record nearest to French Guiana. We discovered *Wy.* (*Cae.*) sp. larvae (Ecofog-ST10117, 0118) from collection in the leaf axils of *Guzmania lingulata* growing on the slopes (600 m above sea level) of Mont Itoupé, Camopi, French Guiana. This discovery in one of the most remote areas of French Guiana was made possible by the DIADEMA project (CEBA, ref. ANR-10-LABX-25-01). Considering that our two fourth instar larvae show some discrepancies with the description of *Wy.* (*Cae.*) *fernandezyepezi*, we decided to withhold judgement on the specific identification until we are able to study males. The presence of this subgenus of *Wyeomyia* is reported in French Guiana for the first time.

36. *Wyeomyia (Den.) ypsipola* were sampled at the larval stage in the leaf axils of different plant-held waters (Marantaceae and Cyclanthaceae) at the three following sites: Kaw (Ecofog-MB10772, ST10204, 0205), Montsinéry (Ecofog-MB10551, 0552) and Petit-Saut (Ecofog-MB10602-0604, in part), French Guiana. Identifications were made on fourth instar larvae based on the invaluable key proposed by **Motta and Lourenço-de-Oliveira** (**2000**) in their revision of the subgenus *Dendromyia* of the *Wyeomyia*. These constitute the first records of the presence of this species in French Guiana; therefore, it is included here.

37. Preliminary identifications for the project "Mosquitoes of Middle America" (**Heinemann & Belkin 1978**) reported the presence of an unidentified species of the subgenus *Hystatomyia* from larval collection in bromeliad leaf axils along the Sinnamary River. We obtained several *Hystatomyia* larvae from *Vriesea splendens* leaf axils at Petit-Saut on the Sinnamary River (Ecofog-MB10043-0045, in part) and from the La Virginie inselberg (Ecofog-MB10209-0211, in part), both in French Guiana. Examinations of genitalia mounted on microscope slides (Ecofog-ST10186, 0190-0193) permitted us to confirm that the specimens belong to *Wy. (Hys.) lamellata*; thus, this species has been included in the present list.

38. *Wy.* (*Wyo.*) *oblita* Theobald 1907 (*nec* Lutz 1904) was reported by **Floch and Abonnenc** (**1947c**) from larval collection in bamboo at the Rorota, Remire-Montjoly, French

Guiana. Because of the ancient synonymy with *Wy.* (*Wyo.*) *medioalbipes*; these records refer without a doubt to *Wy.* (*Wyo.*) *pertinans* (**Fauran 1961**). A few larvae of *Wy.* (*Miamyia*) *oblita* (Lutz 1904) were sampled in perforated *Guadua latifolia* internodes at the locality of Saül, French Guiana. Identification was based on fourth instar larvae (Ecofog-MB10844, 0853, 0854) and one link-reared male (Ecofog-ST10275). These records constitute the first citation of the subgenus *Miamyia* of *Wyeomyia* in French Guiana.

39. The presence of *Wy.* (*Prl.*) *confusa* was reported from an unknown number of females captured at Montagne Tigre, Cayenne (**Floch 1949**). Unfortunately, the report in which this observation was written is missing from the archives of the Pasteur Institute of French Guiana. Finally, the revision of the Flui Group by **Lourenço-de-Oliveira *et al.*** (**1999**) concluded that *Wy.* (*Prl.*) *confusa* is only known to be present in Brazil and is restricted to the Atlantic rainforest system between the latitudes 8° and 30°S. Records of the presence of this species in French Guiana should be interpreted as misidentifications and therefore the species is not included in the present list.

40. The presence of *Wy.* (*Spi.*) *mystes* was reported from a unique female from Montagne Tigre, Cayenne, French Guiana (**Floch & Abonnenc 1947c**). Considering that the characters which can distinguish different species within the *Spilonympha* subgenus were unknown at that time (**Motta & Lourenço-de-Oliveira 2005**), the record of the presence of this species in French Guiana is definitely not reliable. Therefore, the species is not included here.

41. *Wyeomyia luciae* and *Wy. rorotai* were both originally described from French Guiana (**Senevet *et al.* 1942**). These species were synonymized by **Lane** in **1951** to *Wy. chalcocephala* and *Wy. pseudopecten*, respectively. Seventeen years later, a reexamination of both species by **Belkin** (**1968**) resulted in their resurrection. However, *Wy. luciae* is still considered a synonym of *Wy. chalcocephala* in **Knight and Stone**'s catalog (**1977**) certainly because **Belkin** (**1968**) did not make a clear-cut statement on this species. The taxonomic status of *Wy. luciae* is definitely ambiguous, but, because we chose to use the catalog by **Knight and Stone** (**1977**) for species validity, we decided to keep *Wy. chalcocephala* in the present list until more information becomes available on this species.

42. *Wyeomyia surinamensis* was originally described by **Bruijning** (**1959**) in his "Notes on the *Wyeomyia* Mosquitoes of Suriname". Sampling for the project "Mosquitoes of Middle America" reports the presence of this species in pieces of cut or broken bamboo at Montagne Tigre, Cayenne, French Guiana (**Heinemann & Belkin 1978**). We obtained several larvae (Ecofog-MB10482-0487), both males (Ecofog-MB10550, 0579, 0587, 0656) and females (Ecofog-MB10533, 0555, 0561), with associated pupal skin from pieces of cut bamboo (*Bambusa vulgaris*) in Matoury, French Guiana; therefore, this species has been included in the present list.

43. We are the first to report the presence of *Tx.* (*Lyn.*) *guadeloupensis* in French Guiana. Specimens were sampled as larvae from pieces of cut bamboo (*Bambusa vulgaris*) in the region of Montsinéry, French Guiana. Identification was based on three specimens including one link-reared female (Ecofog-MB10540) and two fourth instar larvae (Ecofog-MB10638, 0639). The species is, thus, included in the list.

44. The presence of *Tx.* (*Lyn.*) *theobaldi* was reported in the region around the Oyapock River by Fauran in a mysterious unpublished report (but see **Fauran 1961**). A recent examination of the lectotype from Bogota by **Zavortink and Chaverri** (**2009**) has led to the restriction of *Tx.* (*Lyn.*) *theobaldi* to its typical locality, and to the resurrection of *Tx.* (*Lyn.*) *moctezuma* and *Tx.* (*Lyn.*) *hypoptes*. Records of the presence of *Tx.* (*Lyn.*) *theobaldi* in French Guiana should be seen as misidentifications of the species. The recent examination of a male captured at the Montagne des Singes, Kourou, French Guiana (Ecofog-ST10035) confirms the existence of at least one species with white markings in males in the Guianese *département*. Our male specimen matches the description of *Tx.* (*Lyn.*) *moctezuma*, which extends the eastern geographical distribution of that species to French Guiana.

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Chapitre 2: A DNA reference library of French Guiana mosquitoes for barcoding (Talaga *et al.*, en préparation)

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Abstract: The mosquito family (Diptera: Culicidae) constitutes the most medically important group of arthropods because of the ability of certain species to transmit pathogens to humans. In some parts of the world, the diversity is so high that the accurate delimitation and/or identification of species is challenging. During the last decade a DNA-based identification system for all animals on the planet was proposed, the so-called DNA barcoding approach. In this study, we used this approach to examine the mosquito fauna of French Guiana. Our objectives were (i) to establish a DNA barcode library for the French Guiana mosquito fauna and (ii) to evaluate its utility in delimiting and identifying species. A total of 274 specimens belonging to 76 morphologically identified species or morphospecies were analyzed. Analyses allowed to delimit 87 DNA clusters with only 22 of them already present in the BOLD database. We thus provide a substantial contribution to the global mosquito barcoding initiative. Our results confirm that the COI barcode can be successfully used to delimit and identify mosquito species with only a few cases where the marker could not distinguish closely related species. Our results also confirm the presence of new species identified based on morphology plus potential cases of cryptic species.

Keywords: Culicidae, Diversity, DNA taxonomy, Neotropics, Species delimitation, Vector.

INTRODUCTION

The mosquito family (Diptera: Culicidae) is composed of 3,549 valid species distributed throughout most types of ecosystems worldwide (**Harbach 2015**). It also constitutes the most medically important group of arthropods because of the ability of certain species to transmit pathogens to humans, causing major health issues in some parts of the world (**Gubler 1998**). In French Guiana, a French overseas region (84,000 km²) situated in South America, mosquito-borne diseases are frequent. Malaria is transmitted by *Anopheles* species mainly in inland areas of the territory (**Dusfour *et al.* 2012**), whereas dengue, chikungunya and zika are transmitted by *Aedes* (*Stegomyia*) *aegypti* in urban areas (**Fouque *et al.* 2001; Chouin-Carneiro *et al.* 2016**). Furthermore, many lesser known crypto-arboviroses occur in rural and/or sylvan environments (**Chippaux *et al.* 1983**). Because these pathogens are often transmitted by a limited number of vector species, their precise taxonomic identification is of primary importance for medical entomology.

French Guiana harbors one of the highest relative species densities of mosquitoes anywhere in the world (**Foley *et al.* 2007, 2008**). A recent revision of the mosquitoes of French Guiana established that 235 species can be found in the territory to date (**Talaga *et al.* 2015b**). In this situation, identification based on morphological characteristics can be challenging, especially when basic descriptive references are obsolete or incomplete. Even when a complete description is available, morphological identification also entails several operational drawbacks. First, for many species only the adults are known, which can prevent the identification of immature stages if not reared in the laboratory. Second, morphological identification is often reliable only when the adults are in perfect condition, which is rarely the case with field-caught specimens subjected to natural and/or sampling-induced damages.

Hebert *et al.* (**2003b**) proposed using the mitochondrial gene cytochrome *c* oxidase subunit I (COI) as DNA-based identification system for all animals on the planet, the so-called DNA barcoding approach. Despite the limitations of the method (**Moritz & Cicero 2004**), COI barcoding has also proven to be reliable in delimiting species for many groups of organisms like ants, birds or fishes (**Smith *et al.* 2005; Hebert *et al.* 2004a; Ward *et al.* 2005**). The suitability of the COI gene for species identification was first tested for mosquitoes by **Cywinska *et al.*** (**2006**) on 37 species occurring in Canada. Since then, barcoding has been used for mosquito species in many parts of the world, including India (**Kumar *et al.* 2007**), Iran (**Azari-Hamidian *et al.* 2010**), China (**Wang *et al.* 2012**), Argentina (**Laurito *et al.* 2013**), Amazonian Ecuador (**Linton *et al.* 2013**), Pakistan (**Ashfaq**

***et al.* 2014**), Singapore (**Chan *et al.* 2014**), Belgium (**Versteirt *et al.* 2015**) and Colombia (**Rozo-Lopez & Mengual 2015**). In most cases, these studies show a high correspondence between morphological species delimitation and mtDNA barcode clusters, but others point out the inability of the method to separate some closely related species distinguished by traditional taxonomy (**Laurito *et al.* 2013**).

In this study, our objectives were (i) to establish a DNA barcode library for the French Guiana mosquito fauna and (ii) to evaluate its utility in identifying and delimiting species.

MATERIAL AND METHODS

Sampling and a priori *identification*

The sampling was conducted in various locations and habitats in French Guiana, between 2013 and 2015 (**Talaga *et al.* 2015c**). Immature container-breeding mosquitoes were collected by pouring water out using a great variety of sucking devices in order to fit the great variety of structures and water volumes. On several occasions natural and artificial ovitraps were used, including bamboo stumps and artificial bromeliads installed at ground or canopy level. Immature mosquitoes from larger bodies of water were collected using a kick net. Adult mosquitoes were attracted in the field by human bait and captured using a butterfly net or, if setteled, a tube. All of the samples used in this study were integrated into an online database record (**Talaga *et al.* 2015c**) available through the Global Biodiversity Information Facility (GBIF) data portal at http://www.gbif.org/dataset/5a8aa2ad-261c-4f61-a98e-26dd752fe1c5/ or through the Guyanensis platform (http://guyanensis.ups-tlse.fr/).

Whenever possible, samples were brought back alive to the laboratory. Immature mosquitoes were individually reared in 2 mL tubes and placed in an environmental chamber at 28°C in order to obtain adults. When a sufficient number of adults was obtained, some of them were stored in individual tubes containing 96 % ethanol. Fourth instar and pupal skins were also sorted and stored in individual tubes containing 70 % ethanol. Reared adults and those captured in the field were freeze-killed. Three legs from the right lateral side of each specimen were then carefully dissected on ice and kept in a separate vial containing 96 % ethanol and stored at -20°C for further molecular investigations. Adults were mounted on their right side on a pin point and stored in entomological boxes. Specimen codes are based on the name of the collection followed by a unique serial number as proposed by **Gaffigan and Pecor** (**1997**). The same code was used for all of the biological material issued from the same specimen. When it was not possible to bring live samples back to the laboratory or to rear

them, specimens were stored directly in the field in 96 % ethanol. The identifications of specimens to the species level were made by the first author, most often based on the examination of both immature and adult specimens, and by using the latest publications on the genus or on the subgenus concerned (see **Talaga *et al.* 2015b**).

Sequencing and data analyses

DNA was extracted from two legs of each adult specimen or from a larva head (**Table 2.1**) using the DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA). The standard 658 base pairs barcode of the mitochondrial cytochrome *c* oxidase subunit I gene (COI) was amplified using the primers LCO1490/HCO2198 (**Folmer *et al.* 1994**). The total PCR volume was 25 µL and consisted of 2.5 µL of 10X reaction buffer, 2 µL of 2.5 mM dNTPs, 2 µL of 25 mM $MgCl_2$, 0.5 µL of each 10 µM primer, 0.2 µL of 5U/L Taq Polymerase, 15.3 µL of H_2O and 2 µL of template DNA. The PCR cycles were as follows: 94°C for 2 min, 40 cycles of 94°C for 30 s, 49°C for 45 s and 72°C for 45 s, and then a final extension at 72°C for 1 min. The products were verified on 2 % agarose gel and were commercially sequenced on an ABI3730 by Genoscreen. Forward and reverse sequences were edited and assembled using Geneious 9 (http://www.geneious.com/; **Kearse *et al.* 2012**). All sequences were uploaded to the Barcode of Life Data Systems (BOLD; **Ratnasingham *et al.* 2007**) and are available under the FGMOS project.

We used the REfin Single Linkage clustering approach (RESL; **Ratnasingham & Hebert 2013**) to define Barcode Index Numbers (BINs) based on our COI dataset. The RESL algorithm has the advantage of using a two-step procedure: an initial clustering at a 2.2 % divergence threshold followed by a refinement step using Markov clustering. In addition, it uses all of the sequences present in the BOLD database for clustering, allowing for a direct comparison of our dataset with sequences produced from other barcoding projects such as ACMC (Mosquitoes of North America), CULBE (DNA barcoding of Belgian mosquito species), MEA (Mosquitoes of the Ecuadorian Amazon) or mined from Genbank (BBDCU).

RESULTS

A total of 274 morphologically identified specimens belonging to 76 species or morphospecies were analyzed (**Table 2.1**). The RESL clustering approach applied to the COI marker permitted us to distinguish 87 BINs (**Table 2.2**). The results of the clustering approach

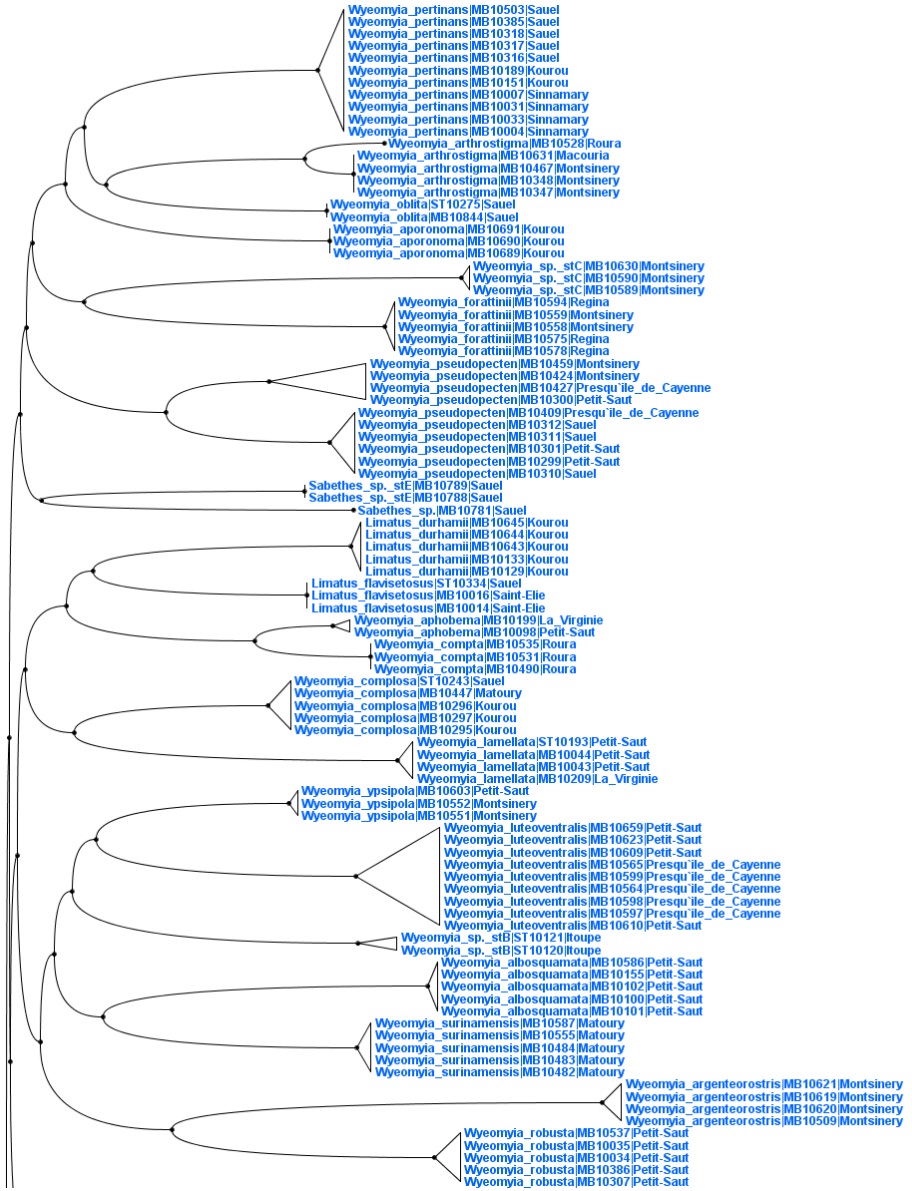
were largely congruent with the morphological delimitations (**Fig. 2.1**). We found one case where two nominal species (namely, *Cx.* (*Car.*) *infoliatus* and *Cx.* (*Car.*) *urichii*) were clustered into a single BIN (AAG3837). In 11 cases, nominal species were split into one or more BINs; namely, *Ae.* (*Och.*) *serratus* (BINs AAN3110 and ACF2113), *Cx.* (*Mcx.*) *stonei* (BINs ACZ3799, ACZ4071 and ACZ4175), *Ru.* (*Cte.*) *magna* (BINs ACZ3754 and ACZ3755), *Sa.* (*Pey.*) *hadrognathus* (BINs ACZ3825 and ACZ3826), *Sh. fluviatilis* (BINs ACZ4319 and ACZ4320), *Sh. schedocyclia* (BINs ACZ3895 and ACZ3896), *Tr. digitatum* (BINs AAG3842 and ACZ3792), *Tr. pallidiventer* (BINs ACZ3837 and ACZ3838), *Wy.* (*Dec.*) *pseudopecten* (BINs AAG3839 and ACZ4104), *Wy.* (*Wyo.*) *arthrostigma* (BINs ACZ3855 and ACZ3856) and *Tx.* (*Lyn.*) *haemorrhoidalis superbus* (BINs ACZ3913, ACZ3996 and ACZ4119).

Table 2.1 List of the mosquito species or morphospecies (hereafter 'taxa') corresponding to the voucher specimens that were COI sequenced in this study. Taxa are listed alphabetically and ranked by subfamily, tribe, genus and subgenus. The life stage is indicated for each taxa (M: male; F: female; L: larvae).

Species/morphospecies	Voucher specimen	Life stage
Anophelinae		
Anopheles (*Anopheles*) *eiseni* Coquillett 1902	ST10078, ST10226	M/L
Anopheles (*Kerteszia*) *neivai* Howard, Dyar & Knab 1913	MB10165, MB10252, MB10253, MB10254	F/L
Culicinae: Aedini		
Aedes (*Georgecraigius*) *fluviatilis* (Lutz 1904)	MB10723, MB10724	L
Aedes (*Ochlerotatus*) *scapularis* (Rondani 1848)	ST10038, ST10040, ST10288	F/L
Aedes (*Ochlerotatus*) *serratus* (Theobald 1901)	ST10046, ST10048, ST10286	F/L
Aedes (*Howardina*) *arborealis* Bonne-Wepster & Bonne 1920	ST10102, ST10103	L
Aedes (*Stegomyia*) *aegypti* (Linnaeus 1762)	ST10178, MB10185, MB10186	M/F/L
Haemagogus (*Haemagogus*) *janthinomys* Dyar 1921	MB10692, MB10693, ST10222	F/L
Psorophora (*Janthinosoma*) *ferox* (von Humboldt 1819)	ST10041, ST10049, ST10293	F/L
Culicinae: Culicini		
Culex (*Carrollia*) *infoliatus* Bonne-Wepster & Bonne 1920	MB10038, MB10039	M/F
Culex (*Carrollia*) *urichii* (Coquillett 1906)	ST10175, ST10188, ST10194	M/F/L
Culex (*Carrollia*) sp.stI	MB10840, ST10257, ST10258	M/F/L
Culex (*Culex*) *coronator* Dyar & Knab 1906	MB10046, MB10049, ST10322, ST10323, ST10326	M/F/L
Culex (*Culex*) *mollis* Dyar & Knab 1906	MB10225, MB10226, MB10227	L
Culex (*Culex*) *quinquefasciatus* Say 1823	MB10474, MB10475, MB10476, MB10496, MB10499	M/F/L
Culex (*Microculex*) *imitator* Theobald 1903	MB10810, MB10811	L
Culex (*Microculex*) *pleuristriatus* Theobald 1903	MB10159, MB10166, MB10231, MB10232, MB10233	M/F/L
Culex (*Microculex*) *stonei* Lane & Whitman 1943	MB10154, MB10156, MB10173, MB10240, MB10241, MB10242	M/F/L
Culex (Uncertain) *nigrimacula* Lane & Whitman 1943	MB10236, MB10237, MB10238	L
Culex (Uncertain) *ocellatus* Theobald 1903	MB10246, MB10247, MB10248, ST10187, ST10201	M/F/L
Culex sp.stJ	MB10030, MB10806, MB10807	F/L
Culex sp.stK	ST10310, ST10311	L
Culex sp.stL	ST10180	F

Lutzia (*Lutzia*) *allostigma* Dyar & Knab 1915	ST10002, ST10003	M/F
Culininae: Orthopodomyiini		
Orthopodomyia fascipes (Coquillett 1906)	ST10356, ST10357	L
Culicinae: Sabethini		
Johnbelkinia longipes (Fabricius 1805)	MB10278, MB10279, MB10280, MB10399, MB10462, MB10802	M/F/L
Johnbelkinia ulopus (Dyar & Knab 1906)	MB10683, MB10802	M/F/L
Limatus durhamii Theobald 1901	MB10129, MB10133, MB10643, MB10644, MB10645	M/F/L
Limatus flavisetosus de Oliveira Castro 1935	MB10014, MB10016, ST10334	M/F/L
Onirion sp.stA	MB10351, MB10618, MB10637, ST10280, ST10282	M/F/L
Runchomyia (*Ctenogoeldia*) *magna* (Theobald 1905)	MB10557, MB10591, MB10592, MB10593, ST10245	M/F/L
Sabethes (*Peytonulus*) *hadrognathus* Harbach 1995	MB10794, MB10798, ST10208	M/L
Sabethes (*Peytonulus*) *paradoxus* Harbach 2002	MB10793, MB10797	L
Sabethes (*Peytonulus*) *soperi* Lane & Cerqueira 1942	MB10795, ST10248, ST10264	M/F/L
Sabethes (*Peytonulus*) *undosus* (Coquillett 1906)	MB10339, MB10340, MB10341, MB10450, MB10662	M/F/L
Sabethes (*Peytonulus*) sp.stD	ST10059	L
Sabethes (*Sabethes*) *cyaneus* (Fabricius 1805)	ST10091	F
Sabethes (*Sabethes*) *purpureus* (Theobald 1901)	MB10782	L
Sabethes (*Sabethes*) sp.stE	MB10788, MB10789	L
Sabethes (*Sabethes*) sp.stM	MB10781	L
Sabethes (*Sabethinus*) *idiogenes* Harbach 1994	MB10849, ST10269, ST10276	M/F/L
Sabethes (*Sabethinus*) sp.stF	MB10845, ST10267	F/L
Shanoniana fluviatilis (Theobald 1903)	MB10816, ST10214	M/L
Shanoniana schedocyclia (Dyar & Knab 1908)	MB10817, ST10061, ST10062, ST10241, ST10249	M/F/L
Trichoprosopon compressum Lutz 1905	ST10251	M
Trichoprosopon digitatum (Rondani 1848)	MB10001, MB10002, ST10350	M/F/L
Trichoprosopon pallidiventer (Lutz 1905)	MB10796, ST10247, ST10233	M/F/L
Trichoprosopon sp.stG	MB10832	L
Trichoprosopon sp.stH	ST10209	F
Wyeomyia (*Caenomyiella*) sp.stB	ST10120, ST10121	L
Wyeomyia (*Cruzmyia*) *forattinii* Clastrier 1974	MB10558, MB10559, MB10575, MB10578, MB10594	F/L
Wyeomyia (*Decamyia*) *pseudopecten* Dyar & Knab 1906	MB10299, MB10300, MB10301, MB10310, MB10311, MB10312, MB10409, MB10424, MB10427, MB10459	M/F/L

Wyeomyia (*Dendromyia*) *complosa* (Drar 1928)	MB10295, MB10296, MB10297, MB10447, ST10243	M/F/L
Wyeomyia (*Dendromyia*) *luteoventralis* Theobald 1901	MB10564, MB10565, MB10597, MB10598, MB10599, MB10609, MB10610, MB10623, MB10659	M/F/L
Wyeomyia (*Dendromyia*) *testei* Senevet & Abonnenc 1939	MB10370, MB10369, MB10416, MB10611, MB10612, MB10627, MB10628	F/L
Wyeomyia (*Dendromyia*) *ypsipola* Dyar 1922	MB10551, MB10552, MB10603	L
Wyeomyia (*Dodecamyia*) *aphobema* Dyar 1918	MB10098, MB10199	L
Wyeomyia (*Hystatomyia*) *lamellata* (Bonne-Wepster & Bonne 1919)	MB10043, MB10044, MB10209, ST10193	M/L
Wyeomyia (*Miamyia*) *oblita* (Lutz 1904)	MB10844, ST10275	M/L
Wyeomyia (*Phoniomyia*) *splendida* Bonne-Wepster & Bonne 1919	MB10217, MB10585, MB10652, MB10653, MB10655	M/F/L
Wyeomyia (*Spilonympha*) *bourrouli* (Lutz 1905)	MB10701, ST10250	F/L
Wyeomyia (*Triamya*) *aporonoma* Dyar & Knab 1906	MB10689, MB10690, MB10691	L
Wyeomyia (*Wyeomyia*) *pertinans* (Williston 1896)	MB10004, MB10007, MB10031, MB10033, MB10151, MB10189, MB10316, MB10317, MB10318, MB10385, MB10503	M/F/L
Wyeomyia (*Wyeomyia*) *arthrostigma* (Lutz 1905)	MB10347, MB10348, MB10467, MB10528, MB10631	M/F/L
Wyeomyia (*Wyeomyia*) *robusta* Sevenet & Abonnenc 1939	MB10034, MB10035, MB10307, MB10386, MB10537	M/F/L
Wyeomyia (Uncertain) *albosquamata* Bonne-Wepster & Bonne 1919	MB10100, MB10101, MB10102, MB10155, MB10586	M/F/L
Wyeomyia (Uncertain) *argenteorostris* (Bonne-Wepster & Bonne 1919)	MB10509, MB10619, MB10620, MB10621	M/F/L
Wyeomyia (Uncertain) *compta* Senevet & Abonnenc 1939	MB10490, MB10531, MB10535	M/F/L
Wyeomyia (Uncertain) *melanocephala* Dyar & Knab 1906	MB10264, MB10262, MB10263, MB10322, MB10393	M/F/L
Wyeomyia (Uncertain) *occulta* Bonne-Weptser & Bonne 1919	MB10270, MB10271, MB10272, MB10432, MB10457, MB10522	M/F/L
Wyeomyia (Uncertain) *surinamensis* Bruijning 1959	MB10482, MB10483, MB10484, MB10555, MB10587	M/F/L
Wyeomyia sp.stC	MB10589, MB10590, MB10630	L
Culicinae: Toxorhynchitini		
Toxorhynchites (*Lynchiella*) *guadeloupensis* (Dyar & Knab 1906)	MB10540, MB10638, MB10639, ST10266	M/F/L
Toxorhynchites (*Lynchiella*) *haemorrhoidalis haemorrhoidalis* (Fabricius 1787)	MB10124, MB10126, MB10670, MB10671, MB10672	M/F/L
Toxorhynchites (*Lynchiella*) *haemorrhoidalis superbus* (Dyar & Knab 1906)	MB10570, MB10673, MB10674, MB10675, MB10676, MB10677, MB10678, MB10679, MB10680, ST10004	M/F/L
Toxorhynchites (*Lynchiella*) *moctezuma* (Dyar & Knab 1906)	ST10035	M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Wyeomyia_pertinans|MB10385|Sauel
Wyeomyia_pertinans|MB10318|Sauel
Wyeomyia_pertinans|MB10317|Sauel
Wyeomyia_pertinans|MB10316|Sauel
Wyeomyia_pertinans|MB10189|Kourou
Wyeomyia_pertinans|MB10151|Kourou
Wyeomyia_pertinans|MB10007|Sinnamary
Wyeomyia_pertinans|MB10031|Sinnamary
Wyeomyia_pertinans|MB10033|Sinnamary
Wyeomyia_pertinans|MB10004|Sinnamary
Wyeomyia_arthrostigma|MB10528|Roura
Wyeomyia_arthrostigma|MB10631|Macouria
Wyeomyia_arthrostigma|MB10467|Montsinery
Wyeomyia_arthrostigma|MB10348|Montsinery
Wyeomyia_arthrostigma|MB10347|Montsinery
Wyeomyia_oblita|ST10275|Sauel
Wyeomyia_oblita|MB10844|Sauel
Wyeomyia_aporonoma|MB10691|Kourou
Wyeomyia_aporonoma|MB10690|Kourou
Wyeomyia_aporonoma|MB10689|Kourou
Wyeomyia_sp._stC|MB10630|Montsinery
Wyeomyia_sp._stC|MB10590|Montsinery
Wyeomyia_sp._stC|MB10589|Montsinery
Wyeomyia_forattinii|MB10594|Regina
Wyeomyia_forattinii|MB10559|Montsinery
Wyeomyia_forattinii|MB10558|Montsinery
Wyeomyia_forattinii|MB10575|Regina
Wyeomyia_forattinii|MB10578|Regina
Wyeomyia_pseudopecten|MB10459|Montsinery
Wyeomyia_pseudopecten|MB10424|Montsinery
Wyeomyia_pseudopecten|MB10427|Presqu`ile_de_Cayenne
Wyeomyia_pseudopecten|MB10300|Petit-Saut
Wyeomyia_pseudopecten|MB10409|Presqu`ile_de_Cayenne
Wyeomyia_pseudopecten|MB10312|Sauel
Wyeomyia_pseudopecten|MB10311|Sauel
Wyeomyia_pseudopecten|MB10301|Petit-Saut
Wyeomyia_pseudopecten|MB10299|Petit-Saut
Wyeomyia_pseudopecten|MB10310|Sauel
Sabethes_sp._stE|MB10789|Sauel
Sabethes_sp._stE|MB10788|Sauel
Sabethes_sp.|MB10781|Sauel
Limatus_durhamii|MB10645|Kourou
Limatus_durhamii|MB10644|Kourou
Limatus_durhamii|MB10643|Kourou
Limatus_durhamii|MB10133|Kourou
Limatus_durhamii|MB10129|Kourou
Limatus_flavisetosus|ST10334|Sauel
Limatus_flavisetosus|MB10016|Saint-Elie
Limatus_flavisetosus|MB10014|Saint-Elie
Wyeomyia_aphobema|MB10199|La_Virginie
Wyeomyia_aphobema|MB10098|Petit-Saut
Wyeomyia_compta|MB10535|Roura
Wyeomyia_compta|MB10531|Roura
Wyeomyia_compta|MB10490|Roura
Wyeomyia_complosa|ST10243|Sauel
Wyeomyia_complosa|MB10447|Matoury
Wyeomyia_complosa|MB10296|Kourou
Wyeomyia_complosa|MB10297|Kourou
Wyeomyia_complosa|MB10295|Kourou
Wyeomyia_lamellata|ST10193|Petit-Saut
Wyeomyia_lamellata|MB10044|Petit-Saut
Wyeomyia_lamellata|MB10043|Petit-Saut
Wyeomyia_lamellata|MB10209|La_Virginie
Wyeomyia_ypsipola|MB10603|Petit-Saut
Wyeomyia_ypsipola|MB10552|Montsinery
Wyeomyia_ypsipola|MB10551|Montsinery
Wyeomyia_luteoventralis|MB10659|Petit-Saut
Wyeomyia_luteoventralis|MB10623|Petit-Saut
Wyeomyia_luteoventralis|MB10609|Petit-Saut
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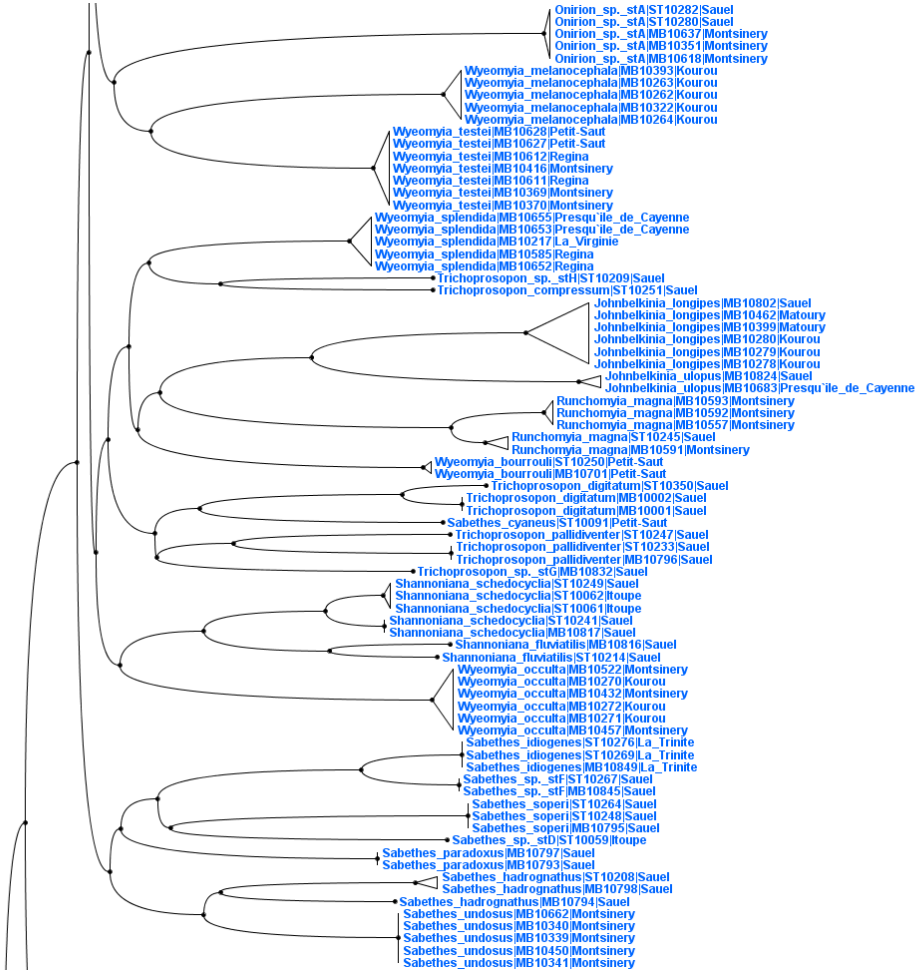
Wyeomyia_luteoventralis|MB10610|Petit-Saut
Wyeomyia_sp._stB|ST10121|Itoupe
Wyeomyia_sp._stB|ST10120|Itoupe
Wyeomyia_albosquamata|MB10586|Petit-Saut
Wyeomyia_albosquamata|MB10155|Petit-Saut
Wyeomyia_albosquamata|MB10102|Petit-Saut
Wyeomyia_albosquamata|MB10100|Petit-Saut
Wyeomyia_albosquamata|MB10101|Petit-Saut
Wyeomyia_surinamensis|MB10587|Matoury
Wyeomyia_surinamensis|MB10555|Matoury
Wyeomyia_surinamensis|MB10484|Matoury
Wyeomyia_surinamensis|MB10483|Matoury
Wyeomyia_surinamensis|MB10482|Matoury
Wyeomyia_argenteorostris|MB10621|Montsinery
Wyeomyia_argenteorostris|MB10619|Montsinery
Wyeomyia_argenteorostris|MB10620|Montsinery
Wyeomyia_argenteorostris|MB10509|Montsinery
Wyeomyia_robusta|MB10537|Petit-Saut
Wyeomyia_robusta|MB10035|Petit-Saut
Wyeomyia_robusta|MB10034|Petit-Saut
Wyeomyia_robusta|MB10386|Petit-Saut
Wyeomyia_robusta|MB10307|Petit-Saut


Onirion_sp._stA|ST10282|Sauel
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Onirion_sp._stA|MB10618|Montsinery
Wyeomyia_melanocephala|MB10393|Kourou
Wyeomyia_melanocephala|MB10263|Kourou
Wyeomyia_melanocephala|MB10262|Kourou
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Wyeomyia_melanocephala|MB10264|Kourou
Wyeomyia_testei|MB10628|Petit-Saut
Wyeomyia_testei|MB10627|Petit-Saut
Wyeomyia_testei|MB10612|Regina
Wyeomyia_testei|MB10416|Montsinery
Wyeomyia_testei|MB10611|Regina
Wyeomyia_testei|MB10369|Montsinery
Wyeomyia_testei|MB10370|Montsinery
Wyeomyia_splendida|MB10655|Presqu'ile_de_Cayenne
Wyeomyia_splendida|MB10653|Presqu'ile_de_Cayenne
Wyeomyia_splendida|MB10217|La_Virginie
Wyeomyia_splendida|MB10585|Regina
Wyeomyia_splendida|MB10652|Regina
Trichoprosopon_sp._stH|ST10209|Sauel
Trichoprosopon_compressum|ST10251|Sauel
Johnbelkinia_longipes|MB10802|Sauel
Johnbelkinia_longipes|MB10462|Matoury
Johnbelkinia_longipes|MB10399|Matoury
Johnbelkinia_longipes|MB10280|Kourou
Johnbelkinia_longipes|MB10279|Kourou
Johnbelkinia_longipes|MB10278|Kourou
Johnbelkinia_ulopus|MB10824|Sauel
Johnbelkinia_ulopus|MB10683|Presqu'ile_de_Cayenne
Runchomyia_magna|MB10593|Montsinery
Runchomyia_magna|MB10592|Montsinery
Runchomyia_magna|MB10557|Montsinery
Runchomyia_magna|ST10245|Sauel
Runchomyia_magna|MB10591|Montsinery
Wyeomyia_bourrouli|ST10250|Petit-Saut
Wyeomyia_bourrouli|MB10701|Petit-Saut
Trichoprosopon_digitatum|ST10350|Sauel
Trichoprosopon_digitatum|MB10002|Sauel
Trichoprosopon_digitatum|MB10001|Sauel
Sabethes_cyaneus|ST10091|Petit-Saut
Trichoprosopon_pallidiventer|ST10247|Sauel
Trichoprosopon_pallidiventer|ST10233|Sauel
Trichoprosopon_pallidiventer|MB10796|Sauel
Trichoprosopon_sp._stG|MB10832|Sauel
Shannoniana_schedocyclia|ST10249|Sauel
Shannoniana_schedocyclia|ST10062|Itoupe
Shannoniana_schedocyclia|ST10061|Itoupe
Shannoniana_schedocyclia|ST10241|Sauel
Shannoniana_schedocyclia|MB10817|Sauel
Shannoniana_fluviatilis|MB10816|Sauel
Shannoniana_fluviatilis|ST10214|Sauel
Wyeomyia_occulta|MB10522|Montsinery
Wyeomyia_occulta|MB10270|Kourou
Wyeomyia_occulta|MB10432|Montsinery
Wyeomyia_occulta|MB10272|Kourou
Wyeomyia_occulta|MB10271|Kourou
Wyeomyia_occulta|MB10457|Montsinery
Sabethes_idiogenes|ST10276|La_Trinite
Sabethes_idiogenes|ST10269|La_Trinite
Sabethes_idiogenes|MB10849|La_Trinite
Sabethes_sp._stF|ST10267|Sauel
Sabethes_sp._stF|MB10845|Sauel
Sabethes_soperi|ST10264|Sauel
Sabethes_soperi|ST10248|Sauel
Sabethes_soperi|MB10795|Sauel
Sabethes_sp._stD|ST10059|Itoupe
Sabethes_paradoxus|MB10797|Sauel
Sabethes_paradoxus|MB10793|Sauel
Sabethes_hadrognathus|ST10208|Sauel
Sabethes_hadrognathus|MB10798|Sauel
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Sabethes_undosus|MB10662|Montsinery
Sabethes_undosus|MB10340|Montsinery
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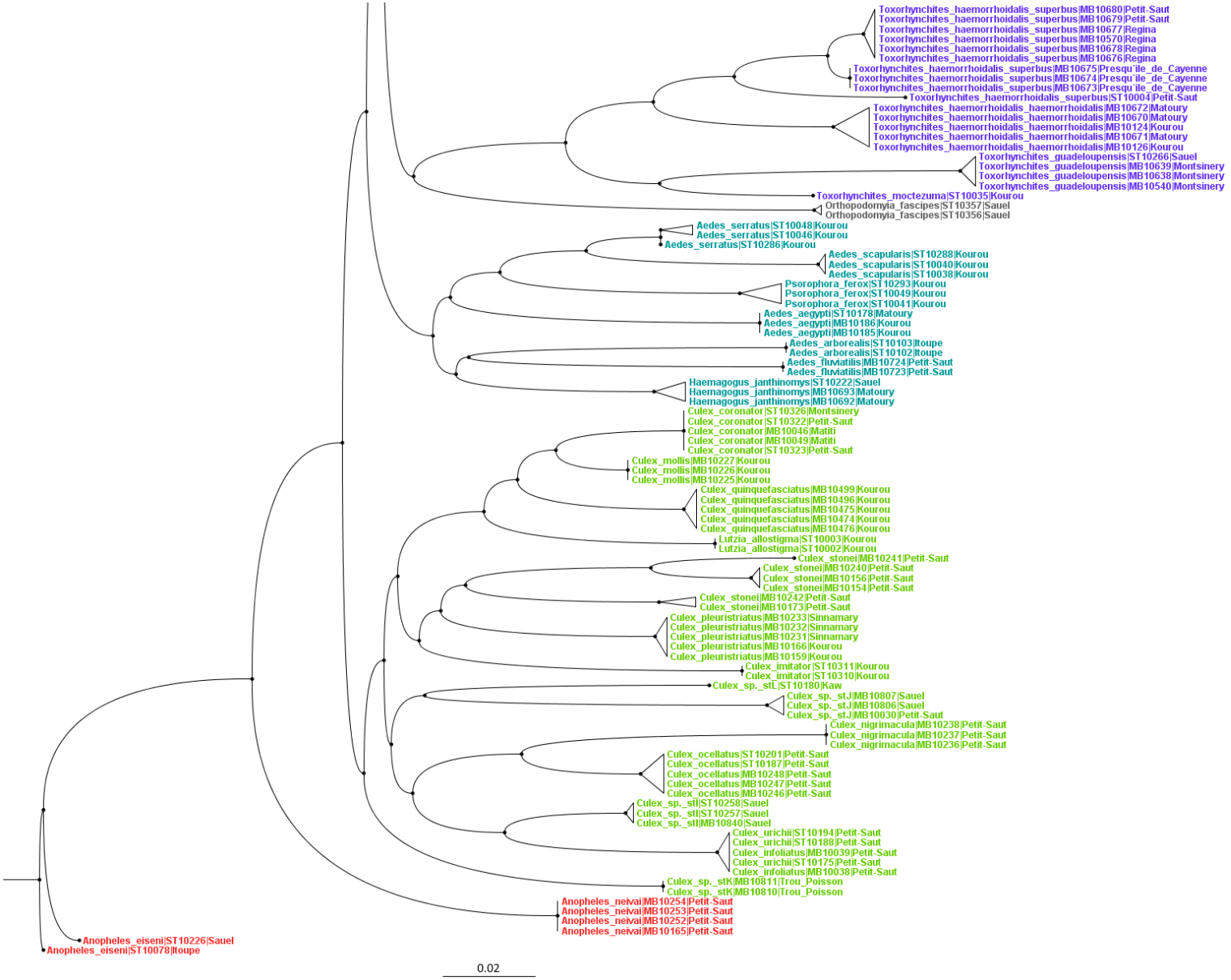
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Toxorhynchites_haemorrhoidalis_superbus|MB10570|Regina
Toxorhynchites_haemorrhoidalis_superbus|MB10678|Regina
Toxorhynchites_haemorrhoidalis_superbus|MB10676|Regina
Toxorhynchites_haemorrhoidalis_superbus|MB10675|Presqu'ile_de_Cayenne
Toxorhynchites_haemorrhoidalis_superbus|MB10674|Presqu'ile_de_Cayenne
Toxorhynchites_haemorrhoidalis_superbus|MB10673|Presqu'ile_de_Cayenne
Toxorhynchites_haemorrhoidalis_superbus|ST10004|Petit-Saut
Toxorhynchites_haemorrhoidalis_haemorrhoidalis|MB10672|Matoury
Toxorhynchites_haemorrhoidalis_haemorrhoidalis|MB10670|Matoury
Toxorhynchites_haemorrhoidalis_haemorrhoidalis|MB10124|Kourou
Toxorhynchites_haemorrhoidalis_haemorrhoidalis|MB10671|Matoury
Toxorhynchites_haemorrhoidalis_haemorrhoidalis|MB10126|Kourou
Toxorhynchites_guadeloupensis|ST10266|Sauel
Toxorhynchites_guadeloupensis|MB10639|Montsinery
Toxorhynchites_guadeloupensis|MB10638|Montsinery
Toxorhynchites_guadeloupensis|MB10540|Montsinery
Toxorhynchites_moctezuma|ST10035|Kourou
Orthopodomyia_fascipes|ST10357|Sauel
Orthopodomyia_fascipes|ST10356|Sauel
Aedes_serratus|ST10048|Kourou
Aedes_serratus|ST10046|Kourou
Aedes_serratus|ST10286|Kourou
Aedes_scapularis|ST10288|Kourou
Aedes_scapularis|ST10040|Kourou
Aedes_scapularis|ST10038|Kourou
Psorophora_ferox|ST10293|Kourou
Psorophora_ferox|ST10049|Kourou
Psorophora_ferox|ST10041|Kourou
Aedes_aegypti|ST10178|Matoury
Aedes_aegypti|MB10186|Kourou
Aedes_aegypti|MB10185|Kourou
Aedes_arborealis|ST10103|Itoupe
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Aedes_fluviatilis|MB10724|Petit-Saut
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Haemagogus_janthinomys|ST10222|Sauel
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Culex_coronator|ST10326|Montsinery
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Culex_coronator|MB10046|Matiti
Culex_coronator|MB10049|Matiti
Culex_coronator|ST10323|Petit-Saut
Culex_mollis|MB10227|Kourou
Culex_mollis|MB10226|Kourou
Culex_mollis|MB10225|Kourou
Culex_quinquefasciatus|MB10499|Kourou
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Culex_quinquefasciatus|MB10475|Kourou
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Culex_quinquefasciatus|MB10476|Kourou
Lutzia_allostigma|ST10003|Kourou
Lutzia_allostigma|ST10002|Kourou
Culex_stonei|MB10241|Petit-Saut
Culex_stonei|MB10240|Petit-Saut
Culex_stonei|MB10156|Petit-Saut
Culex_stonei|MB10154|Petit-Saut
Culex_stonei|MB10242|Petit-Saut
Culex_stonei|MB10173|Petit-Saut
Culex_pleuristriatus|MB10233|Sinnamary
Culex_pleuristriatus|MB10232|Sinnamary
Culex_pleuristriatus|MB10231|Sinnamary
Culex_pleuristriatus|MB10166|Kourou
Culex_pleuristriatus|MB10159|Kourou
Culex_imitator|ST10311|Kourou
Culex_imitator|ST10310|Kourou
Culex_sp._stL|ST10180|Kaw
Culex_sp._stJ|MB10807|Sauel
Culex_sp._stJ|MB10806|Sauel
Culex_sp._stJ|MB10030|Petit-Saut
Culex_nigrimacula|MB10238|Petit-Saut
Culex_nigrimacula|MB10237|Petit-Saut
Culex_nigrimacula|MB10236|Petit-Saut
Culex_ocellatus|ST10201|Petit-Saut
Culex_ocellatus|ST10187|Petit-Saut
Culex_ocellatus|MB10248|Petit-Saut
Culex_ocellatus|MB10247|Petit-Saut
Culex_ocellatus|MB10246|Petit-Saut
Culex_sp._stI|ST10258|Sauel
Culex_sp._stI|ST10257|Sauel
Culex_sp._stI|MB10840|Sauel
Culex_urichii|ST10194|Petit-Saut
Culex_urichii|ST10188|Petit-Saut
Culex_infoliatus|MB10039|Petit-Saut
Culex_urichii|ST10175|Petit-Saut
Culex_infoliatus|MB10038|Petit-Saut
Culex_sp._stK|MB10811|Trou_Poisson
Culex_sp._stK|MB10810|Trou_Poisson
Anopheles_neivai|MB10254|Petit-Saut
Anopheles_neivai|MB10253|Petit-Saut
Anopheles_neivai|MB10252|Petit-Saut
Anopheles_neivai|MB10165|Petit-Saut
Anopheles_eiseni|ST10226|Sauel
Anopheles_eiseni|ST10078|Itoupe
0.02

Figure 2.1 Neighbour-joining analysis of Kimura 2-parameter (K2P) distances of COI mosquito sequences from French Guiana. Specimens are clustered according to their BIN. The main taxonomic groups are color-coded: Anophelinae in red, among the Culicinae, Aedini in turquoise, Culicini in green, Orthopodomyiini in grey, Sabethini in blue and Toxorhynchitini in purple. 'Sauel' mean Saül.

Table 2.2 List of BINs with their associated species or morphospecies (hereafter 'taxa') obtained from BOLD. Taxa are listed alphabetically and ranked by subfamily, tribe, genus and subgenus. Distances correspond to the percentage of dissimilar pairwise nucleotides and counts correspond to the number of voucher specimens included in this study followed, between brackets, by the total number of specimens (including ours) present in the BOLD database.

BIN	Species/morphospecies	Average distance	Maximum distance	Distance to nearest neighbor	Count
Anophelinae					
ACZ3766	*An.* (*Ano.*) *eiseni*	0.99	0.99	7.06	2
ACZ4390	*An.* (*Ker.*) *neivai*	0	0	6.74	4
Culicinae: Aedini					
ABW1628	*Ae.* (*Gec.*) *fluviatilis*	1.08	1.50	10.09	2(6)
ACZ4358	*Ae.* (*How.*) *arborealis*	NA	NA	9.32	1
AAH9007	*Ae.* (*Och.*) *scapularis*	1.19	5.06	6.68	3(301)
AAN3110	*Ae.* (*Och.*) *serratus*	0.85	1.24	1.04	1(4)
ACF2113	*Ae.* (*Och.*) *serratus*	0.70	0.96	1.04	1(4)
AAA4210	*Ae.* (*Stg.*) *aegypti*	1.07	4.86	1.58	3(536)
AAU1467	*Hg.* (*Hag.*) *janthinomys*	1.09	2.09	6.88	3(12)
AAO0580	*Ps.* (*Jan.*) *ferox*	1.23	2.09	1.77	3(13)
Culicinae: Culicini					
AAG3837	*Cx.* (*Car.*) *infoliatus/urichii*	0.37	0.81	7.14	5(14)
ACZ3921	*Cx.* (*Car.*) sp.stI	0.16	0.16	4.51	2
AAN3636	*Cx.* (*Cux.*) *coronator*	0.68	3.08	1.17	5(128)
AAF1735	*Cx.* (*Cux.*) *mollis*	1.45	5.07	1.59	3(190)
AAA4751	*Cx.* (*Cux.*) *quinquefasciatus*	0.14	4.01	0.98	5(3162)
ABX7935	*Cx.* (*Mcx.*) *imitator*	0.64	0.96	4.17	2(4)
ACZ4187	*Cx.* (*Mcx.*) *pleuristriatus*	0.31	0.64	7.16	5
ACZ3799	*Cx.* (*Mcx.*) *stonei*	0.82	0.82	8.23	2
ACZ4071	*Cx.* (*Mcx.*) *stonei*	0.21	0.32	4.65	3
ACZ4175	*Cx.* (*Mcx.*) *stonei*	NA	NA	4.01	1
ACZ4194	*Cx.* (Uncertain) *nigrimacula*	0	0	8.62	3
ACZ4158	*Cx.* (Uncertain) *ocellatus*	0.44	0.96	8.30	5
ACZ4398	*Culex* sp.stJ	0.43	0.64	11.17	3
ACZ4266	*Culex* sp.stK	0	0	2.89	2
ACZ3899	*Culex* sp.stL	NA	NA	9.63	1
AAW1435	*Lt.* (*Lut.*) *allostigma*	0.06	0.16	5.62	2(5)
Culicinae: Orthopodomyiini					
ACZ4163	*Or. fascipes*	0	0	2.41	2
Culicinae: Sabethini					
ACZ4070	*Jb. Longipes*	0.59	1.77	8.24	6
ACZ4300	*Jb. ulopus*	0.65	0.65	9.06	2

ACN9473	*Li. durhamii*	0.14	0.32	1.12	5(6)
AAW1293	*Li. flavisetosus*	0.03	0.16	7.54	3(10)
ACN0508	*On.* sp.stA	0.14	0.33	11.08	5(6)
ACZ3754	*Ru.* (*Cte.*) *magna*	0.11	0.16	2.57	3
ACZ3755	*Ru.* (*Cte.*) *magna*	0.80	0.80	2.57	2
AAW5410	*Sa.* (*Pey.*) *undosus*	0.11	0.32	6.10	5(6)
ACZ3825	*Sa.* (*Pey.*) *hadrognathus*	NA	NA	5.94	1
ACZ3826	*Sa.* (*Pey.*) *hadrognathus*	0.48	0.48	5.94	2
ACZ3779	*Sa.* (*Pey.*) *paradoxus*	0	0	8.19	2
ACZ3827	*Sa.* (*Pey.*) *soperi*	0	0	8.99	3
ACZ3811	*Sa.* (*Pey.*) sp.stD	NA	NA	9.47	1
ACZ3883	*Sa.* (*Sab.*) *cyaneus*	NA	NA	7.72	1
ACZ4359	*Sa.* (*Sab.*) sp.stE	0	0	1.77	2
ACZ3810	*Sa.* (*Sab.*) sp.stM	NA	NA	8.84	1
ACZ3828	*Sa.* (*Sbn.*) *idiogenes*	0	0	3.21	3
ACZ4350	*Sa.* (*Sbn.*) sp.stF	0	0	3.21	2
ACZ4319	*Sh. fluviatilis*	NA	NA	3.70	1
ACZ4320	*Sh. fluviatilis*	NA	NA	3.70	1
ACZ3895	*Sh. schedocyclia*	0	0	1.93	2
ACZ3896	*Sh. schedocyclia*	0.11	0.16	1.93	3
ACZ3752	*Tr. compressum*	NA	NA	6.90	1
AAG3842	*Tr. digitatum*	0.24	0.48	2.57	1(4)
ACZ3792	*Tr. digitatum*	0	0	2.57	2
ACZ3837	*Tr. pallidiventer*	NA	NA	7.06	1
ACZ3838	*Tr. pallidiventer*	0	0	7.06	2
ACZ4400	*Trichoprosopon* sp.stG	NA	NA	8.51	1
ACZ4399	*Trichoprosopon* sp.stH	NA	NA	6.90	1
ACZ4113	*Wy.* (*Cae.*) sp.stB	1.12	1.12	8.18	2
ACZ3978	*Wy.* (*Cru.*) *forattinii*	0.13	0.32	8.35	5
AAG3839	*Wy.* (*Dec.*) *pseudopecten*	1.45	2.57	4.49	4(7)
ACZ4104	*Wy.* (*Dec.*) *pseudopecten*	0.30	0.82	5.24	6
ACA0978	*Wy.* (*Den.*) *complosa*	1.63	3.05	7.84	5(14)
ACZ3898	*Wy.* (*Den.*) *luteoventralis*	1.32	2.89	4.49	9
ACZ3881	*Wy.* (*Den.*) *testei*	0.14	0.33	8.20	7
ACZ4034	*Wy.* (*Den.*) *ypsipola*	0.23	0.34	7.50	3
ACZ4140	*Wy.* (*Dod.*) *aphobema*	0.48	0.48	2.73	2
ACZ3890	*Wy.* (*Hys.*) *lamellata*	0.16	0.33	4.29	4
ACZ3891	*Wy.* (*Myamyia*) *oblita*	0	0	5.94	2
ACZ4220	*Wy.* (*Pho.*) *splendida*	0.35	0.64	7.38	5
ACZ4080	*Wy.* (*Spi.*) *bourrouli*	0.16	0.16	8.67	2
ACZ4142	*Wy.* (*Triamyia*) *aporonoma*	0	0	3.05	3
ACZ3855	*Wy.* (*Wyo.*) *arthrostigma*	NA	NA	2.29	1
ACZ3856	*Wy.* (*Wyo.*) *arthrostigma*	0.00	0.00	2.29	4
ACZ4079	*Wy.* (*Wyo.*) *pertinans*	0.48	1.77	1.44	11(12)
ACZ3847	*Wy.* (*Wyo.*) *robusta*	0.26	0.65	10.48	5
ACZ4171	*Wy.* (Uncertain) *albosquamata*	0.06	0.16	9.19	5
ABW3718	*Wy.* (Uncertain) *argenteorostris*	0.17	0.32	11.46	4(6)
ACZ4141	*Wy.* (Uncertain) *compta*	0	0	3.08	3
ACZ3830	*Wy.* (Uncertain) *melanocephala*	0.22	0.48	2.25	5

ACZ4130	*Wy.* (Uncertain) *occulta*	0.38	0.51	9.66	6
ACZ4312	*Wy.* (Uncertain) *surinamensis*	0.13	0.33	7.20	5
ACZ4143	*Wyeomyia* sp.stC	0.11	0.16	10.00	3
Culicinae: Toxorhynchitini					
ACZ4355	*Tx.* (*Lyn.*) *guadeloupensis*	0.32	0.64	8.26	4
ACZ4120	*Tx.* (*Lyn.*) *haemorrhoidalis haemorrhoidalis*	0.51	0.80	7.06	5
ACZ3913	*Tx.* (*Lyn.*) *haemorrhoidalis superbus*	0.26	0.49	1.44	6
ACZ3996	*Tx.* (*Lyn.*) *haemorrhoidalis superbus*	0	0	1.44	3
ACZ4119	*Tx.* (*Lyn.*) *haemorrhoidalis superbus*	NA	NA	6.22	1
ACZ4278	*Tx.* (*Lyn.*) *moctezuma*	NA	NA	8.20	1

Among the 87 BINs present in our dataset, 22 BINs include sequences already present in BOLD. We observed 12 cases of perfect clustering: *Ae.* (*Gec.*) *fluviatilis* (BIN ABW1628), *Ae.* (*Och.*) *scapularis* (BIN AAH9007), *Ae.* (*Och.*) *serratus* (BINs AAN3110 and ACF2113), *Ae.* (*Stg.*) *aegypti* (BIN AAA4210; despite a few BOLD specimens that might have been misidentified), *Hg.* (*Hag.*) *janthinomys* (BIN AAU1467), *Ps.* (*Jan.*) *ferox* (BIN AAO0580), *Cx.* (*Mcx.*) *imitator* (BIN ABX7935), *Lt.* (*Lut.*) *allostigma* (BIN AAW1435), *Li. durhamii* (BIN ACN9473), *Li. flavisetosus* (BIN AAW1293) and *Wy.* (*Den.*) *complosa* (BIN ACA0978).

In five cases, there was a mismatch between our identifications and the one present in the other dataset: BIN AAG3837 included *Cx.* (*Car.*) *infoliatus* and *Cx.* (*Car.*) *urichii* and clusters with *Cx.* (*Car.*) *urichii* (9 counts); BIN AAN3636 identified as *Cx.* (*Cux.*) *coronator* clusters with *Cx.* (*Cux.*) *maxi* Dyar 1928 (76 counts), *Cx.* (*Cux.*) *coronator* (21 counts) and others identified/unidentified *Culex* species (26 counts); BIN AAF1735 identified as *Cx.* (*Cux.*) *mollis* clusters with *Cx.* (*Cux.*) *nigripalpus* Theobald 1901 (64 counts), *Cx.* (*Cux.*) *interfor* Dyar 1928 (43 counts) and several others identified/unidentified *Culex* species (80 counts); and BIN AAA4751 identified as *Cx.* (*Cux.*) *quinquefasciatus* clusters with *Cx.* (*Cux.*) *quinquefasciatus* (1971 counts) and *Cx.* (*Cux.*) *pipiens* s.l. Linnaeus 1758 (1186 counts); BIN ACZ4079 identified as *Wy.* (*Wyo.*) *pertinans* clusters with one specimen of *Wy.* (*Wyo.*) *mitchellii* (Theobald 1905) from Venezuela.

In five others cases, the BINs clustered with only unidentified specimens in BOLD: *Onirion* sp.stA (BIN ACN0508), *Sa.* (*Pey.*) *undosus* (BIN AAW5410), *Tr. digitatum* (BIN AAG3842), *Wy.* (Uncertain) *argenteorostris* (BIN ABW3718) and *Wy.* (*Dec.*) *pseudopecten* (BIN AAG3839).

DISCUSSION

Overall we obtained 11 % more taxa using molecular delimitation than with morphology-based identification. This difference might be due to three factors: the presence of complexes of closely related species (i.e. cryptic species), the ongoing divergence of species and the gap in basic taxonomic knowledge. We discuss below which is the most likely hypothesis for each taxa split into more than one BIN.

Culex (Mcx.) stonei specimens (MB10154, 0156, 0173, 0240, 024, 0242) clustered in three different BINs. This result is unexpected because the specimens were collected on the same date and at the same location which might suggest the presence of cryptic species occurring in sympatry.

Sabethes (*Pey.*) *hadrognathus* was described by Harbach as part of the thorough revision of the subgenus which began in 1991 (**Harbach 1991; Harbach 1995a, b; Hall *et al.* 1999; Harbach & Howard 2002**). MB10794, 0798 and STI0208 constitute the three sole specimens of *Sa.* (*Pey.*) *hadrognathus* ever caught in French Guiana (**Talaga *et al.* 2015c**). The molecular delimitation of *Sa.* (*Pey.*) *hadrognathus* into two BINs suggests the presence of two closely related species, which might be one of the three species of *Peytonulus* whose larval stage is unknown (i.e. *Sa.* (*Pey.*) *gorgasi* Duret 1971, *Sa.* (*Pey.*) *ignotus* Harbach 1995 or *Sa.* (*Pey.*) *xenismus* Harbach 1995) or an undescribed species (**Harbach & Howard 2002**). Further examination of additional specimens at all life stages will be needed to determine if morphological criteria support the presence of another species or simply that intraspecific divergence within this taxon is high.

All of the nominal species *Ru.* (*Cte.*) *magna, Sh. fluviatilis, Sh. schedocyclia, Tr. digitatum* and *Tr. pallidiventer* were split into two BINs. These species belong to the same taxonomic group (formerly *Trichoprosopon sensu*; **Lane & Cerqueira 1942**) which was the subject of a key revision by **Zavortink** in **1979**. In this revision, Zavortink pointed out the difficulties in identifying the different species belonging to the subgenera *Runchomyia, Shannoniana* and *Trichoprosopon* given that most of the available descriptions are insufficient and/or incomplete. The situation has not evolved since 1979 and our results probably reflect the lack of existing accurate description.

Wyeomyia (*Dec.*) *pseudopecten* was also split into two BINs. The three species currently included in the subgenus *Decamyia* have not been studied in detail, particularly immatures (**Harbach 2015**). For example, at the larval stage, *Wy.* (*Dec.*) *pseudopecten* and *Wy.* (*Dec.*) *ulocoma* (Theobald 1903) cannot be unfailingly distinguished. The two sequenced

males (MB10424, 0427) belonged to the same BIN and definitely harbored characters of *Wy.* (*Dec.*) *pseudopecten* that belongs to a group of species including *Wy.* (*Dec.*) *ulocoma* (Theobald 1903), *Wy.* (*Dec.*) *felicia* (Dyar & Núñez Tovar 1927) and probably *Wy.* (Uncertain) *rorotai* Senevet, Chabelard & Abonnenc 1942. The *Decamyia* subgenus of *Wyeomyia* would deserve a thorough revision.

It is likely that *Tx.* (*Lyn.*) *haemorrhoidalis superbus* constitutes a complex of closely related species because the specimens were split into three BINs. Two BINs grouped specimens based on their sampling site: Cayenne (MB10673, 0674, 0675) or Régina and Petit-Saut (MB10570, 0676, 0677, 0678, 0679, 0680). The third BIN corresponded to one individual (ST10004) collected in the deep primary forest of Petit-Saut; this fact is unusual as all other specimens were collected along forest edges.

In few cases, there was a mismatch between our identifications and the one present in BOLD. For example, our specimens identified as *Wy.* (*Wyo.*) *pertinans* clustered with one specimen identified as *Wy.* (*Wyo.*) *mitchellii* from Venezuela. Both species belong to the Pertinans group of *Wyeomyia* which includes at least 13 close related species distributed across the Americas (**Belkin *et al.* 1970**). According to **Belkin *et al.*** (**1970**) records of *Wy.* (*Wyo.*) *mitchellii* in Central and South America are erroneous. Therefore, this record should be interpreted as a misidentification.

Our specimens of *Cx.* (*Cux.*) *coronator* (MB10046, 0049 and ST10322, 0323, 0326) clustered with *Cx.* (*Cux.*) *maxi, Cx.* (*Cux.*) *coronator* and others *Culex* species. The specimens were identified at the larval stage indicated by the presence of strong spines at the apical end of the siphon. Because this feature is unique among the *Culex* subgenus, we are quite confident of our identification (**Bram 1967; Casal & García 1968**). In addition, our specimens identified as *Cx.* (*Cux.*) *mollis* (MB10225, 0226, 0227) clustered with *Cx.* (*Cux.*) *nigripalpus*, *Cx.* (*Cux.*) *interfor* and others *Culex* species in BOLD. Morphological identifications in this case were only based on the larval stage, yet the differences at the larval stage between these species are slight, so that our identification is questionable. Also, C*x.* (*Cux.*) *quinquefasciatus* clustered with *Cx.* (*Cux.*) *quinquefasciatus* as well as with *Cx.* (*Cux.*) *pipiens* s.l., its temperate equivalent (**Harbach 1988**). As already reported by other authors, it seems that the COI barcode does not contain enough information to distinguish closely related species among the subgenus *Culex* (**Laurito *et al.* 2013**).

All the morphospecies included in the analyses (namely, sp.stA to sp.stM) have been confirmed to be distinct from other related taxa and did not match any identified species in BOLD. Potentially, each of them represents an undescribed species, or, at least an undescribed life stage of an incompletely described species. Because most of them are represented by very few specimens, further field missions will be necessary to gather enough biological material to allow their description. In the other cases (i.e. *Onirion* sp.stA and *Cx.* (*Car.*) sp.stI), descriptions are already under way.

Conclusions

Our analysis of 274 mosquito specimens from French Guiana resulted in the definition of 87 DNA clusters (BINs) with only 22 BINs already present in the BOLD database. We thus provide a substantial contribution to the global mosquito barcoding initiative. Our results confirm that the COI barcode can be successfully used for delimiting and identifying container-breeding mosquito species, with only a few cases where the marker could not distinguish closely related species. Our results also confirm the presence of several new species identified based on their morphology plus several potential cases of cryptic species.

Acknowledgment: We would like to thank Olivier Dézerald, Marceau Minot and Hector Rodriguez for their field help, and Andrea Yockey-Dejean for proofreading the manuscript. This study was funded by *Investissement d'Avenir* grants managed by the French *Agence Nationale de la Recherche* (CEBA: ANR-10-LABX-25-01; TULIP: ANR-10-LABX-41, ANR-11-IDEX-0002-02). ST was funded by a PhD fellowship from the *Université Antilles-Guyane*.

Chapitre 3: Online database for mosquito (Diptera: Culicidae) occurrence records in French Guiana (Talaga *et al.* 2015, *ZooKeys*, 532**, 107–115)**

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Abstract: We present a database providing information on mosquito specimens (Arthropoda: Diptera: Culicidae) collected in French Guiana. Field collections were initiated in 2013 under the auspices of the CEnter for the study of Biodiversity in Amazonia (CEBA: www.labexceba.fr/en/). This study is part of an ongoing process aiming to understand the distribution of mosquitoes, including vector species, across French Guiana. Occurrences are recorded after each collecting trip in a database managed by the laboratory *Evolution et Diversité Biologique* (EDB), Toulouse, France. The dataset is updated monthly and is available online. Voucher specimens and their associated DNA are stored at the laboratory *Ecologie des Forêts de Guyane* (Ecofog), Kourou, French Guiana. The latest version of the dataset is accessible through EDB's Integrated Publication Toolkit at http://130.120.204.55:8080/ipt/resource.do?r=mosquitoes_of_french_guiana/ or through the Global Biodiversity Information Facility data portal at http://www.gbif.org/dataset/5a8aa2ad-261c-4f61-a98e-26dd752fe1c5/ It can also be viewed through the Guyanensis platform at http://guyanensis.ups-tlse.fr/

Keywords: Diversity, French Guiana, Mosquitoes, Neotropics, Occurrence.

INTRODUCTION

Mosquitoes (Diptera: Culicidae) are probably the most medically important group of arthropods worldwide because of the ability of some species to transmit pathogens to humans (**Clements 2011**), causing major health issues in some parts of the world. Mosquito-borne diseases are frequent in French Guiana with malaria occurring mainly in inland areas, dengue and chikungunya in urban areas, while many lesser known crypto-arboviruses occur in sylvan and/or rural environments (**Chippaux *et al.* 1983**). To date, 3,549 valid species of mosquitoes have been described (**Harbach 2015**) and French Guiana, with 235 species, harbors one of the highest relative species densities of mosquitoes anywhere in the world (**Foley *et al.* 2008; Talaga *et al.* 2015b**). Understanding the biology, ecology and distribution of this group is thus of primary importance.

French Guiana is mainly covered by primary rainforest and its inhabitants (*ca*. 250,000) are mostly distributed along the coast (**Gond *et al.* 2011**). While some evidence suggests that the Guiana Shield could be an early center of speciation for mosquitoes in the Neotropics (**Navarro *et al.* 2007**), the mechanisms explaining the high mosquito diversity in the region remain poorly understood.

This work is an ongoing process and should help to understand mosquito distribution across French Guiana. This database will also be used to disseminate biodiversity information related to future studies on mosquito distribution in French Guiana in general and in medical entomology and ecology in particular. We aim to promote the best practices for recording and sharing biodiversity data within our research community, and highly encourage foreign institutions to do the same. Our goal is to provide data on Guianese mosquitoes and to make available a fast and efficient tool for sharing and tracking reliable information on specimens in the form of an online database.

TAXONOMIC COVERAGE

Description: This database concerns all mosquito (Diptera: Culicidae) species inhabiting French Guiana. Most specimens have been identified to species level or at least to genus level. The identifications were made by the first author based most of the time on the examination of immature and adult specimens, and by using the latest taxonomic publications on the genus or on the subgenus concerned (e.g. **Zavortink 1979; Harbach & Peyton 2000; Motta & Lourenço-de-Oliveira 2000**). The validation of species and subspecies is based on "A

Catalog of the Mosquitoes of the World (Diptera: Culicidae)" (**Knight & Stone 1977**) and its supplements (**Knight 1978; Ward 1984, 1992; Gaffigan & Ward 1985**), and the "Systematic Catalog of Culicidae" (**WRBU 2015**). The internal classification of the tribe Aedini is based on **Wilkerson *et al.*** (**2015**).

Until now, the database was mostly filled with data from studies conducted on mosquitoes breeding in phytotelmata, which explains why the Sabethini are particularly well represented in the current dataset (**Fig. 3.1**). Consequently, clades like the Anophelinae, Culicini and Mansoniini are highly underrepresented and the tribes Aedeomyiini and Uranotaeniini are not at all represented (**Fig. 3.1**). The dataset presently contains 19 genera and 81 species, including occurrences of twelve species recently recorded in French Guiana (**Talaga *et al.* 2015**), namely: *Onirion* sp. cf. **Harbach & Peyton** (**2000**), *Sabethes* (*Peytonulus*) *hadrognathus* Harbach 1995, *Sa.* (*Pey.*) *paradoxus* Harbach 2002, *Sa.* (*Pey.*) *soperi* Lane & Cerqueira 1942, *Sa.* (*Sabethinus*) *idiogenes* Harbach 1994, *Sa.* (*Sabethes*) *quasicyaneus* Peryassú 1922, *Runchomyia* (*Ctenogoeldia*) *magna* (Theobald 1905), *Wyeomyia* (*Caenomyiella*) sp. cf. **Harbach & Peyton** (**1990**), *Wy.* (*Dendromyia*) *ypsipola* Dyar 1903, *Wy.* (*Hystatomyia*) *lamellata* (Bonne-Wepster & Bonne 1920), *Wy.* (*Miamyia*) *oblita* (Lutz 1904), and *Toxorhynchites* (*Lynchiella*) *guadeloupensis* (Dyar & Knab 1906).

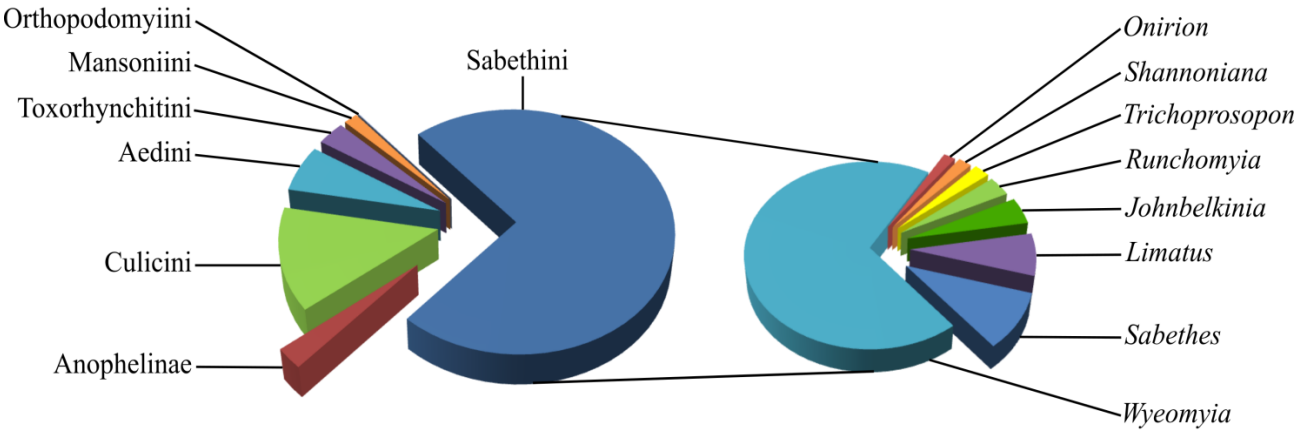

Figure 3.1 Taxonomic coverage by tribe (pie chart on the left) with a focus on the distribution of specimens by genus for the tribe Sabethini (pie chart on the right) from the dataset the "Mosquitoes of French Guiana" up to 2015. Because there are no tribes in the Anophelinae, they are represented at the subfamily level on the pie chart.

Taxa include:

Kingdom: Animalia

Phylum: Arthropoda

Class: Insecta

Order: Diptera

Family: Culicidae

Subfamilies: Anophelinae, Culicinae.

Tribes: Aedeomyiini, Aedini, Culicini, Mansoniini, Orthopodomyiini, Sabethini, Toxorhynchitini, Uranotaeniini.

Genera: *Aedeomyia*, *Aedes*, *Anopheles*, *Chagasia*, *Coquillettidia*, *Culex*, *Deinocerites*, *Haemagogus*, *Johnbelkinia*, *Limatus*, *Lutzia*, *Mansonia*, *Onirion*, *Orthopodomyia*, *Psorophora*, *Runchomyia*, *Sabethes*, *Shannoniana*, *Toxorhynchites*, *Trichoprosopon*, *Uranotaenia*, *Wyeomyia*.

SPATIAL COVERAGE

Description: French Guiana (83,534 km²) is a French overseas region situated in South America at the eastern limit of the Guiana Shield. The latter is a mountainous tableland extending, from West to East, across Guyana, Suriname, French Guiana, as well as parts of Colombia, Venezuela and Brazil. The sampling area is delimited by the current administrative boundaries of the territory of French Guiana (**Fig. 3.2**). To the East, the Oyapock River delimits the border with Brazil. To the West, the Maroni River delimits the border with Suriname. The territory's borders have not been constant throughout history and a large portion of northern Brazil was disputed between France and Brazil during the 19th century. As a result, the type locality of Counani, French Guiana where the *nomen dubium Culex americanus* **Neveu-Lemaire 1902** was described (**Belkin *et al.* 1971**) is currently in Brazil. Even though French Guiana is a French overseas region, all occurrences have been recorded under the country 'French Guiana' to comply with the ISO 3166-1 standard.

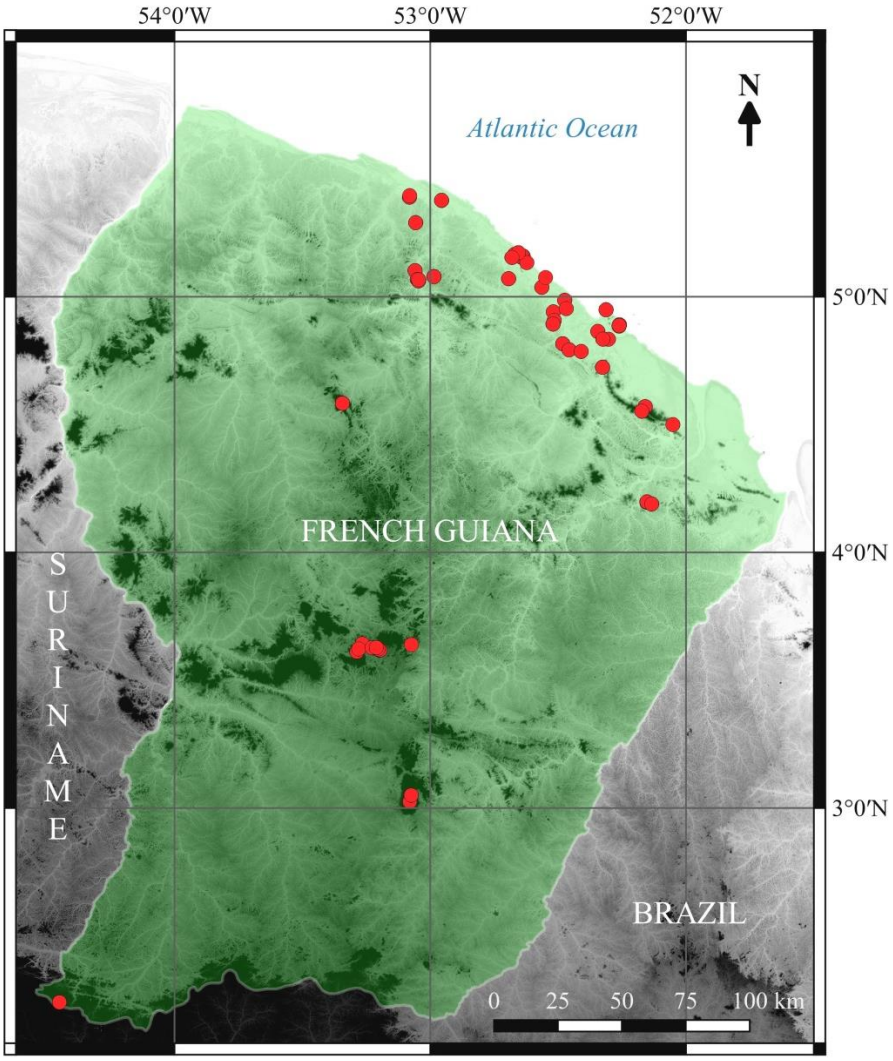

Figure 3.2 Geographical coverage of the dataset (green shade) and collecting localities (red dots) up to 2015.

Geographical methods: GPS coordinates were obtained using a Garmin GPSmap 60CSx device or higher equivalent of the GPSmap series. The World Geodetic System 1984 (WGS 84) was used as geodetic system and associated with UTM 21-22 N for map projection.

Coordinates: 2°5'24"N and 5°50'60"N Latitude; 54°36'36"W and 51°31'48"W Longitude.

PROJECT DESCRIPTION

Title: Mosquitoes of French Guiana

Personnel: Stanislas Talaga

Study area descriptions: Collecting trips were conducted in various locations throughout French Guiana ranging from urban to pristine environments.

Design description: This database was originally built from studies on mosquito-phytotelm associations at the scale of French Guiana. Immature mosquitoes were collected from at least 30 water-holding structures per phytotelm species, per locality. However, the extent of the sampling area was not standardized between the different localities. The database also contains some records of opportunistically sampled immature and adult mosquitoes conducted by the first author.

Funding: Data for this resource have been obtained within the framework of the projects BIOHOPSYS and DIADEMA from the CEBA (CEnter for the study of Biodiversity in Amazonia) and thanks to a PhD fellowship from the *Université Antilles-Guyane* awarded to Stanislas Talaga. CEBA is funded by an *Investissement d'Avenir* grant managed by the French *Agence Nationale de la Recherche* (ANR) under grant number: ANR-10-LABX-25-01.

METHODS

Study extent description: Study sites were located throughout French Guiana.

Sampling description: The following techniques were used; however, not all techniques were used at every collecting site and the sampling design may not have been the same at all sites. Immature container mosquitoes were collected by extracting plant-held water using a great variety of sucking devices in order to fit the great variety of plant structures and water volumes. On some occasions, natural and artificial ovitraps were used, including bamboo stumps, CDC ovitraps and artificial bromeliads installed at ground or canopy level. Immature mosquitoes from larger bodies of water were collected by using a kick net. Adult mosquitoes

were attracted in the field by human bait and captured with a butterfly net or with an entomological aspirator when they alighted.

Processing: Whenever possible, samples were brought back alive to the laboratory. Immature mosquitoes were individually reared in 2 mL Eppendorf tubes and placed in a climatic chamber at 28°C to obtain adults. When a sufficient number of adults was obtained, some of them were stored in individual tubes containing 96 % ethanol. Fourth instar and pupal skins were also sorted and stored in individual tubes containing 70 % ethanol. Laboratory-reared adults and adults issued from field capture were killed by freezing. Three legs from the right side of each specimen were then carefully dissected and kept in a separate vial containing 96 % ethanol and stored at -20°C for further molecular investigations. Adults were mounted on their right side on a pin point attached to a No. 3 stainless steel insect pin and stored in entomological boxes. Specimen codes are based on the name of the collection followed by a unique serial number as proposed by **Gaffigan and Pecor** (**1997**). The same code was used for all of the biological material issued from the same specimen. When it was impossible to bring live samples back to the laboratory and rearing was not possible either, specimens were stored directly in 96 % ethanol in the field.

Quality control description: Considering different sources of GPS errors (such as ionosphere delay and signal multipath), we estimate the accuracy of the coordinates to be around 30 meters at a 95 % confidence level.

MB10794

Sabethes hadrognathus Harbach, 1995
authority from EOL

Specimen name			
Order	Diptera	Subfamily	Culicinae
Family	Culicidae	Tribe	Sabethini
Genus	Sabethes	Subtribe	Peytonulus
Species	hadrognathus	Host org.	
Subspecies		Auctor	
Type species?		don't know	

DNA	
Extraction	Tube
Extractor	
Date	

Locality Information		
Country		
French Guiana		
Specific Locality		
Saül		
Latitude	Longitude	Altitude
3°38' N	53°13' W	100

Collector Information		
Code in VoSeq	Collector	Collection date
MB10794	S. Talaga	2015-03-06
Voucher Locality	Voucher	Sex
Ecofog-Kourou	95% EtOH	I
	Voucher Code	Determined By
	MB1#0794	S. Talaga

Sequence Information						
Region	bp	Amb.	Lab.	Accession	local Blast	ncbi Blast
16SIns	230	0	GenoScre			
COI	654	0	GenoScre			
add seq						

Publication and Notes	
Published in	Notes
	Larval collection - Hollow stem Guadua latifolia

Figure 3.3 Sample data entry of our online database (http://mosquitoes.ups-tlse.fr/ with restricted access) holding the "Mosquitoes of French Guiana" dataset.

Selected specimens were photographed using a Leica DFC450 camera mounted on a Leica MZ16 macroscope under a light dome simulating natural light. Images were Z-stacked using the Leica LAS Z-stacking module. Montage pictures and collecting information for each specimen are stored in an online Voseq database (**Peña & Malm 2012**) managed by the EDB laboratory (**Fig. 3.3**) and viewable through the Guyanensis GIS web platform at http://guyanensis.ups-tlse.fr/, through the Global Biodiversity Information Facility (GBIF) at http://www.gbif.org/dataset/5a8aa2ad-261c-4f61-a98e-26dd752fe1c5/ or alternatively through the local Integrated Publishing Toolkit (IPT) at http://130.120.204.55:8080/ipt/resource.do?r=mosquitoes_of_french_guiana/ Specimens are initially curated at the Ecofog laboratory by Stanislas Talaga and can be deposited in museums for further taxonomic study.

DATA RESSOURCES

Dataset title: Mosquitoes of French Guiana
Resource: r=mosquitoes_of_french_guiana
Character encoding: UTF-8
Format name: Darwin Core Archive (**Darwin Core Task Group 2009**)
Format version: 1.0
Distribution: http://130.120.204.55:8080/ipt/resource.do?r=mosquitoes_of_french_guiana/
Publication date of data: 2015-06-12
Language of database: English
License of use: Other
Date of metadata creation: 2014-12-10
Hierarchy level: Dataset

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Chapitre 4: Convergent evolution of intraguild predation in phytotelm-breeding mosquitoes (Talaga *et al.*, soumis à *Evolutionary Ecology*)

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Abstract: Intraguild predation (IGP) is a type of biological interaction involving the killing and eating of competing species that exploit similar and often limited resources. This phenomenon, widespread among a great variety of taxonomic groups and has already been reported in mosquito (Diptera: Culicidae) larvae. Moreover, the larvae of certain mosquito species have evolved modified mouthparts ending in rigid apical structures signaling their capacity to be effective intraguild predators. We assumed that IGP confer a selective advantage under severe competitive conditions by both providing an immediate energetic gain and by reducing potential competition. Because potential competition is likely to increase with decreasing habitat size, we hypothesized that the proportion of species with modified mouthparts would increase in smaller aquatic habitats. We tested this hypothesis by examining the mosquito species naturally associated with phytotelmata of decreasing sizes in French Guiana. We show that the degree of specialization in mosquito-phytotelm associations is high, suggesting a long coevolutive process. Indeed, short-term interaction experiments confirmed that species with modified mouthparts are able to prey upon similarly-sized intraguild prey and are, thus, effective intraguild predators. In addition these species are larger and associated with smaller phytotelmata than those with typical mouthparts. Moreover, below a certain threshold of phytotelm size, only species with modified mouthparts remained. These results show that IGP is a selective advantage under severe competitive conditions and results from the coadaptation of mosquito species to their specific phytotelm habitat. The

selection of functionally analogous structures in different mosquito genera also implies that IGP has emerged from convergent evolution in small phytotelmata.

Keywords: Coadaptation, Interaction networks, Mosquito-plant associations, Neotropics, Sabethini.

INTRODUCTION

Intraguild predation (IGP) is a type of biological interaction midway between predation and competition which involves the killing and eating of competing species that exploit similar and often limited resources (**Polis *et al.* 1989**). It differs from traditional concepts of competition by the immediate energetic gains for one participant and from classical predation because it also reduces potential competition (**Holt & Polis 1997**). This phenomenon is widespread among a great variety of taxonomic groups and understanding the reasons for the selection of such behavior is challenging (**Arim & Marquet 2004**).

The life cycle of mosquitoes (Diptera: Culicidae) is complex and implies an ontogenetic niche shift between an aquatic immature stage and a terrestrial adult stage (**Wilbur 1980**). Much of the biomass of individuals is obtained during their aquatic life, so that food acquisition at this stage is a limiting factor for their fitness (**Clements 1990**). The most common feeding mode used by mosquito larvae is particle capture through filtration, but some species have evolved alternative or complementary feeding modes such as scraping, shredding or predation (**Merritt *et al.* 1992**). IGP has been documented in mosquitoes of the genus *Aedes* and has proven to be context dependent and enhanced under limited food conditions (**Edgerly *et al.* 1999**). It was also noted in the malaria vector *Anopheles gambiae* s.s. under laboratory conditions and has been suggested to be common in natural conditions (**Muturi *et al.* 2010**). This age-structured IGP is likely due to the inadapted structure of larval mouthparts (i.e. mandible or maxilla) to prey upon larger individuals (**Knight *et al.* 1977**). In both cases, IGP only occurs between late instars preying upon first instar larvae. In this situation, the benefit of IGP (i.e. energetic gain and the elimination of a competitor) is relatively limited because competition is expected to occur between similarly-sized intraguild individuals more than between a large and a smaller individual.

Mosquitoes have colonized a great variety of water collections, from the largest lakes to the smallest phytotelmata (‘plant-held waters’) (**Mogi & Sembel 1996**). The relative intensity of biological interactions such as predation and competition are thought to change across

habitat size. For example, predation by higher trophic levels is supposed to be high in large aquatic habitats as a result of greater prey production and longer habitat persistence (**Sunahara *et al.* 2002**). On the contrary, interference and exploitative competition are thought to be high in small aquatic habitats as a result of greater promiscuity and lower food resources (**Summers & McKeon 2004**). Furthermore, it has already been shown in mosquitoes that species exposed to similar selective forces have independently evolved analogous and convergent feeding strategies (**Lounibos 1983**).

The size of phytotelmata can range from a few milliliters to several liters depending on the plant species (**Kitching 2000**), and their associated mosquito species have likely evolved different strategies to face the long-term selective forces imposed by phytotelm size. Among phytotelm-breeding mosquitoes, several species of the tribe Sabethini have evolved modified mouthparts, including maxilla ending in rigid apical structures (i.e. maxillary bundle, claw or prominent tooth) (**Harbach & Peyton 1993**) or hypertrophied mandibles (**Zavortink 1979**). These structural modifications are probably detrimental to their filtration performance, but have been postulated to be functional adaptations for collecting food by sweeping, scraping or clasping (**Harbach & Peyton 1993**).

We assumed that IGP confers a selective advantage under severe competitive conditions by both providing an immediate energetic gain and by reducing potential competition. Because potential competition is likely to increase with decreasing habitat size, we hypothesized that the proportion of species with modified mouthparts would increase in smaller aquatic habitats. Moreover, because larger species have more chance to prey upon than to be preyed on than do smaller species, the intensification of IGP may have selected larger species in small aquatic habitats. We tested these hypotheses by examining the mosquito species naturally associated with phytotelmata of decreasing sizes in French Guiana.

We selected 22 species of the most common plants forming phytotelmata and identified the mosquito species associated with them as well as their level of association. Second, based on the assumption that competition is higher in small phytotelmata than in larger ones, we verified if the proportion of mosquito species with modified mouthparts increases with the decreasing size of the phytotelmata and if these species are larger, an advantage in IGP. Third, we conducted short-term interaction experiments under laboratory conditions to confirm that species with modified mouthparts have the capacity to prey upon similarly-sized intraguild species.

MATERIALS AND METHODS

This study was conducted in French Guiana between 2013 and 2015 in seven localities: Cayenne (4°55′N, 52°19′W), Itoupé (3°01'N, 53°04'W), Kaw Mountain, from Roura (04°43'N, 52°19'W) to Kaw (4°36'N, 52°07'W), Kourou (5°09', 52°39'W), inselberg La Virginie (4°11'N, 52°09'W), Montsinéry (04°53'N, 52°29'W), Petit-Saut (52°21'N, 53°41'W) and Saül (3°37'N, 53°12'W) (**Talaga *et al.* 2015c**). We selected 22 phytotelm plant species from eight families based on their contrasting phytotelm size (**Table 4.1**). Immature mosquitoes were collected from 30 phytotelm structures (i.e. leaf axil, flower bract or hollow stem) per phytotelm plant species (fully grown individuals were chosen to avoid ontogenetic variations). The water volume of each for the phytotelm sampled was used as a proxy of phytotelm size.

Table 4.1 List of the 22 plant species forming phytotelmata that were sampled. Species are ranked alphabetically by family, genus and species. The occurrence in French Guiana as well the validity of species names is based on **Funk *et al.*** (**2007**). Type of phytotelm structures have been divided into leaf axil (LA), flower bract (FB) and hollow stem (HS), and indicated for each species.

Family	Genus	Species	Author	Type of phytotelm		
ARACEAE	*Dieffenbachia*	*seguine*	(Jacq.) Schott	LA		
BROMELIACEAE	*Aechmea*	*aquilega*	(Salisbery) Grisebach	LA		
		bromeliifolia	(Rudge) Baker	LA		
		melinonii	Hooker	LA		
		mertensii	(Meyer) J.H.Schultes	LA		
	Ananas	*comosus*	(L.) Merrill	LA		
	Guzmania	*lingulata*	(L.) Mez	LA		
		melinonis	Regel	LA		
	Vriesea	*amazonica*	(Baker) Mez	LA		
		splendens	(Brongniart) Lemaire	LA		
COSTACEAE	*Costus*	*claviger*	Benoist	LA		
CYCLANTHACEAE	*Cyclanthus*	*bipartitus*	Poit.	LA		
	Ludovia	*lancifolia*	Brongn.	LA		
HELICONIACEAE	*Heliconia*	*acuminata*	L.C.Rich.	LA		
		bihai	(L.) L.	LA	FB	
		psittacorum	L.f.	LA		
MARANTACEAE	*Calathea*	*maasiorum*	H.Kennedy	LA		
	Ischnosiphon	*obliquus*	(Rudge) Korn.	LA		
POACEAE	*Bambusa*	*vulgaris*	Schrad. ex J.C.Wendl.			HS
	Guadua	*latifolia*	(Humb. & Bonpl.) Kunth			HS
	Lasiacis	*sorghoidea*	(Desv. ex Ham.) Hitchc. & Chase			HS
STRELITZIACEAE	*Phenakospermum*	*guyannense*	(L.C.Rich.) Endl. ex Miq.	LA		

Immature mosquitoes were collected by extracting plant-held water using several sucking devices adapted to the various shapes and volumes of each phytotelm plant species. Specimens were isolated in transparent 2 ml Eppendorf Tubes® filled with the water from their phytotelm and transported alive to the laboratory in order to obtain adults. In the laboratory, immature individuals were placed into a climatic chamber with a constant temperature of 28°C under a 12h:12h photoperiod. Specimens were raised in their tubes, fed with flake fish food (Tetra®), and the water level was kept constant by the regular addition of rainwater. Emerging adults were freeze-killed and pin-mounted along with their fourth instar and pupal exuviae following the protocol proposed by **Gaffingan and Pecor** (**1997**). Surplus larvae were killed and preserved in 96 % alcohol. Most of the specimens sampled were identified to species level and all useful information on their sampling conditions was noted in an online database (see **Talaga *et al.* 2015c** for details).

To study the level of association between mosquito species and phytotelm plants, we created three interaction networks based on presence/absence data; the plants were grouped by species, genus and family. For each network, the connectance (C; number of species associations at the network-level; **Dunne *et al.* 2002**), Fisher's alpha diversity (Fα; diversity of interactions at the network level; **Fisher *et al.* 1943**) and the specialization index (H'_2; specialization in interactions at the network level, **Blüthgen & Menzel 2006**) were calculated.

The mean size of each sabethine species was approximated by measuring the head capsule width of fourth instar larvae under a stereomicroscope equipped with a micrometer (six individuals per species; only two for infrequent species, namely: *Sabethes* (*Peytonulus*) sp.stD, *Sabethes* (*Sabethinus*) sp.stF, *Trichoprosopon compressum*, *Trichoprosopon* sp.stG, *Trichoprosopon* sp.stH, *Wyeomyia* (*Caenomyiella*) sp.stB). The mean water volume for the phytotelmata and mosquito size were compared between species with and without modified mouthparts using Student's t-test or the Wilcoxon Rank Sum test when the normality assumption was violated. Network and statistical analyses were conducted using R (R software; **R Development Core Team 2013**) with 'bipartite' and 'stats' packages.

Short-term interaction experiments were conducted under laboratory conditions using eight sabethine species to verify if modified mouthparts permit them to prey upon similarly-sized intraguild species. Four of them were chosen due to different types of modified mouthparts: *Runchomyia* (*Ctenogoeldia*) *magna* have maxillary bundles, *Sabethes* (*Peytonulus*) *undosus* have prominent maxillary teeth, *Shannoniana fluviatilis* have maxillary claws and *Trichoprosopon pallidiventer* have hypertrophied mandibles (**Fig. 4.1c, d**). The four other species -*Wyeomyia* (*Decamyia*) *pseudopecten*, *Wy.* (*Dodecamyia*) *aphobema*, *Wy.*

(*Wyo.*) *pertinans*, and *Wy. occulta*- exhibited typical mouthparts (i.e. unmodified maxillae or mandibles; **Fig. 4.1a, b**).

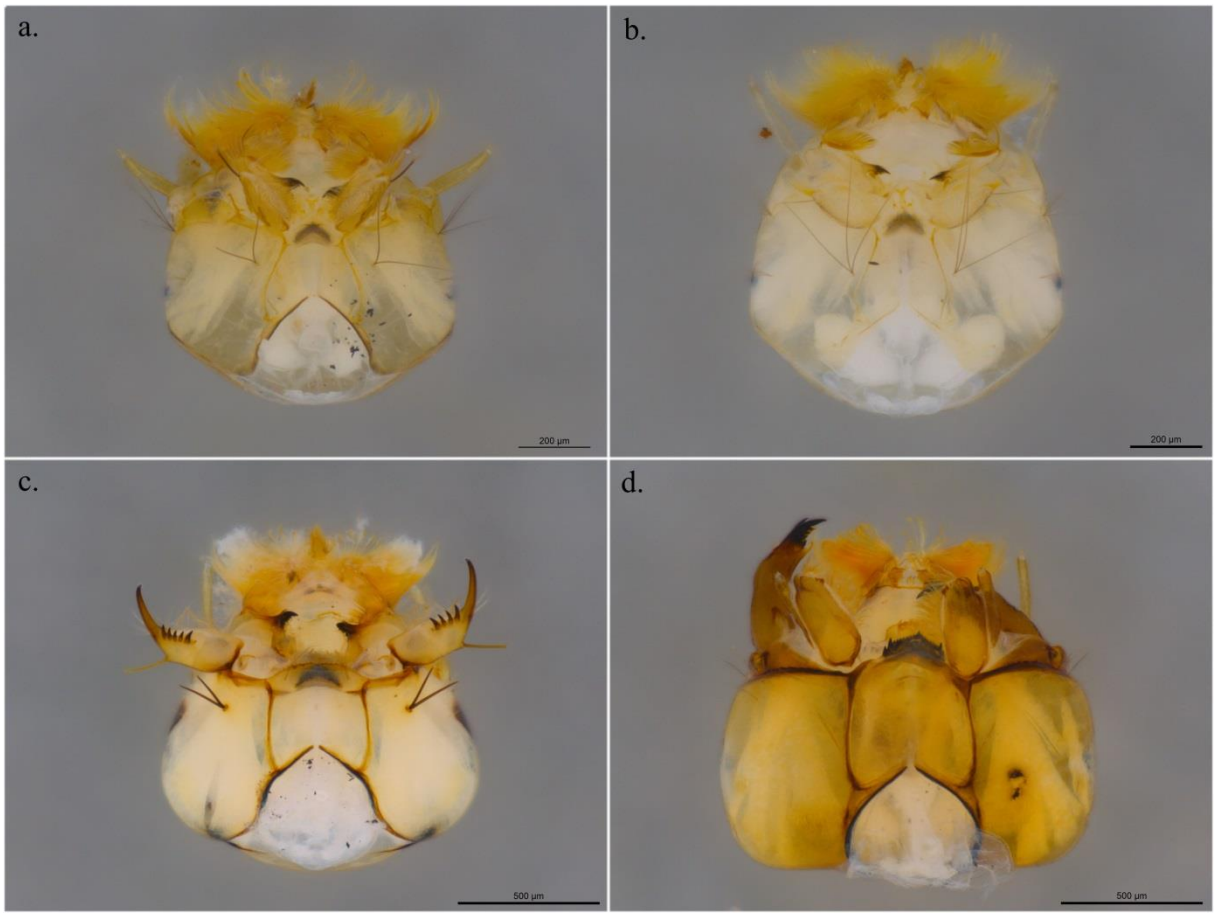


Figure 4.1 Ventral view of the head capsule of fourth instar Sabethini mosquito larvae. a. *Wyeomyia* (*Dodecamyia*) *aphobema* and b. *Wy.* (*Wyo.*) *pertinans* have typical mouthparts. c. *Sabethes* (*Peytonulus*) *undosus* has prominent maxillary teeth. d. *Trichoprosopon pallidiventer* possesses hypertrophied mandibles. Mandibles and maxillae are abbreviated Md and Mx, respectively.

For each species to be tested, 20 wild-collected fourth instar larvae (except for *Sh. fluviatilis*, N = 15) were isolated in 2 ml transparent tubes filled with 1.5 ml of mineral water (Volvic®) and starved during 7 days. Because they are easy to rear and their size corresponded to the median size of the tested sabethine species, third instar *Aedes* (*Stegomyia*) *aegypti* larvae were used as the intraguild, co-occuring species. At the beginning of each trial, a drop of water containing an *Ae.* (*Stg.*) *aegypti* larva was added to each tube. The tubes, aligned in a transparent rack, were checked every 5 minutes during 1 hour and the amount of predation upon the *Ae.* (*Stg.*) *aegypti* larvae was recorded. The experiment was repeated for the pool of *Ru.* (*Cte.*) *magna* larvae 1 hour after the end of the first trial by the addition of a new *Ae.* (*Stg.*) *aegypti* larva to each tube.

RESULTS

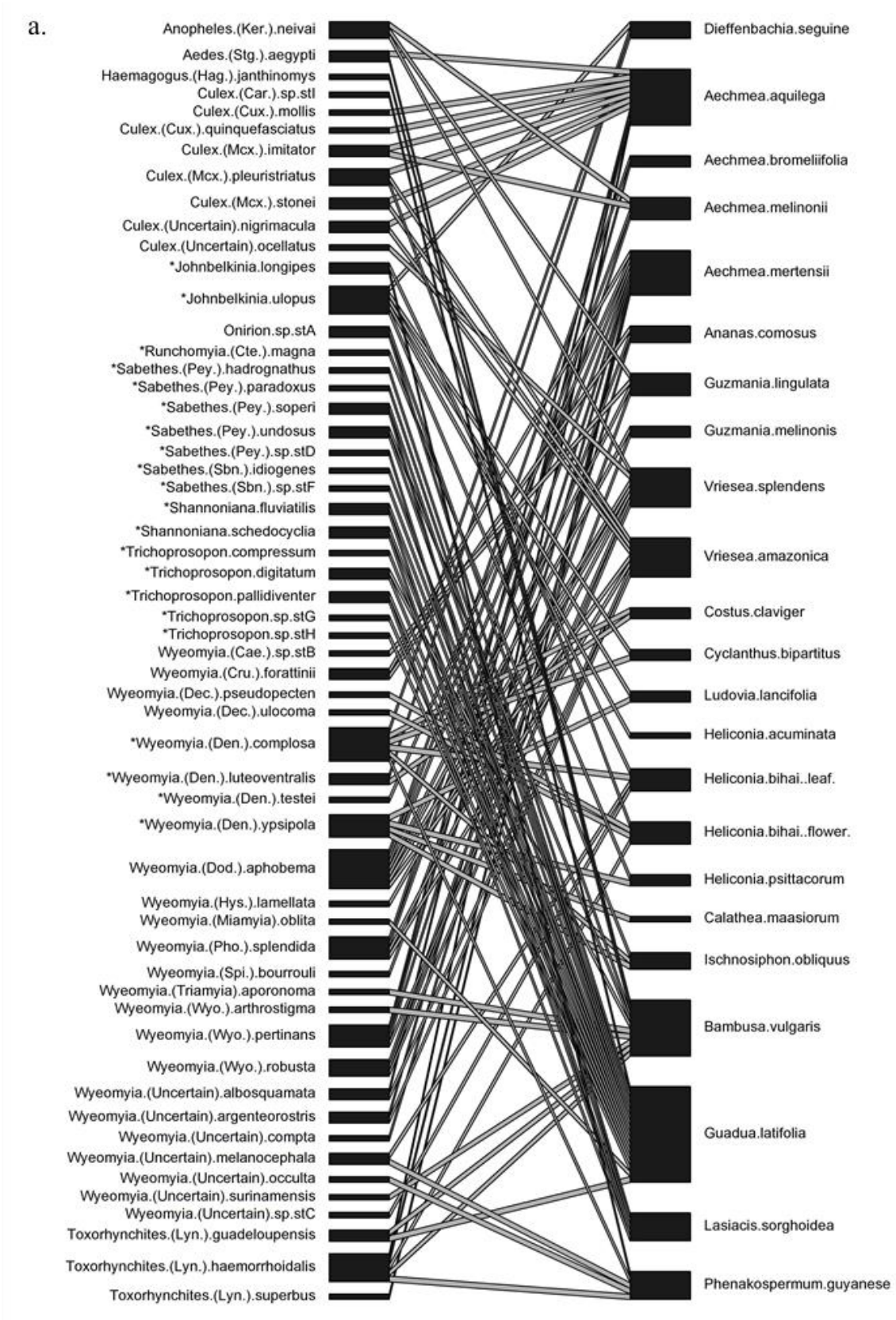
The phytotelmata of the 22 plant species sheltered the immature individuals of 56 mosquito species, of which 55 belong to the subfamily Culicinae and the remaining species, *Anopheles* (*Kerteszia*) *neivai*, is an Anophelinae (**Table 4.2; Fig. 4.2a**). The Culicinae were represented by the tribes Sabethini (76.4 %), Culicini (14.5 %), Toxorhynchitini (5.5 %) and Aedini (3.6 %). Note that the invasive mosquito *Ae.* (*Stg.*) *aegypti* was retrieved from the tank bromeliad *Aechmea aquilega* and bamboo stumps (i.e. from *Bambusa vulgaris*; **Fig. 4.2a**).

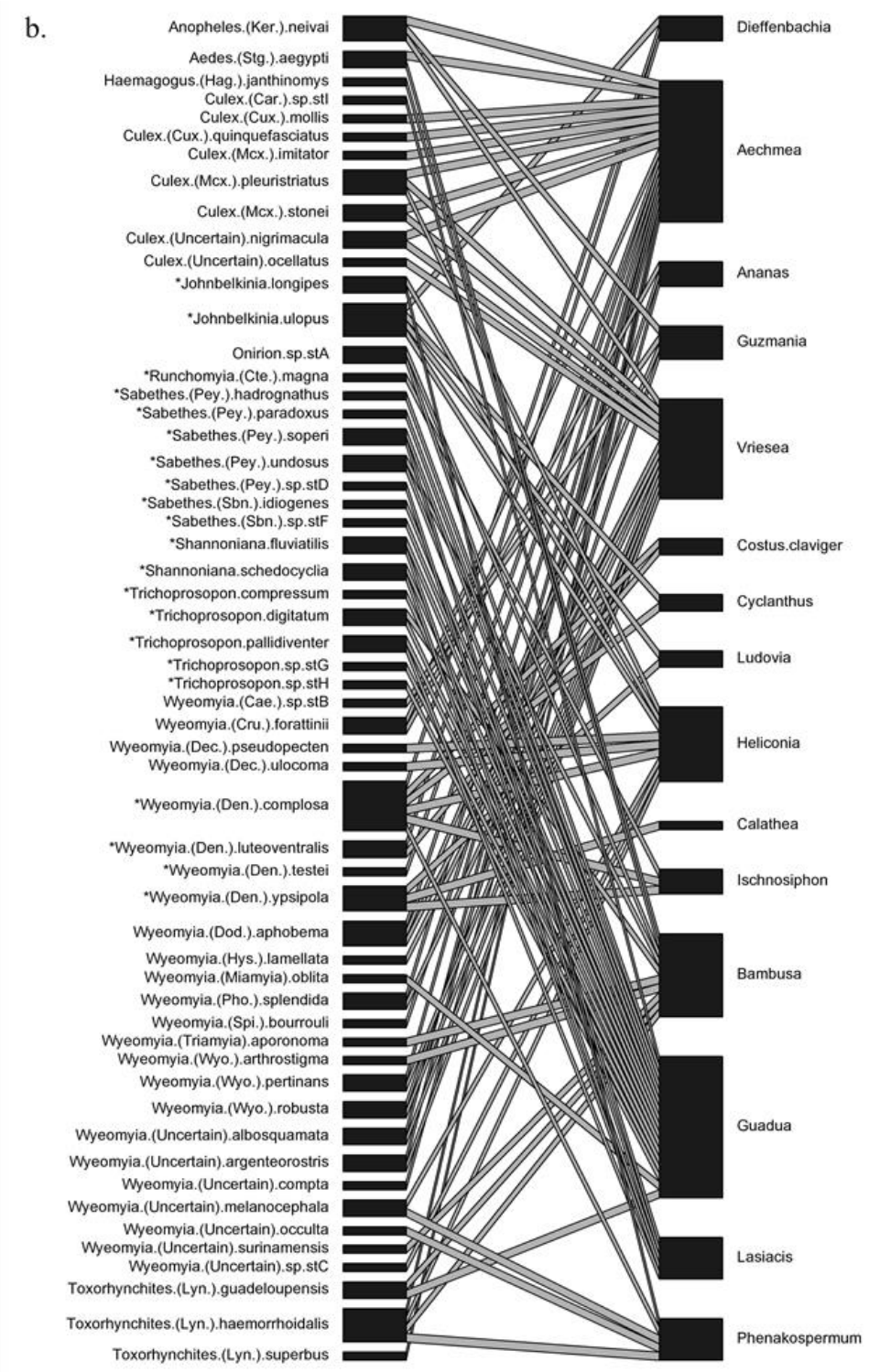
Table 4.2 List of mosquito species found in phytotelm plants in French Guiana. Species are ranked alphabetically by subfamily, genus, subgenus and species. The type of mouthparts is indicated for each species; -: Typical mouthparts, MB: Maxillary bundle, MC: Maxillary claw, MT: prominent Maxillary tooth, HM: Hypertrophied mandible. Species with modified mouthparts are highlighted in bold.

Subfamily	Tribe	Genus	Subgenus	Species	Author	Modified mouthpart
Anophelinae		*Anopheles*	*Kerteszia*	*neivai*	Howard Dyar & Knab 1913	-
Culicinae	Aedini	*Aedes*	*Stegomyia*	*aegypti*	(Linnaeus 1762)	-
		Haemagogus	*Haemagogus*	*janthinomys*	Dyar 1921	-
	Culicini	*Culex*	*Carrollia*	sp.stI	cf. Valencia (1973)	-
		Culex	*Culex*	*mollis*	Dyar & Knab 1906	-
		Culex	*Culex*	*quinquefasciatus*	Say 1823	-
		Culex	*Microculex*	*imitator*	Theobald 1903	-
		Culex	*Microculex*	*pleuristriatus*	Theobald 1903	-
		Culex	*Microculex*	*stonei*	Lane & Whitman 1943	-
		Culex	Uncertain	*nigrimacula*	Lane & Whitman 1943	-
		Culex	Uncertain	*ocellatus*	Theobald 1903	-
	Sabethini	***Johnbelkinia***		***longipes***	**(Fabricius 1805)**	**MB**
		Johnbelkinia		***ulopus***	**(Dyar & Knab 1906)**	**MB**
		Onirion		sp.stA	cf. Harbach & Peyton (2000)	-
		Runchomyia	***Ctenogoeldia***	***magna***	**(Theobald 1905)**	**MB**
		Sabethes	***Peytonulus***	***hadrognathus***	**Harbach 1995**	**MT**
		Sabethes	***Peytonulus***	***paradoxus***	**Harbach 2002**	**MT**
		Sabethes	***Peytonulus***	***soperi***	**Lane & Cerqueira 1942**	**MT**
		Sabethes	***Peytonulus***	***undosus***	**(Coquillett 1906)**	**MT**
		Sabethes	***Peytonulus***	**sp.stD**	**cf. Harbach (1991)**	**MT**
		Sabethes	***Sabethinus***	***idiogenes***	**Harbach 1994**	**MT**
		Sabethes	***Sabethinus***	**sp.stF**	**cf. Harbach (1994)**	**MT**
		Shannoniana		***fluviatilis***	**(Theobald 1903)**	**MC**
		Shannoniana		***schedocyclia***	**(Dyar & Knab 1908)**	**MC**
		Trichoprosopon		***compressum***	**Lutz 1905**	**HM**
		Trichoprosopon		***digitatum***	**(Rondani 1848)**	**HM**
		Trichoprosopon		***pallidiventer***	**(Lutz 1905)**	**HM**

	Trichoprosopon		**sp.stG**	**cf. Zavortink (1979)**	**HM**
	Trichoprosopon		**sp.stH**	**cf. Zavortink (1979)**	**HM**
	Wyeomyia	*Caenomyiella*	sp.stB	cf. Harbach & Peyton (1990)	-
	Wyeomyia	*Cruzmyia*	*forattinii*	Clastrier 1974	-
	Wyeomyia	*Decamyia*	*pseudopecten*	Dyar & Knab 1906	-
	Wyeomyia	*Decamyia*	*ulocoma*	(Theobald 1903)	-
	Wyeomyia	***Dendromyia***	***complosa***	**(Dyar 1928)**	**MT**
	Wyeomyia	***Dendromyia***	***luteoventralis***	**Theobald 1901**	**MT**
	Wyeomyia	***Dendromyia***	***testei***	**Senevet & Abonnenc 1939**	**MT**
	Wyeomyia	***Dendromyia***	***ypsipola***	**Dyar 1922**	**MT**
	Wyeomyia	*Dodecamyia*	*aphobema*	Dyar 1918	-
	Wyeomyia	*Hystatomyia*	*lamellata*	(Bonne-Wepster & Bonne 1919)	-
	Wyeomyia	*Miamyia*	*oblita*	(Lutz 1904)	-
	Wyeomyia	*Phoniomyia*	*splendida*	Bonne-Wepster & Bonne 1919	-
	Wyeomyia	*Spilonympha*	*bourrouli*	(Lutz 1905)	-
	Wyeomyia	*Triamyia*	*aporonoma*	Dyar & Knab 1906	-
	Wyeomyia	*Wyeomyia*	*arthrostigma*	(Lutz 1905)	-
	Wyeomyia	*Wyeomyia*	*pertinans*	(Williston 1896)	-
	Wyeomyia	*Wyeomyia*	*robusta*	Senevet & Abonnenc 1939	-
	Wyeomyia	Uncertain	*albosquamata*	Bonne-Wepster & Bonne 1919	-
	Wyeomyia	Uncertain	*argenteorostris*	(Bonne-Wepster & Bonne 1920)	-
	Wyeomyia	Uncertain	*compta*	Senevet & Abonnenc 1939	-
	Wyeomyia	Uncertain	*melanocephala*	Dyar & Knab 1906	-
	Wyeomyia	Uncertain	*occulta*	Bonne-Wepster & Bonne 1919	-
	Wyeomyia	Uncertain	*surinamensis*	Bruijning 1959	-
	Wyeomyia	Uncertain	sp.stC	cf. Lane (1953)	-
Toxorhynchitini	*Toxorhynchites*	*Lynchiella*	*guadeloupensis*	(Dyar & Knab 1906)	-
	Toxorhynchites	*Lynchiella*	*haemorrhoidalis*	(Fabricius 1787)	-
	Toxorhynchites	*Lynchiella*	*superbus*	(Dyar & Knab 1906)	-

The majority of the mosquito species were found in one (50 %) or two (32.1 %) phytotelm plant species; we noted an average of 1.38 links per species at the network level (**Fig. 4.2a**). The network specialization index, high overall, was the highest when the phytotelmata were grouped by family (H_2' = 0.7683); it then decreased with increasing taxonomic resolution (H_2' = 0.7248 and H_2' = 0.7045 when grouped by genus and species, respectively) (**Fig. 4.2a, b, c**). The same was true for the connectance (C = 0.1607; C = 0.1131; and C = 0.0838 when grouped by family, genus and species, respectively). The Fisher's alpha diversity was higher when the phytotelmata were grouped by genus (Fα = 5.37e+10) than by species (Fα = 1.34e+10) or family (Fα = 2.68e+10).


a.
Anopheles.(Ker.).neivai
Aedes.(Stg.).aegypti
Haemagogus.(Hag.).janthinomys
Culex.(Car.).sp.stI
Culex.(Cux.).mollis
Culex.(Cux.).quinquefasciatus
Culex.(Mcx.).imitator
Culex.(Mcx.).pleuristriatus
Culex.(Mcx.).stonei
Culex.(Uncertain).nigrimacula
Culex.(Uncertain).ocellatus
*Johnbelkinia.longipes
*Johnbelkinia.ulopus
Onirion.sp.stA
*Runchomyia.(Cte.).magna
*Sabethes.(Pey.).hadrognathus
*Sabethes.(Pey.).paradoxus
*Sabethes.(Pey.).soperi
*Sabethes.(Pey.).undosus
*Sabethes.(Pey.).sp.stD
*Sabethes.(Sbn.).idiogenes
*Sabethes.(Sbn.).sp.stF
*Shannoniana.fluviatilis
*Shannoniana.schedocyclia
*Trichoprosopon.compressum
*Trichoprosopon.digitatum
*Trichoprosopon.pallidiventer
*Trichoprosopon.sp.stG
*Trichoprosopon.sp.stH
Wyeomyia.(Cae.).sp.stB
Wyeomyia.(Cru.).forattinii
Wyeomyia.(Dec.).pseudopecten
Wyeomyia.(Dec.).ulocoma
*Wyeomyia.(Den.).complosa
*Wyeomyia.(Den.).luteoventralis
*Wyeomyia.(Den.).testei
*Wyeomyia.(Den.).ypsipola
Wyeomyia.(Dod.).aphobema
Wyeomyia.(Hys.).lamellata
Wyeomyia.(Miamyia).oblita
Wyeomyia.(Pho.).splendida
Wyeomyia.(Spi.).bourrouli
Wyeomyia.(Triamyia).aporonoma
Wyeomyia.(Wyo.).arthrostigma
Wyeomyia.(Wyo.).pertinans
Wyeomyia.(Wyo.).robusta
Wyeomyia.(Uncertain).albosquamata
Wyeomyia.(Uncertain).argenteorostris
Wyeomyia.(Uncertain).compta
Wyeomyia.(Uncertain).melanocephala
Wyeomyia.(Uncertain).occulta
Wyeomyia.(Uncertain).surinamensis
Wyeomyia.(Uncertain).sp.stC
Toxorhynchites.(Lyn.).guadeloupensis
Toxorhynchites.(Lyn.).haemorrhoidalis
Toxorhynchites.(Lyn.).superbus
Dieffenbachia.seguine
Aechmea.aquilega
Aechmea.bromeliifolia
Aechmea.melinonii
Aechmea.mertensii
Ananas.comosus
Guzmania.lingulata
Guzmania.melinonis
Vriesea.splendens
Vriesea.amazonica
Costus.claviger
Cyclanthus.bipartitus
Ludovia.lancifolia
Heliconia.acuminata
Heliconia.bihai..leaf.
Heliconia.bihai..flower.
Heliconia.psittacorum
Calathea.maasiorum
Ischnosiphon.obliquus
Bambusa.vulgaris
Guadua.latifolia
Lasiacis.sorghoidea
Phenakospermum.guyanese


b.
Anopheles.(Ker.).neivai
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Culex.(Cux.).quinquefasciatus
Culex.(Mcx.).imitator
Culex.(Mcx.).pleuristriatus
Culex.(Mcx.).stonei
Culex.(Uncertain).nigrimacula
Culex.(Uncertain).ocellatus
*Johnbelkinia.longipes
*Johnbelkinia.ulopus
Onirion.sp.stA
*Runchomyia.(Cte.).magna
*Sabethes.(Pey.).hadrognathus
*Sabethes.(Pey.).paradoxus
*Sabethes.(Pey.).soperi
*Sabethes.(Pey.).undosus
*Sabethes.(Pey.).sp.stD
*Sabethes.(Sbn.).idiogenes
*Sabethes.(Sbn.).sp.stF
*Shannoniana.fluviatilis
*Shannoniana.schedocyclia
*Trichoprosopon.compressum
*Trichoprosopon.digitatum
*Trichoprosopon.pallidiventer
*Trichoprosopon.sp.stG
*Trichoprosopon.sp.stH
Wyeomyia.(Cae.).sp.stB
Wyeomyia.(Cru.).forattinii
Wyeomyia.(Dec.).pseudopecten
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*Wyeomyia.(Den.).ypsipola
Wyeomyia.(Dod.).aphobema
Wyeomyia.(Hys.).lamellata
Wyeomyia.(Miamyia).oblita
Wyeomyia.(Pho.).splendida
Wyeomyia.(Spi.).bourrouli
Wyeomyia.(Triamyia).aporonoma
Wyeomyia.(Wyo.).arthrostigma
Wyeomyia.(Wyo.).pertinans
Wyeomyia.(Wyo.).robusta
Wyeomyia.(Uncertain).albosquamata
Wyeomyia.(Uncertain).argenteorostris
Wyeomyia.(Uncertain).compta
Wyeomyia.(Uncertain).melanocephala
Wyeomyia.(Uncertain).occulta
Wyeomyia.(Uncertain).surinamensis
Wyeomyia.(Uncertain).sp.stC
Toxorhynchites.(Lyn.).guadeloupensis
Toxorhynchites.(Lyn.).haemorrhoidalis
Toxorhynchites.(Lyn.).superbus
Dieffenbachia
Aechmea
Ananas
Guzmania
Vriesea
Costus.claviger
Cyclanthus
Ludovia
Heliconia
Calathea
Ischnosiphon
Bambusa
Guadua
Lasiacis
Phenakospermum

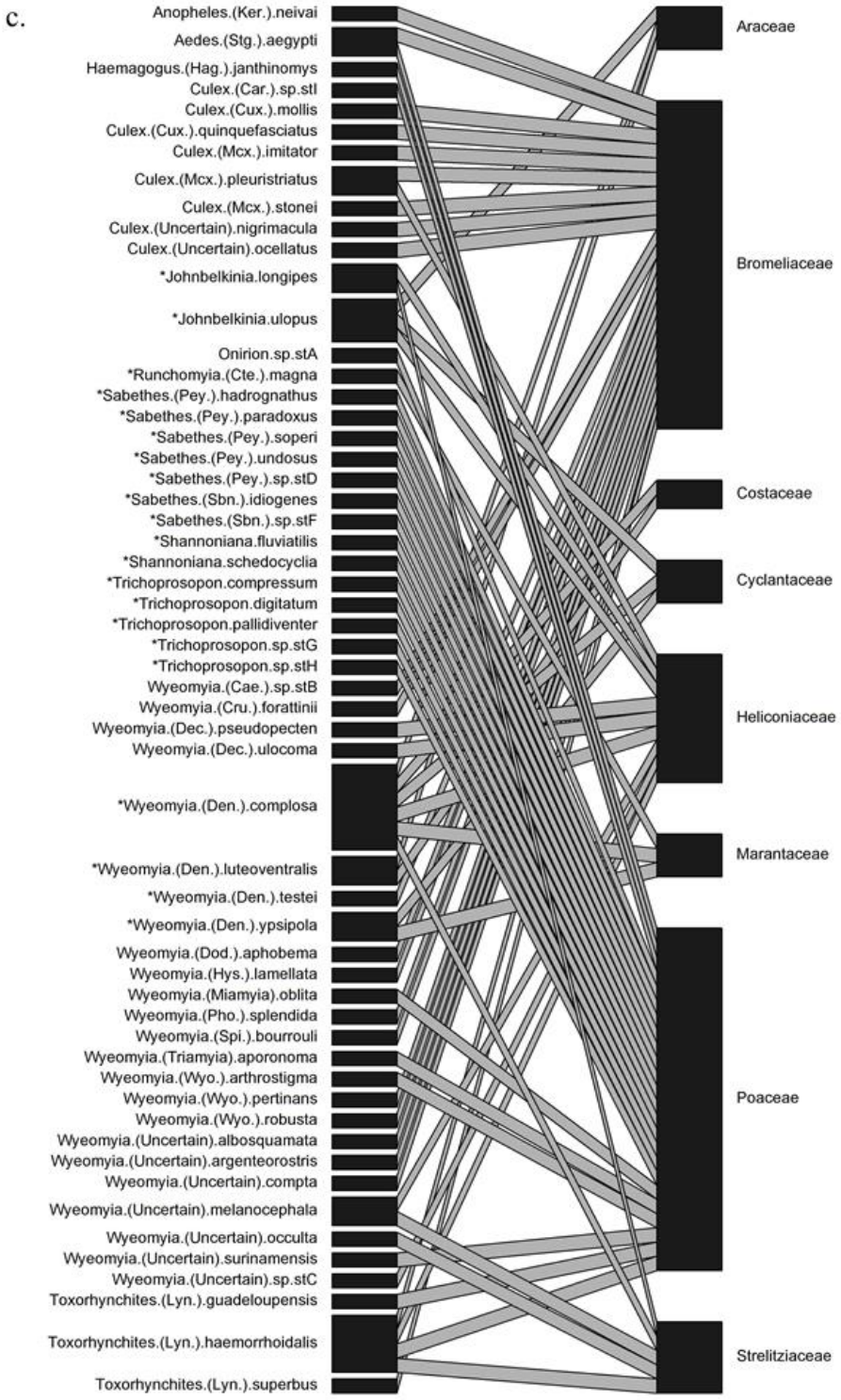

Figure 4.2 Network of interactions between mosquitoes (on the left) and their phytotelm host plants (on the right). Mosquito species are listed alphabetically and ranked by subfamily, tribe, genus and subgenus; stars indicate mosquito species with modified mandibles or maxilla. a. Phytotelm species (listed alphabetically and ranked by family and genus); 22 species tested, two types of phytotelm were distinguished for *Heliconia bihai*. b. Phytotelm genera (listed alphabetically and ranked by family). c. Phytotelm families listed alphabetically.

The mean volume of water held per phytotelm structure ranged from 1.18 ±0.08 ml up to 88.17 ±6.37 ml, these values corresponding to *Ischnosiphon obliquus* and *B. vulgaris*, respectively. The proportion of species with modified mouthparts did not show a clear increasing pattern along phytotelm size (**Fig. 4.3**). Nevertheless, all of the mosquito species associated with phytotelmata holding a mean volume of water equal to or less than 6.1 ml were sabethine with modified mouthparts (**Fig. 4.3**). Furthermore, the latter species were significantly more often found in association with smaller phytotelmata than were species with typical mouthparts (11.06 ±0.60 ml *versus* 35.42 ±0.89 ml; Wilcoxon rank sum test; W = 187,720; P < 0.0001); moreover, the former have a significantly larger head width than the latter (1162.79 ±16.39 µm *versus* 904 ±9.18 µm; Welch t-test; t = 13.7; df = 159.7; P < 0.001).

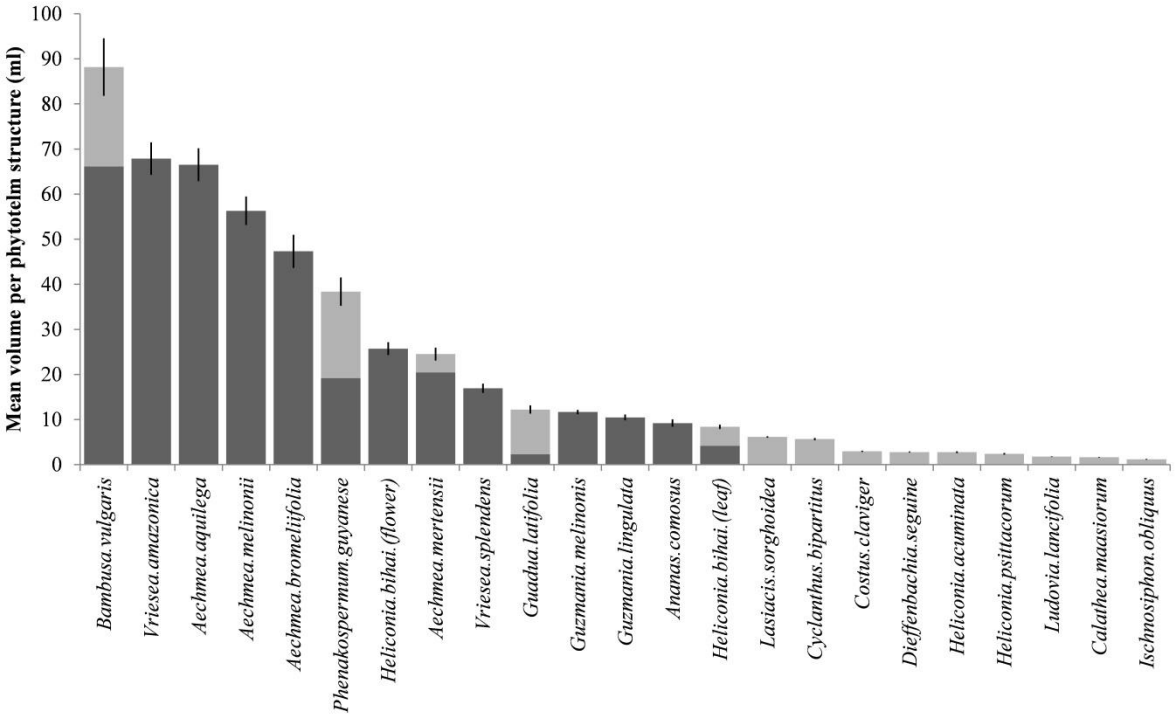

Figure 4.3 Mean volume of water held (per phytotelm structure) by 22 monocotyledon plant species forming phytotelmata in French Guiana. Plant species are ranked in decreasing order of their mean volume. Bars are filled to indicate the relative proportions of associated mosque to species with (light grey, N = 21) and without modified mouthparts (dark grey, N = 35).

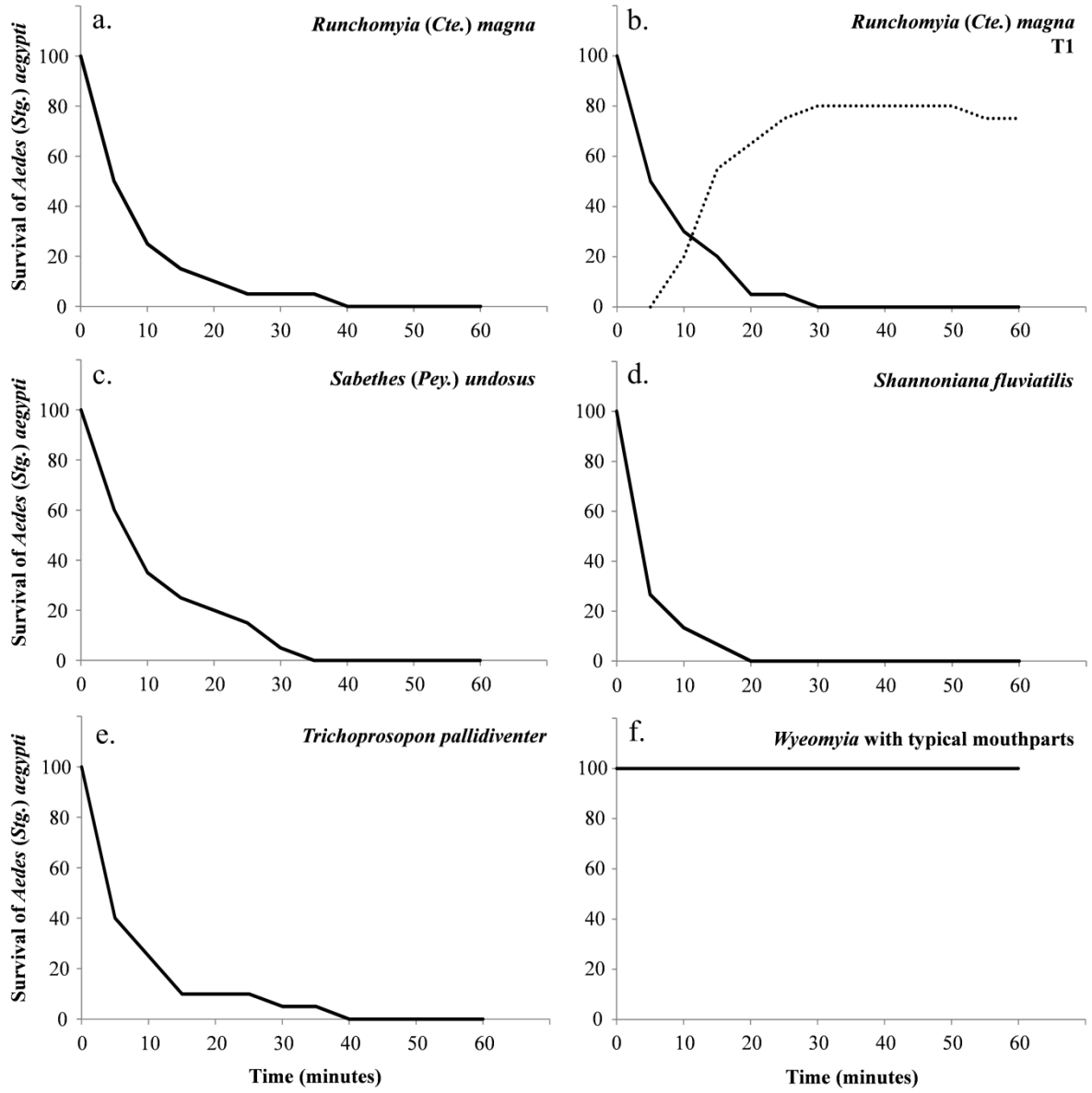

Figure 4.4 Percentage of survival of third instar *Aedes* (*Stegomyia*) *aegypti* larvae (solid lines) as a function of time and the presence of the fourth instar larvae of different mosquito species. a. *Runchomyia* (*Cte.*) *magna* (N = 20). b. A second *Ae.* (*Stg.*) *aegypti* larvae was provided (dotted line represents the percentage of these larvae released before being entirely eaten) (N = 20). c. *Sabethes* (*Pey.*) *undosus* (N = 20). d. *Shannoniana fluviatilis* (N = 15). e. *Trichoprosopon pallidiventer* (N = 20). f. Mosquitoes with typical mouthparts (N = 20 for each of the four species tested).

Short-term interaction experiments showed that sabethine species with modified mouthparts were effective intraguild predators of similarly-sized intraguild species (**Fig. 4.4a, b, c, d, e**). In all cases, *Ae.* (*Stg.*) *aegypti* larvae were rapidly attacked, killed and eaten (in 10.75 ±2.04 mn for *Ru.* (*Cte.*) *magna*; 13 ±2.26 mn for *Sa.* (*Pey.*) *undosus*; 7.33 ±1.22 mn for *Sh. fluviatilis*; and 10.25 ±2.15 mn for *Tr. pallidiventer*) leaving behind only chitinized structures. During the supplementary trial conducted on the pool of *Ru.* (*Cte.*) *magna* larvae,

all of the *Ae.* (*Stg.*) *aegypti* larvae were rapidly attacked and killed (10.5 ±1.66 mn; **Fig. 4.4b**), yet 80 % of them (16/20) were released before being entirely eaten. On the contrary, mosquito larvae having typical mouthparts (i.e. *Wy.* (*Dec.*) *pseudopecten*, *Wy.* (*Dod.*) *aphobema*, *Wy.* (*Wyo.*) *pertinans* and *Wy. occulta*) did not prey upon the *Ae.* (*Stg.*) *aegypti* larvae with which they were confronted (**Fig. 4.4f**). It is worth noting that no mortality occurred among the sabethine larvae during these trials.

DISCUSSION

In the Neotropics, the number of mosquito species breeding in phytotelmata rivals with the number of mosquito species breeding in ground bodies of water. In French Guiana, almost half of the 235 mosquito species known has been reported breeding in phytotelmata (**Talaga *et al.* 2015b**). Taxonomic studies conducted on mosquitoes have long noted that many mosquito species preferentially develop in certain types of phytotelmata (**Dyar 1928**), but the level of association remains poorly studied (but see **Navarro *et al.* 2007**). The degrees of specialization of the mosquito-phytotelm associations that we found in French Guiana are high and comparable to those found in pollination and mutualistic ant-myrmecophyte networks (see **Blüthgen *et al.* 2006**). In other words, each mosquito species interacts with a limited number of phytotelm plant species, resulting in a low number of links per species in the network. Moreover, the diversity of interactions at the network level (i.e. Fisher's alpha diversity) was higher when the phytotelmata were grouped by genus, suggesting that the association between mosquitoes and their host plants is stronger at this taxonomic rank than at the species or family levels. All of these results indicate that phytotelm-breeding mosquito species are mainly associated with their host plants and suggest a long coevolutive process.

Harbach and Peyton (**1993**) postulated that structural modifications of the maxilla in the Sabethini should be considered functional adaptations for collecting food by sweeping, scraping or clasping. In addition, we show that sabethine species with modified mouthparts (i.e. maxillary bundles, claws, prominent teeth or hypertrophied mandibles) are able to attack, kill and eat similarly-sized intraguild species and are, thus, effective intraguild predators. This situation is different from the highly age-structured IGP already reported for *Aedes* and *Anopheles* species (**Edgerly *et al.* 1999; Muturi *et al.* 2010**) and can be supposed to have a greater influence on the structure of communities. Furthermore, we show that satiated *Ru.* (*Cte.*) *magna* larvae killed potential competitors but then do not necessarily eat them. This 'aggressive behavior', already reported for *Ru.* (*Cte.*) *magna* and also known in species of the

subgenus *Dendromyia* of *Wyeomyia* (**Zavortink 1979; Motta & Lourenço-de-Oliveira 2000**), indicates that IGP in this case likely results from the evolution of interference competition (**Polis *et al.* 1989**).

The high proportion of species with modified mouthparts developing in small phytotelmata suggests that IGP provides a selective advantage in such habitats. Indeed, below a certain threshold of phytotelm size, all associated mosquito species displayed modified mouthparts making clear that effective IGP is the only alternative under severe competitive conditions. We also found that, in addition to being associated with smaller phytotelmata, mosquito species with modified mouthparts were larger than those with typical mouthparts. Being larger in a small habitat seems counterproductive, but because larger species have more chance to prey upon than to be preyed upon, this might be an adaptive response to an environment structured by IGP.

In the relationship between habitat size and the occurrence of species with modified mouthparts, there are some exceptions. Two explanations can be put forward to explain this phenomenon. First, modified mouthparts may have evolved in response to other selective forces than those imposed by competition alone. It can easily be imagined that modified mouthparts evolved first to exploit other food resources such as biofilms or large fragments of detritus. Second, varying food inputs between phytotelmata are also likely to influence competition; for example, the 'trash basket' morphology of tank bromeliads allows them to intercept a greater amount of detritus than phytotelmata with cryptic openings such as the leaf axils of *Phenakospermum guyannense* or the perforated internodes of *Guadua latifolia* where we found species with modified mouthparts, despite a relatively large volume of water (**Fig. 4.3**).

Therefore, certain mosquitoes breeding in phytotelm plants have evolved feeding strategies including predation (i.e. IGP and cannibalism) conferring to them an advantage when the habitat is small (**Church & Sherratt 1996**). Interestingly, this situation is reminiscent of the evolutionary history of poison frogs (Anura: Dendrobatidae) which have evolved novel reproductive and feeding strategies in response to small aquatic habitats (**Brown *et al.* 2008**). In particular, tadpoles have shifted from strict herbivory in large aquatic habitats to facultative or obligatory predation/cannibalism in small phytotelmata (**Summers & McKeon 2004**). Our results show that IGP is a selective advantage under severe competitive conditions and results from the coadaptation of mosquito species to their specific phytotelm habitat. The selection of functionally analogous structures in different mosquito

genera also implies that IGP evolved independently in different lineages, strongly suggesting that IGP emerged from convergent evolution in small phytotelmata.

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Partie II

Chapitre 5: Urbanization decreases taxonomic and functional diversity in Neotropical bromeliad invertebrates (Talaga *et al.*, soumis à *Urban Ecosystems*)

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Abstract: Due to habitat fragmentation, resource disruption and pollution, urbanization is one of the most destructive forms of anthropization affecting ecosystems worldwide. Generally, human-mediated perturbations dramatically alter species diversity in urban areas compared to the surroundings, thus influencing the functioning of the entire ecosystem. We investigated the taxonomic and functional diversity patterns of aquatic macroinvertebrate communities in tank bromeliads by comparing those found in a small Neotropical city with those from an adjacent rural site. Changes in the quality of detrital inputs in relation to lower tree diversity and the presence of synanthropic species are likely important drivers of the observed structural changes in the urban area, though alpha diversity was primarily affected. Leaf litter processors (i.e. shredders, scrapers) were positively affected in the urban area, while filter-feeders that process smaller particles produced by the activity of the shredders were negatively affected. Because we cannot ascertain whether the decline in filter-feeder diversity is related to food web-mediated effects or to competitive exclusion (*Aedes* (*Stegomyia*) *aegypti* mosquitoes were present in urban bromeliads only), further studies are necessary to account for the effects of weekly insecticide spraying (a practice intended to control disease

vectors) on both target and non-target insects and the subsequent effects in terms of intraguild competition or interguild facilitation.

Keywords: Aedes aegypti, Bioindicator, Diversity, Functional traits, Tank bromeliads.

INTRODUCTION

Urbanization is one of the most destructive forms of anthropogenic disturbance experienced by ecosystems worldwide (**McKinney 2002**). Generally, species diversity is altered dramatically in urban areas compared to the surroundings; habitat fragmentation, resource disruption and pollution (i.e. runoff; atmospheric, acoustic and streetlight pollution) are probably the three main causes (**McKinney 2002, 2008**). Urbanization is also frequently characterized by a greater density of artificial, man-made habitats (e.g. ponds, domestic gardens) that foster colonization by either native or synanthropic species (**Santoul *et al.* 2009; Talaga *et al.* 2015a**). Even if the presence and abundance of most species is influenced by urbanization, community-level responses cannot only be interpreted as a simplification equivalent to a decrease in alpha diversity, and counterintuitive patterns of urban diversity have been noted (**McIntyre 2000**). Indeed, the negative or positive effects of urbanization upon community diversity differ markedly between taxonomic groups, and explanations for the contrasting patterns lie in the nature of the processes acting on the focal taxa studied (**Henle *et al.* 2004**). For example, habitat fragmentation, which is inherent to urban areas, has different impacts on vertebrates, which are adversely affected due to gene flow disruption between populations (**Delanay *et al.* 2010**), than on invertebrates which are less affected given the low habitat size needed to sustain a population (**Jones & Leather 2013**). Moreover, a greater pattern of beta diversity can be detected within urban areas where habitat fragmentation increases habitat heterogeneity, promotes edge species, and/or creates specific niches for invertebrates (**Jones & Leather 2013**).

Most studies on urban ecosystems have been conducted in temperate regions in Europe and North America which raises the question of the representativeness of general patterns (**Savard *et al.* 2000**). In the Tropics, with the exception of megacities of millions of inhabitants that are not different from their temperate counterparts, most urban areas are represented by medium to small urban settlements displaying comparatively low levels of urbanization, and are often located adjacent to natural habitats (**Grau *et al.* 2008**). A reduction

in the range of the natural-to-urban gradient is likely to favor exchanges between the two environments and thus limit the influence of urbanization on communities.

In the Neotropics, tank bromeliads form a highly discontinuous aquatic meta-habitat embedded within a terrestrial matrix. These phytotelmata ('plant-held waters') provide a habitat to aquatic organisms ranging from bacteria to small vertebrates (**Kitching 2000**; **Carrias *et al.* 2001**). Interestingly, this spatially discrete microecosystem can be sampled exhaustively, providing unbiased records of community-level diversity, and forming a relevant model system to bring out environmental effects on community assembly (**Srivastava *et al.* 2004**). The aquatic macroinvertebrate communities in tank bromeliads have been investigated in natural environments throughout their range. The key environmental determinants structuring these communities are related to the characteristics of the aquatic compartment like habitat size and complexity, food resources, the presence of a top predator, and to the characteristics of the terrestrial matrix most of the time evaluated as open *versus* closed environments (**Brouard *et al.* 2012; Dézerald *et al.* 2013, 2014**). Tank bromeliads are common in Neotropical cities so that human-mediated pressures can influence both directly and indirectly the structure of their aquatic communities (**Talaga *et al.* 2015a**). The fragmentation of the terrestrial matrix consecutive to urbanization definitely increases the patchiness of the aquatic meta-habitat formed by tank bromeliads. This phenomenon can have a negative influence on dispersal and therefore on the colonization of tank bromeliads. Responses are thought to be different between species and we might expect that the disruption of tree cover will negatively influence species dependent on shade for dispersal and promote edge species adapted to living in more open environments. The aquatic compartment might also be directly affected by a reduction in tree canopy cover that leads to a reduction in incoming detritus (e.g. leaf litter) and to an increase in incident radiation.

We here investigate the influence of urbanization on biological diversity by comparing the taxonomic and functional structure of aquatic bromeliad invertebrate communities in urban and rural sites in French Guiana. The city of Sinnamary displays a moderate level of urbanization representative of the most common form of urbanization in the Neotropics. Besides typical human-mediated perturbations, the urban site is regularly sprayed with an insecticide in an attempt to control the proliferation of adult *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) (Diptera: Culicidae), a well-known vector of yellow-fever, dengue and chikungunya (**Christophers 1960**). We hypothesized that urbanization can affect the structure of the aquatic communities in three different ways. First, the alpha and beta diversity of the meta-community will be lower and higher, respectively, in the urban area compared to the

surrounding rural area as a result of habitat fragmentation and insecticide spraying within the city limits. Second, the concomitant effects of human settlements like the occurrence of synanthropic and/or exotic species should be expected. We assume, therefore, that some of these species will appear in the urban aquatic metacommunity and not in the rural area. Third, trophic cascades are likely to alter food webs: lower litter inputs in the urban area might notably have a bottom-up influence on the food web, negatively affecting detritivorous organisms (e.g. scrapers, shredders).

MATERIALS AND METHODS

Study area

This study was conducted in French Guiana in the coastal region of Sinnamary (05°22'39"N 52°57'35"W). The area has an equatorial monsoon climate corresponding to an average of 2,800 mm of yearly rainfall, distributed over 251 days (**Peel *et al.* 2007**). There is a major drop in rainfall from mid-July to mid-November (dry season) and a shorter and more irregular dry period in March. Minimum and maximum monthly mean temperatures, relatively stable, vary between 23.6°C and 31.6°C.

In this region, the tank bromeliad *Aechmea aquilega* (Salisb.) Griseb. occurs along a gradient of anthropogenic disturbance from rural to urban areas. Sampling sites, separated by *ca.* 2 km, extended over comparable surface areas of *ca.* 10 ha (rural: 9.74 ha, urban: 10.09 ha). The first sampling site was situated along a dead-end road (*Route de l'Anse*) in a habitat characterized by very few dwellings among large fragments of an old secondary forest. The second site was located in the city of Sinnamary, a residential urban area home to most of the 3,165 inhabitants recorded within the municipality (**INSEE 2015**), where *A. aquilega* abound on medium to large trees in yards, mostly mango trees (**Talaga *et al.* 2015a**). Each street in the city of Sinnamary is sprayed twice weekly with a solution of 1 gram of deltamethrin (Aqua K-Othrine®, Bayer, Leverkusen, Germany) per hectare (*Centre de démoustication de Sinnamary*, personal communication).

Impervious surface areas were calculated within the convex hulls formed by sampled *A. aquilega* at each site using QGIS software (**QGIS Development Team 2015**). The percentages of impervious surface areas were 14.23 % and 47.59 % in the rural and urban sites, respectively, and falling into the low (<20 % impervious surface area) and moderate (20-50 % impervious surface area) category proposed by **McKinney** (**2002**).

Sampling methods

Field sampling was carried out at the start of the dry season in July 2011 on 13 mature *A. aquilega* sampled at each of the two sites (26 in total). Before being collected, each *A. aquilega* was geolocated with a GPS, its elevation above ground (EG) was measured (in meters), and the percentage of incident radiation (IR) was quantified using the hemispherical photography technique (see **Leroy *et al.* 2009**). Each plant was then removed from its supporting tree or building and placed into an individual sealed plastic bag to prevent spillage and contamination. In the laboratory, the number of leaves forming wells (NW) was recorded, plant height (PH) was measured as the distance from the insertion of the outer leaves to the top of the crown, and plant width (PW) as the maximum distance between the tips of the leaves (both in centimeters). Subsequently, aquatic and semi-aquatic invertebrates were extracted using the following method. First, the bromeliads were turned upside down in a bucket, and the water filtered through a 150 µm mesh. The water filtered from the wells was measured as the total volume of water (in milliliters) held by the plant (WV). The invertebrates retained by the 150 µm net were sorted and kept for identification (see below). The organic matter contained by the plant was separated into two classes: fine particulate organic matter (FPOM; 1000-0.45 µm in size) and coarse particulate organic matter (CPOM; small pieces of fragmented material). Both were expressed in dry mass (in grams) after being placed in an oven until a constant weight was reached.

Diversity assessments

The plants were totally dismantled and each leaf was separated from the base and cleaned with a jet of water directed into a bucket. This technique allowed us to exhaustively collect the remaining aquatic macroinvertebrates, especially benthic organisms living deep in the wells (see **Jocqué *et al.* 2010**). All aquatic and semi-aquatic macroinvertebrate organisms were separated from the organic material under a stereomicroscope at 10X constant magnification. The individuals collected were separated into species or morphospecies, enumerated and preserved in 70 % alcohol. Mosquitoes were identified to species level using the **Lane** (**1953**) keys and individuals belonging to other families were identified using the **Merritt and Cummins** larval keys (**2008**). For convenience, both morphospecies and species are regrouped under the term ‘taxa’ in the rest of the text.

Because functional diversity, or the diversity of species traits in ecosystems, considers the complementarity and redundancy of co-occurring species, it is accepted as a good predictor of ecosystem productivity and vulnerability. Among the metrics of functional

diversity available, we used three indices based mostly on quantitative traits: functional richness (FRic) or the amount of niche space occupied by species in the community; functional evenness (FEve) or the evenness of the abundance distribution in the occupied niche space; and functional divergence (FDiv) the degree to which the abundance distribution in the niche space maximizes the divergence in functional characters within the community (**Villéger *et al.* 2008**). We also used functional dispersion (FDis), an index that takes into account the species' relative abundances, that is independent of species richness and represents the average distance of species to the abundance-weighted centroid of all species in the community in the trait space (**Laliberté &Legendre 2010**). All diversity indices were calculated from species scores in a trait space defined by a Fuzzy Correspondence Analysis of the abundance-weighted species traits (see **Dézerald *et al.* 2015**). The biological traits examined were: maximum body size (BS), aquatic developmental stage (AS), reproduction mode (RE), dispersal mode (DM), resistance forms (RF), food (FD), respiration mode (RM), locomotion (LO), and feeding group (FG). The latter comprises predators (Pr) and detritivores composed of: shredders (Sh) that feed on intact leaves which fall into the phytotelmata and produce fine organic matter; scrapers (Sc) that feed on layers of algae, bacteria and organic matter attached to the substrate; filtering-collectors (FC) that feed by filtering small particles of organic matter and microorganisms from the water column; and gathering-collectors (GC) that feed on the organic matter that accumulates at the bottom of the phytotelmata (see details on the biological traits of each taxon in **Merritt & Cummins 2008; Céréghino *et al.* 2011; Dézerald *et al.* 2013**). The categories for each trait were either ordinal or nominal. The information on the biological traits was then structured using a fuzzy-coding technique (**Chevenet *et al.* 1994**): scores ranged from 0, indicating 'no affinity', to 3, indicating 'high affinity' for a given species traits category (**Appendix 3**). This species-traits matrix was analyzed with a Fuzzy Correspondence Analysis (FCA) in order to obtain multivariate scores for the full set of species.

Statistical analyses

The variables characterizing bromeliads (i.e. EG, IR, NW, PH, PW, WV, FPOM, CPOM) were first compared between the two sites in order to confirm that there was no significant difference between the two sites. Because the assumptions of normality were not met, the non-parametric pairwise Wilcoxon Rank Sum test was performed. Significant variation was only observed for the number of wells (NW), which were higher in the urban site ($W = 36$, $P = 0.013$). Consequently, we controlled for the NW in subsequent analyses.

In order to test for differences in the structure of the communities between the two sites, a Permutational Multivariate Analysis of Variance (PERMANOVA) was run on raw abundance data using the Bray-Curtis (abundance-based) and the Jaccard (incidence-based) indexes. The diversity (D) was calculated and partitioned within each site into alpha, beta and gamma diversity based on **Marcon *et al.*** (**2014**). The alpha diversity is defined as the average local community diversity, gamma diversity corresponds to the diversity of the metacommunity composed of all the communities within each site, and beta diversity is understood as the diversity between local communities (or the divergence between each community and the metacommunity). Finally, evenness was calculated as the ratio of diversity (D) on richness (S) (**Tuomisto 2012**).

Statistical analyses were conducted in R (R software; **R Development Core Team 2013**) using 'entropart', 'FD' and 'vegan' packages.

RESULTS

A total of 11,099 aquatic macroinvertebrate individuals belonging to 36 taxa were extracted from the 26 *A. aquilega* bromeliads sampled (**Table 5.1**). Nine taxa out of the 36 were exclusively found in the urban area (**Table 5.1**). Among them, we identified 63 individuals of the mosquito *Ae.* (*Stg.*) *aegypti* distributed in seven out of the 13 *A. aquilega* sampled.

Table 5.1 List of the aquatic macroinvertebrate species or morphospecies occurring in *Aechmea aquilega* in Sinnamary, French Guiana (13 plants in each of the rural and urban areas). Taxa are listed alphabetically according to a classical system and highlighted in bold. The rank number of a taxon's relative abundance is indicated for the rural and the rural metacommunities.

Class	**Order**	**Family**	**Subfamily**	**Morphospecies/species**	**Rank No. of taxa**		**Taxa ID***
					Rural	**Urban**	
Insecta	Coleoptera	Elateridae		**Elateridae sp.**	21	27	1
		Elmidae		**Elmidae sp.**	24	22	2
		Hydrophilidae		**Hydrophilidae sp.1**	-	23	3
				Hydrophilidae sp.2	-	24	4
	Diptera			**Brachycera sp.1**	-	20	5
				Brachycera sp.4	14	9	6
				Brachycera sp.5	20	15	7
				Brachycera sp.6	16	25	8
				Brachycera sp.7	23	-	9
				Brachycera sp.8	-	28	10

			Brachycera sp.9	12	-	11
			Brachycera sp.10	25	14	12
			Brachycera sp.12	-	29	13
			Brachycera sp.15	26	17	14
	Ceratopogonidae	Ceratopogoninae	***Bezzia* sp.1**	7	3	15
			***Bezzia* sp.2**	9	5	16
			Ceratopogoninae sp.2	18	7	17
			Ceratopogoninae sp.3	22	30	18
			***Dasyhelea* sp.**	-	16	19
		Forcipomyiinae	**Forcipomyiinae sp.2**	6	2	20
			Forcipomyiinae sp.5	-	18	21
	Chironomidae	Chironominae	**Chironominae sp.**	2	-	22
		Tanypodinae	**Tanypodinae sp.**	27	-	23
	Culicidae	Culicinae	***Ae.* (*Stg.*) *aegypti***	-	12	24
			Cx.* (*Mcx.*) *pleuristriatus	8	10	25
			Cx.* (*Mcx.*) *imitator	11	-	26
			Wy.* (*Wyo.*) *pertinans	5	11	27
			Tx.* (*Lyn.*) *haemorrhoidalis	10	13	28
	Tipulidae	Limoniinae	***Trentepholia* sp.**	3	-	29
	Psychodidae	Psychodinae	**Psychodinae sp.**	-	21	30
			***Telmatoscopus* sp.**	4	1	31
	Tabanidae		**Tabanidae sp.**	19	19	32
Oligochaeta			**Oligochaeta sp.1**	17	26	33
			Oligochaeta sp.2	13	8	34
Haplotaxida			***Aulophorus superterrenus***	1	6	35
			***Pristina* sp.**	15	4	36

*Taxa ID as in **Appendix 3**.

A significant difference in the structure of the aquatic macroinvertebrate communities was detected between the two sites, using both the Bray-Curtis (PERMANOVA; N = 26; F = 8.23; P < 0.001) and the Jaccard (PERMANOVA; N = 26; F = 5.49; P < 0.001) indices with the number of wells (NW) as random factor.

Most of the taxa belonged to the order Diptera, but some Coleoptera were also found. Species richness was slightly lower in the rural metacommunity (27 taxa) than in the urban metacommunity (30 taxa), with one and three singletons, respectively, and a species turnover of 41.67 % (15/36) between the two sites. The total disappearance from the urban area of Chironominae sp. and *Trentepholia* sp., which were ranked, respectively, second and third in terms of relative frequency in the rural area, should be noted (**Table 5.1**).

The comparison of partitioned alpha, beta and gamma diversity between the rural and the urban area is presented in **Figure 5.1**. The communities were weighted according to their number of wells (NW) in order to control for significant variation in the NW between the two sites. In theory, a community is considered more diverse when its profile is above the others

compared. Diversity profiles reveal that for each order of diversity, local alpha diversities were on average higher in the rural site than in the urban one, but not significantly. The analyses of beta and gamma diversity profiles were less straightforward. While the beta diversity in the rural metacommunity was higher for orders of diversity between 0.5 and 1, mean values were higher in the urban metacommunity for orders of diversity of 0 and 2. We also noted that for each order of diversity, the urban beta diversity showed a higher range of variation: rural beta diversity is always included within the range of variation of urban beta diversity. The gamma diversity of the rural metacommunity was higher than that observed for the urban one, except for an order of diversity of 0 where the urban metacommunity showed a greater gamma diversity (**Table 5.2**). A comparison of evenness (E) was more in keeping with the higher or equal values in the rural site compared to the urban one for all alpha, beta and gamma diversities and for each order of diversity (**Table 5.2**).

Table 5.2 Values of diversity (D) and evenness (E) for each order of diversity q partitioned into alpha, beta and gamma levels for the rural and urban metacommunities. Values of gamma diversity of the order q=0, equivalent to the richness (S), are highlighted in bold for each metacommunity. Evenness is calculated as D:S ratio.

	q=0			**q=1**			**q=2**		
Index	Rural	Urban	Sign R:U	Rural	Urban	Sign R:U	Rural	Urban	Sign R:U
Dα	14.65	14.22	>	6.73	5.80	>	5.11	3.69	>
Dβ	1.84	2.11	<	1.55	1.51	>	1.51	1.63	<
Dγ	**27**	**30**	<	10.40	8.77	>	7.71	6.01	>
Eα	0.542	0.474	>	0.249	0.193	>	0.189	0.123	>
Eβ	0.068	0.070	≈	0.057	0.050	>	0.056	0.054	>
Eγ	1	1	=	0.385	0.292	>	0.285	0.200	>

In terms of functional feeding groups, filtering-collectors and gathering-collectors were significantly more abundant in the rural communities than in the urban ones (Wilcoxon Rank Sum test: W = 125; P = 0.04 and W = 124; P = 0.045, respectively), the contrary being true for shredders and scrapers (Wilcoxon Rank Sum test: W = 22; P = 0.0008 and W = 40; P = 0.024, respectively; **Fig. 5.2**). Predators tended to be more abundant in the rural area, but the difference was not significant (Wilcoxon Rank Sum test: W = 113.5, P = 0.1404; **Fig. 5.2**).

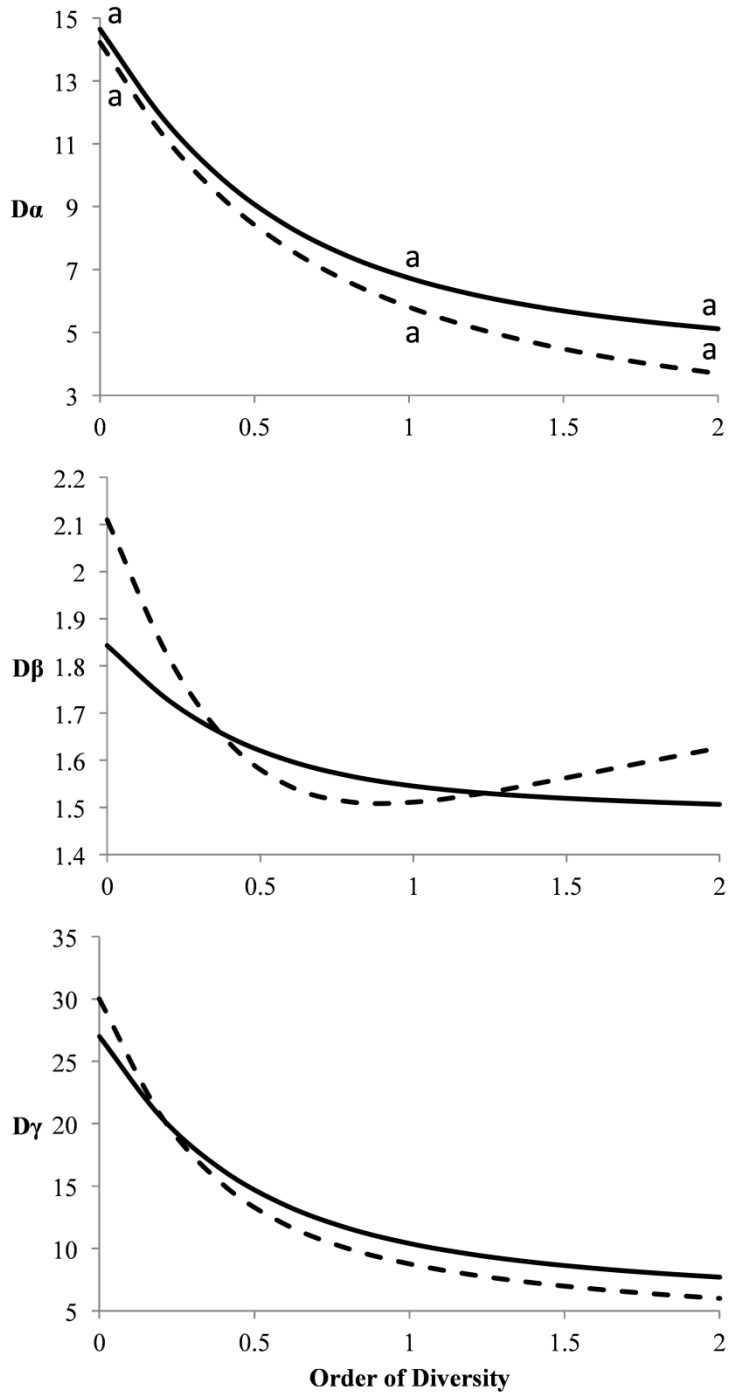

Figure 5.1 Profiles of alpha, beta and gamma diversity (D) of the order q computed for the aquatic macroinvertebrate metacommunities in the rural (solid lines) and urban areas (dashed lines). Small letters indicate a significant difference ($P < 0.01$) between sites for orders of diversity $q = 0$, 1 and 2.

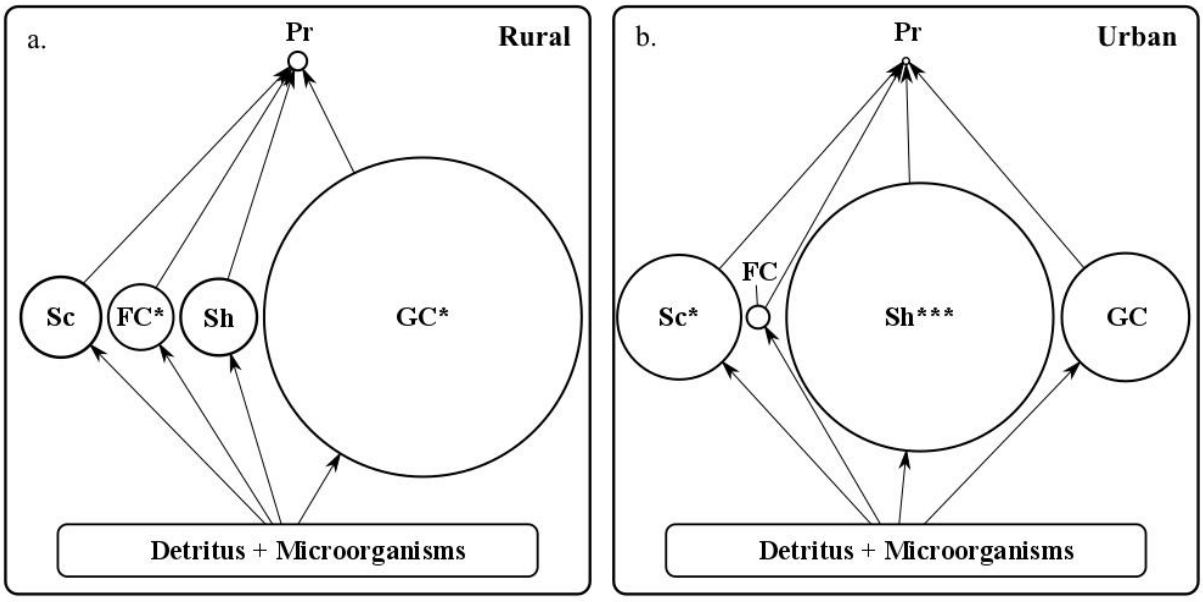

Figure 5.2 Composite food web diagrams showing trophic interactions involving aquatic macroinvertebrate Functional Feeding Groups (FFGs) in rural and urban metacommunities. FFGs are abbreviated as follows: Scraper (Sc), Shredder (Sh), Gathering-collector (GC), Filtering-collector (FC) and Predator (Pr). Circle diameter represents the relative abundance of each FFG standardized by doubling the relative abundance of the least abundant FFG. Predator and detritivore trophic levels are weighted by two and one, respectively, with respect to former functional analyses. Arrows illustrate interactions pointing to the consumer. Asterisks indicate the FFGs with a significantly higher mean abundance after a pairwise, non-parametric comparison between the two sites (* = $P < 0.05$; *** = $P < 0.001$).

Concerning functional diversity, the following indices were not significantly different between the two sites (Welch Two Sample t-tests): FRic ($t = 0.51$; $df = 20.84$; $P = 0.619$), FEve ($t = -1.20$; $df = 20.89$; $P = 0.242$) and FDiv ($t = 1.99$; $df = 20.54$; $P = 0.060$). However, the FDis was significantly lower in urban bromeliads, suggesting that anthropogenic disturbance leads to a convergence in the functional traits of invertebrates in mid-sized, Neotropical cities like Sinnamary (lower dispersion in trait space) ($t = -13.64$; $df = 12.38$; $P < 0.001$).

DISCUSSION

Although the bromeliad habitat (i.e. size, complexity) represented by *A. aquilega* did not differ between an urban and a nearby rural site, the associated macroinvertebrate communities showed significantly lower taxonomic and functional diversity in the urban area. In other words, if taxonomic and functional variations cannot be attributed to differences in

the bromeliad habitat *per se*, we assume that factors associated with the urban environment itself are the primary drivers of community assembly through invertebrate trait filtering.

That tank bromeliads held comparable amounts of detritus (CPOM and FPOM) in the urban and the rural areas was contrary to our initial expectations. However, dry weight measurements only provide an indication of the quantity of the food resource, while the quality of this resource is likely important to macroinvertebrates (**Yanoviak 1999; Yee & Juliano 2006**). Because native tree species occurred in the rural site whereas mango trees strongly dominated in the city (see **Chapter 6**), it is likely that the quality and diversity of the litter (something that is directly related to urbanization in the study area) accounts for the observed impacts on detritivores (see below).

A higher alpha diversity in the rural area compared to the urban one is in accordance with our predictions related to human-mediated disturbances. Moreover, the taxonomic turnover of 41.67 % between the two sites reflects changes within the composition of the metacommunities (the remaining 58.33 % corresponds to an overlap of taxa between the two habitats, showing that many species can live in both areas). Among the detritivores, shredders (Sh) and scrapers (Sc) are positively impacted by the urban environment, while the filtering-collectors (FC) and gathering-collectors (GC) are negatively influenced. However, nothing indicates that predators (Pr), here represented by the mosquito species *Toxorhynchites* (*Lynchiella*) *haemorrhoidalis* (Fabricius 1787), are impacted by urbanization (**Fig. 5.2**). The major restructuration observed for detritivores, associated with the absence of significant variations among predators, strongly suggests an alteration in urban communities through bottom-up processes.

Even if the alpha diversity is affected, the beta diversity was lower in the urban area for an order of diversity of 1, the contrary being true for orders of diversity of 0 and 2. Higher beta diversity reflects larger variations among local communities, a result which is consistent with the hypothesis that habitat fragmentation increases environmental heterogeneity in the urban site. Because diversity measures give more weight to abundant relative to rare species with an increasing order of diversity, the higher beta diversity in the urban area is due to rare species (for which q=0) and the heterogeneous distribution of abundant species (for which q=2). Despite the change in the relative abundance among functional feeding groups, all of them are nevertheless present in the two sites, showing that aquatic macroinvertebrates are relatively tolerant of urbanization.

In terms of functional diversity, the three indices tested first did not reveal significant differences between the two metacommunities. Functional richness (FRic) should increase

when niche complementarity enhances probabilities of species occurrence; functional evenness (FEve), generally used to indicate the under- or overutilization of resources, should increase when the distribution is regular (low values indicate the existence of separate groups of species and/or abundances); functional divergence (FDiv), which measures the degree to which the abundance of a community is distributed toward the extremities of the occupied trait space, should increase when niche complementarity enhances species' relative abundances (**Schleuter 2010; Mason *et al.* 2013**). Yet, that the functional dispersion (FDis) is significantly lower in the city compared to the rural site is in line with previous studies showing a reduction in FDis with higher disturbance intensity (**Mouillot *et al.* 2013**). This is interpreted to indicate that highly disturbed areas only support species able to cope with their conditions (strong environmental filtering), generating clustering and the irregular distribution of abundances of co-occurring species, decreasing FDis values (**Gerisch *et al.* 2012; Mouillot *et al.* 2013**).

The responses of functional feeding groups are also related to the behavior and survival of adult insects directly exposed to human-mediated perturbations in the terrestrial matrix. For instance, in order to control *Ae.* (*Stg.*) *aegypti* adults, each street in the city of Sinnamary is sprayed twice per week with an insecticide. The impact on untargeted organisms is unknown; however, Chironomidae have proven to be sensitive to this insecticide (**Morrill & Neal 1990**). The total disappearance of Chironominae sp. and *Trentepohlia* sp. in the urban metacommunity, although abundant in the rural habitat, might be attributed to the use of this chemical.

The presence of *Ae.* (*Stg.*) *aegypti* larvae in seven of the 13 tank bromeliads sampled in the urban area and its absence from the rural one was not surprising because they are known to be rare in natural containers and very abundant in artificial containers (**Christophers 1960**), something which has been explained as the result of the remnant primitive behavior of the species (**Chadee *et al.* 1998**). This is the first report of the use of tank bromeliads as a breeding site by *Ae.* (*Stg.*) *aegypti* in French Guiana, with a percentage of occurrence which is particularly high compared to Argentina (**Stein *et al.* 2013**), Brazil (**Varejão *et al.* 2005**) and Trinidad (**Chadee *et al.* 1998**), and other natural breeding sites such as rock pools, tree holes, and the leaf axils and flowers of various plants (**Belkin & Heinemann 1973, 1975, 1976**). The restriction of *Ae.* (*Stg.*) *aegypti* to the urban site coincides with a significantly lower abundance of filtering-collectors represented by the mosquito species *Culex* (*Microculex*) *pleuristriatus* Theobald 1903 and *Wyeomyia* (*Wyeomyia*) *pertinans* (Williston 1896). This released niche occupancy by filtering-collectors can itself explain the establishment of a non-

native ecological equivalent, something shown in tank bromeliads in Florida at the range limits of *Aedes (Stegomyia) albopictus* (Skuse 1894) due to the presence of native competitor mosquitoes of the genus *Wyeomyia* (**Lounibos *et al.* 2003**). However, even if reports from rural environments exist (**Stein *et al.* 2013**), the high degree of synanthropy displayed by *Ae.* (*Stg.*) *aegypti* might explain the absence of this species in the rural metacommunity.

Bromeliads represent small and discrete habitats that are abundant in urban and natural areas, and their physical characteristics (small-scale habitat filtering) are not directly affected by the urban environment. They are therefore the deemed suitable model systems to bring out the environmental effects of human-impacted landscapes on the taxonomic and functional structure of biological communities in the Neotropics. In this context, our study highlights the adverse effects of small-scale urbanization on Neotropical invertebrate communities. Changes in the quality of detrital inputs in relation to tree diversity and the presence of synanthropic species are likely important drivers of the observed structural changes, though alpha diversity, rather than beta and gamma diversity was primarily affected. It is worth noting, however, that leaf litter processors (i.e. shredders and scrapers) were positively affected in the urban area, while filter-feeders that process much smaller particles (produced by the activity of the shredders) were negatively affected. Because we cannot ascertain whether the decline in filter-feeder diversity and abundance is related to food web-mediated effects (i.e. shredder x filter-feeder interaction) or competitive exclusion (i.e. presence of *Ae.* (*Stg.*) *aegypti*), further studies are necessary to account for the effects of frequent and massive insecticide spraying on both target and non-target insects, with emphasis on adult dispersal and oviposition and the subsequent effects in terms of intraguild competition or interguild facilitation.

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Chapitre 6: Environmental drivers of community diversity in a Neotropical urban landscape - a multi-scale analysis (Talaga *et al.*, soumis à *Landscape Ecology*)

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Abstract: Many aquatic communities are linked by the aerial dispersal of multiple, interacting species and are thus structured by processes occurring in both the aquatic and terrestrial compartments of the ecosystem. To evaluate the relative influence of urban heterogeneity and habitat characteristics on the structure of aquatic macroinvertebrate communities, including mosquitoes. We worked in a small Neotropical city and used a tank bromeliad species as model system. A land cover map distinguishing buildings, roads, vegetation, ground and water was created to quantify landscape heterogeneity using a high resolution orthophoto. Also, the tank bromeliads were georeferenced in order to assess the spatial distribution of the aquatic meta-habitat in the entire city. We sorted 18,352 aquatic macroinvertebrates into 29 taxa from 32 selected tank bromeliads. The volume of water and the amount of organic matter explained a significant part of the taxa variance whatever the spatial scale. The remaining variance was explained by the meta-habitat size, the distance to the nearest buildings at small scales, and the surface area of buildings plus ground cover at larger scales. At small scales, the meta-habitat size influenced the abundance of the two most frequent mosquito species in opposite ways, suggesting a mechanism of spatial competition coexistence. The presence of a

top predator in this system was favored by greater vegetation cover. Modifications conducted at the landscape scale could have negative consequences on both the terrestrial and aquatic compartments of the urban ecosystem, opening up perspectives for mosquito management during urban planning.

Keywords: Landscape ecology, Mosquitoes, Neotropics, Scale dependency, Tank bromeliads.

INTRODUCTION

Urbanization is one of the most destructive forms of anthropogenic impact experienced by ecosystems worldwide (**McKinney 2002**). Through the construction of roads and buildings, and the creation of gardens, squares and parks, humans have greatly fragmented the habitat with many consequences for the abiotic and biotic environments (**Grimm *et al.* 2008**). The destruction of native vegetation and the development of urban infrastructure often lead to the 'urban heat island effect' characterized by warmer and drier conditions (**Yuan & Bauer 2007**). Consequently, urbanization creates unfavorable conditions for many native species that are unable to adapt, leading to an overall decrease in biodiversity (**Newbold *et al.* 2015**). Yet, the environmental filter created by urbanization selects species adapted to the new conditions, so that they can become very abundant (**Kark *et al.* 2007; Lowe *et al.* 2015**). While species diversity tends to decline with extreme urbanization, several studies have shown that it peaks at a moderate level of urbanization as a result of habitat heterogeneity and the introduction of numerous alien species, particularly exotic plants (**McKinney 2008**). For instance, mango trees, which are native to northeast India, are grown for both their fruits and their shade in many tropical cities, to the point that Belém, a large city in Amazonian Brazil, is also known as the *Cidade das Mangueiras* (the City of Mango Trees).

To understand how biodiversity is maintained in urban landscapes, field surveys can primarily help in revealing patterns in diversity and structure along relevant spatial environmental gradients (**McDonnell *et al.* 1993**). However, because the fragmentation of habitats suitable for native species is inherent to urbanization, these habitats function as islands or as a stepping stone for the installation of invasive species (**Davis & Glick 1978**). Therefore, our understanding of urban biodiversity must include a landscape perspective incorporating metacommunity patterns as well as habitat-level to landscape-level characteristics (**Leibold *et al.* 2004**).

Phytotelmata ('plant-held waters') form discrete freshwater habitats that house aquatic communities interconnected through different dispersal modes arranged in a metacommunity (**Kitching 2000**). Passive dispersers (e.g. worms, crustaceans) colonize new aquatic habitats through phoresy, while active dispersers (e.g. insects with complex life cycles) select new, suitable breeding habitats at the adult stage (**Wilbur 1980**). Hence, because (i) landscape heterogeneity likely plays an important role in determining diversity patterns in both natural (**Simpson 1949;** reviewed in **Tews *et al.* 2004**) and urban (**Grimm *et al.* 2008; Newbold *et al.* 2015**) ecosystems, and (ii) phytotelmata are small, contained and easy to sample exhaustively (**Jocqué *et al.* 2010**), these systems are deemed suitable model systems that will allow us to challenge the currently accepted hierarchy of environmental factors that shape communities in urban landscapes.

Bromeliads (Bromeliaceae) are distributed throughout the Neotropics in environments ranging from pristine forests to cities, and some species have evolved tightly-interlocking leaves that impound water and detritus forming phytotelmata (**Benzing 2000**). Most of these tank bromeliad species are epiphytic and spatially distributed in patches, resulting in a highly heterogeneous aquatic meta-habitat embedded within a terrestrial matrix (**LeCraw *et al.* 2014**). This aquatic habitat is used as a breeding site for a great variety of insects with complex life cycles that make the largest contribution to local-regional species pools in tank bromeliads (reviewed in **Frank & Lounibos 2009**).

Mosquitoes (Diptera: Culicidae) are particularly well represented in tank bromeliads, and, given their medical importance worldwide, a solid body of information on their ecology exists. Oviposition by adult females is modulated by abiotic characteristics related to visual and olfactory cues, both concerning the container habitat (e.g. color, openness) and the water quality (e.g. pH, conductivity, salinity) (**Yanoviak 2001; Navarro *et al.* 2003**). The biotic characteristics of the aquatic habitat also influence oviposition behaviors, repelling or attracting females depending on the nature of the bacterial communities developing in the water (**Huang *et al.* 2006; Ponnusamy *et al.* 2010**). Furthermore, the presence of conspecifics, heterospecifics and/or predators might influence oviposition in many different ways (**Chadee *et al.* 1990; Kiflawi *et al.* 2003**). After oviposition, immature mosquitoes are confined to their aquatic habitat and their survival is strongly determined by trophic interactions such as competition, predation and/or parasitism (**Lounibos *et al.* 2003**). Depending on their flying abilities, adults can move within the terrestrial matrix passively (i.e. physical aggregation due to the wind) or actively (i.e. oriented, flying dispersal), resulting in the heterogeneous spatial distribution of the different populations (**Ellis 2008**). Consequently,

understanding the terrestrial predictors of the spatial distribution of adults can help to explain the differential rate of oviposition and the subsequent outcomes on larval populations. The aggregation of adults might be driven by the availability of aquatic habitats, resting and mating sites, and access to blood meals. First, areas with numerous aquatic habitats are believed to aggregate large numbers of adult mosquitoes because they are easy to locate due to their size and/or their density. This situation generally results in a large adult population and, consequently, a high overall rate of oviposition in these areas because they can sustain greater larval production (**Clements 1999**). Second, ovipositional behavior can be adapted to the availability of aquatic habitats in the immediate surroundings, something interpreted as an adaptation reducing larval competition (**Reiskind & Wilson 2004**). Third, the availability of adult resting sites is also an important predictor of their distribution due to its impact on their survival (**Ellis 2008**). Indeed, although many mosquito species use ground vegetation or tree trunk cavities, synanthropic mosquito species rest near or inside houses, combining resting and mating sites and easy access to blood meals (**Burkett-Cadena *et al.* 2008**). Fourth, some human-mediated perturbations, such as urban insecticide spraying to control populations of vector species, influence the spatial distribution of adult mosquitoes by creating an escape phenomenon or by increasing local mortality (**Kongmee *et al.* 2004; Dusfour *et al.* 2011**).

In this study, we seized the opportunity of the existence of large patches of the tank bromeliad *Aechmea aquilega* in the city of Sinnamary, French Guiana to test the influence of environmental factors at different spatial scales ranging from habitat to landscape. We specifically examined the response of the two most abundant mosquito species as well as the presence of the mosquito species known to be a top predator in this system.

MATERIALS AND METHODS

Study area

This study was conducted in French Guiana between March 2012 and March 2013 within the city limits of Sinnamary (05°22'39"N, 52°57'35"W). The region is characterized by an equatorial monsoon climate corresponding to an average of 2,800 mm of yearly rainfall, distributed over 251 days (**Peel *et al.* 2007**). There is a major drop in rainfall from mid-July to mid-November (the dry season) and a shorter and more irregular dry period in March. Minimum and maximum monthly mean temperatures, relatively stable, vary between 23.6°C and 31.6°C.

Terrestrial habitat characteristics

The first step of this study was to accurately characterize the terrestrial habitat over the entirety of the city of Sinnamary (≈1,500,000 m^2). Variables likely to influence adult mosquitoes whose immatures develop in tank bromeliads were mapped based on a high resolution (pixel size 0.3 m at ground level) color orthophoto of Sinnamary taken in April 2012. A land cover map was created by taking into account the areas covered by buildings, roads, vegetation (i.e. trees and shrubs), ground (i.e. bare soil and grass), and water. Layers corresponding to buildings and roads were extracted from the BDORTHO® of the IGN (pixel size 0.5 m at ground level). Because remote sensing provided only mitigated results for precisely mapping the ground, vegetation and areas covered by water, these layers were created through photointerpretation based on the 2012 orthophoto. The ground cover layer was considered as the surface not covered by buildings, roads, vegetation or water (**Fig. 6.1**). In order to assess the spatial distribution of the aquatic meta-habitat, we conducted a survey of the entire population of *A. aquilega* growing within the city limits (**Fig. 6.1**). During three consecutive weeks in March 2012, each structure supporting tank bromeliads (tree or building) was tagged and geolocated with a GPS (GPSmap® 62st, USA). Host trees were identified to species level and their heights were measured with a laser meter (3D compass LaserAce® 1000 Rangefinder, USA).

The number of tank bromeliads supported by each structure was counted and plant height (i.e. distance from the insertion of the outer leaves to the top of the crown) was used as a surrogate of plant size because it is the most reliable measurement feasible from the ground. Each tank bromeliad was assigned to one of four size classes ($I \leq 20$ cm $< II \leq 50$ cm $< III \leq 100$ cm $< IV \leq 150$ cm), and the mean water volume held by each size class (in milliliters) was established from 30 *A. aquilega* per size class. This permitted us to obtain an estimation of the volume of water held by each georeferenced tree or building supporting *A. aquilega* individuals (used in the models below) as well as the overall volume of water held by these phytotelmata in the city. The meta-habitat size (mhs) refers to the amount of water held by all of the *A. aquilega* within a given surface area. All of the data were entered into the Geographic Information System (GIS) database (QGIS software; **QGIS Development Team 2015**).

Aquatic habitat characteristics

We sampled 32 mature *A. aquilega* in March 2013 within the city limits of Sinnamary in sites selected *a priori* to minimize spatial overlapping between sampling sites (**Fig. 6.1**).

Before being collected, each selected *A. aquilega* was geolocated with a GPS, its elevation above ground (EG) was measured (in meters), and the percentage of incident radiation (IR) around the plant was quantified using hemispherical photography (see **Leroy *et al.* 2009**). Then, each *A. aquilega* was removed from its substrate and placed into a separate, sealed plastic bag to prevent spillage and contamination. In the laboratory, we recorded plant height (PH in centimeters), plant width (PW in centimeters; maximum distance between the tips of the leaves) and the number of wells (NW). Aquatic and semi-aquatic invertebrates were extracted using the following method. First, the bromeliads were turned upside down in a bucket, and the recuperated water filtered through a 150 µm mesh. This primer residue was examined for macroinvertebrates and the water filtered from the phytotelmata was measured (in milliliters) as the volume of water (WV) held by the plant. Second, each plant was totally dismantled; each leaf was separated from the base and cleaned with a jet of water directed into a bucket to collect all remaining aquatic macroinvertebrates, especially benthic organisms living deep in the wells (see **Jocqué *et al.* 2010**). Third, aquatic and semi-aquatic macroinvertebrates were separated from the organic material under a stereomicroscope and collected individuals were sorted by species or morphospecies, enumerated and preserved in 70 % alcohol. Mosquitoes were identified to species level using the **Lane** keys (**1953**), while other macroinvertebrates were identified using the **Merritt and Cummins** larval keys (**2008**). For the sake of convenience, both morphospecies and species are regrouped under the term ‘taxa’ in the rest of the text. Fourth, the organic matter (OM) contained by the plant was expressed in dry mass (in grams) after being dried in an oven until a constant weight was reached.

Statistical analyses

For each tank bromeliad sampled, the surface areas covered by buildings (surf_build), roads (surf_road), vegetation (surf_veget) and ground (surf_ground) were extracted from the GIS at four spatial scales corresponding to radii of 10, 30, 50 and 70 m. The size of the aquatic meta-habitat (mhs) was also estimated (in milliliters) at these four scales. In addition, the distance to the nearest building (dist_build) and the distance to the nearest road (dist_road) were extracted (both in meters) for each tank bromeliad sampled.

Figure 6.1 High resolution orthophoto of Sinnamary, French Guiana, showing the distribution of the 32 sampling sites within the city buffered by a radius of 30 m (orange). Areas covered by buildings (light green), roads (purple) and vegetation (blue) are represented as well as all of the structures (trees and buildings) supporting *Aechmea aquilega* (light blue dots).

Macroinvertebrate distribution was first analyzed with an initial detrended correspondence analysis (DCA). This analysis allowed us to test the first assumption regarding the use of a linear type ordination method. Specifically, the output gives the lengths of the gradient for each ordination axis representing the extent of taxa turnover in community

composition along gradients of newly created ordination axes. In order to use a linear type ordination method, the longest gradient should not exceed 3.0 (**Lepš & Šmilauer 2003**). We analyzed the relative influence of the aquatic and the terrestrial habitat on the structure of the aquatic macroinvertebrate communities using redundancy analyses (RDAs). At each spatial scale, we conducted redundancy analyses with all of the environmental explanatory variables. The significance of the explanatory variables was tested against 1000 Monte Carlo permutations. The P-value was obtained by comparing the F-statistic of the model with that obtained using the null hypothesis (rejected at $P < 0.05$). Note that the reported significance level P-value = 0.001 is the lowest achievable value given the number of permutations we used. The explained variance at each spatial scale was then partitioned into the variance explained by the aquatic habitat and the variance explained by the terrestrial habitat through a partial redundancy analysis (pRDA). In addition, simple linear regressions were used to test the influence of the aquatic habitat size (WV) and the aquatic meta-habitat sizes at the four spatial scales (mhs) on the species richness of local aquatic macroinvertebrate communities.

We analyzed the influence of the aquatic and the terrestrial habitat on the two most abundant mosquito species during this study (namely, *Culex* (*Microculex.*) *pleuristriatus* and *Wyeomyia* (*Wyeomyia*) *pertinans*) and on the top predator species *Toxorhynchites* (*Lynchiella*) *haemorrhoidalis.* In the latter case, because of the relatively low abundances, we transformed the data into presence/absence and we used generalized linear models with a binomial distribution. At each spatial scale, we used six explanatory variables issued from a wide selection of RDAs. The size of the aquatic habitat (WV) and the available food resources (amount of organic matter; OM) are related to the aquatic habitat; the size of the aquatic meta-habitat (mhs), the surface area of vegetation cover (trees and shrubs; surf_veget), the surface area of ground cover (bare ground and grass; surf_ground), and the distance to the nearest buildings (dist_build) are related to the terrestrial habitat. These explanatory variables were tested *a posteriori* for multicollinearity using the Variance Inflation Factor (VIF) at each spatial scale (**Appendix 5a**). We used a multimodel inference approach to examine the relative effects of the predictors on mosquito abundance at different spatial scales. Because the variables were computed for four different spatial scales, we considered four different data sets, each including the six above-cited variables. For each data set, all possible models were ranked using the Akaike information criterion (AIC), and the Akaike weights (w_i) were computed for all models (**Appendix 5b**). Since the Akaike weights are probabilities, we were able to estimate the relative importance of a given variable by summing up the Akaike weights (noted $w+(j)$ for variable j) across all models where this

variable occurred (**Burnham & Anderson 2002**). So, *w*+(j) is the probability that the variable j will appear in the most appropriate model. The larger *w*+(j), the more important variable j is relative to the other variables.

Statistical analyses were conducted in R (R software; **R Development Core Team 2013**) using 'car', 'entropart', 'MuMIn' and 'vegan' packages.

RESULTS

The cartographic census of the entire population of tank bromeliads in Sinnamary permitted us to record 7,359 *A. aquilega* supported by 224 trees belonging to 15 species (70 % of them were mango trees), and 28 individuals growing on six buildings (**Table 6.1**). The mean water volume held by each size class was: I = 1.58 ±0.68 ml; II = 61.43 ±17.72 ml; III = 493.13 ±71.51 ml; and IV = 779.61 ±111.87 ml. Based on these means, we estimated the overall aquatic meta-habitat formed by tank bromeliads in Sinnamary at 3,745 ±553 liters. A total of 18,352 aquatic macroinvertebrate individuals belonging to 29 taxa were sorted out from the 32 *A. aquilega* selected (**Table 6.2**). Most of the individuals were immature (larvae and pupae) Diptera; a few Coleoptera and Oligochaeta specimens were also found. The meta-community sampled contained three singletons and three *Aedes* (*Stegomyia*) *aegypti* individuals gathered from two *A. aquilega*.

Table 6.1 List of the structures supporting the tank bromeliad *Aechmea aquilega* in the city of Sinnamary, French Guiana. Species/structures are ranked in decreasing order of the number of *Aechmea aquilega* supported.

Species	Vernacular name	Mean height	No. of structure	Percent. of structure	No. of *A. aquilega*	Percent. of *A. aquilega*
Mangifera indica L.	Mango tree	10.57 ±0.17	161	70.00	5832	79.25
Chrysophyllum cainito L.	Caimito tree	10.50 ±0.67	10	4.35	635	8.63
Spondias mombin L.	Yellow Mombin	10.82 ±0.63	7	3.04	189	2.57
Artocarpus altilis (Parkinson) Fosberg	Breadfruit tree	12.31 ±0.55	11	4.78	148	2.01
Pinus caribaea Morelet	Caribbean Pine	11.21 ±0.55	10	4.35	121	1.64
Unidentified species	-	9.65 ±1.01	7	3.04	76	1.03
Mammea americana L.	Mammee tree	11.06 ±0.77	3	1.30	69	0.94
Delonix regia (Bojer ex Hook.) Raf.	Flamboyant tree	8.50 ±0.49	2	0.87	68	0.92
Attalea maripa (Aubl.) Mart.	Maripa Palm	9.59 ±1.37	3	1.30	33	0.45
Cocos nucifera L.	Coconut Palm	5.85 ±0.85	2	0.87	30	0.41
Terminalia catappa L.	Bengal Almond tree	23.00 -	1	0.43	29	0.39
Buildings	-	2.43 ±0.29	6	2.61	28	0.38
Spondias dulcis Sol. ex Parkinson	Ambarella tree	8.53 -	1	0.43	26	0.35
Crescentia cujete L.	Calabash tree	5.44 -	1	0.43	23	0.31

Tamarindus indica L.	Tamarind tree	11.00 -	1	0.43	23	0.31
Persea americana Mill.	Avocado tree	8.07 ±0.07	2	0.87	22	0.30
Astrocaryum vulgare Mart.	Awara Palm	9.08 ±2.07	2	0.87	7	0.10
Total			230		7359	

Table 6.2 List of the aquatic and semi-aquatic macroinvertebrate species or morphospecies (hereafter 'taxa') occurring in *Aechmea aquilega* in Sinnamary, French Guiana. The taxa are listed alphabetically. The rank of the relative frequency and the percentage of occurrence are presented for each taxa.

Class	**Order**	**Family**	**Subfamily**	**Morphospecies/species**	**No. rank**	**Percent. of occurrence**
Insecta	Coleoptera			Coleoptera sp.1	27	3.13
				Coleoptera sp.2	15	21.88
		Elateridae		Elateridae sp.	23	9.38
	Diptera			Brachycera sp.1	16	28.13
				Brachycera sp.3	28	3.13
				Brachycera sp.4	12	40.63
				Brachycera sp.5	26	6.25
				Brachycera sp.6	9	75.00
				Brachycera sp.7	14	3.13
				Brachycera sp.8	21	12.50
				Brachycera sp.9	7	37.50
				Brachycera sp.10	8	6.25
				Brachycera sp.11	29	3.13
				Brachycera sp.13	13	9.38
		Ceratopogonidae	Ceratopogoninae	*Bezzia* sp.1	3	93.75
				Bezzia sp.2	18	12.50
				Ceratopogoninae sp.2	20	12.50
			Forcipomyiinae	Forcipomyiinae sp.2	6	93.75
				Forcipomyiinae sp.3	10	46.88
		Chironomidae	Chironominae	Chironominae sp.	25	9.38
		Culicidae	Culicinae	*Aedes* (*Stg.*) *aegypti*	24	6.25
				Culex (*Mcx.*) *pleuristriatus*	2	96.88
				Culex (*Mcx.*) *imitator*	22	3.13
				Wyeomyia (*Wyo.*) *pertinans*	4	96.88
				Toxorhynchites (*Lyn.*) *haemorrhoidalis*	11	50.00
		Psychodidae	Psychodinae	Psychodinae sp.	17	100.00
				Telmatoscopus sp.	1	3.13
Oligochaeta				Oligochaeta sp.1	19	15.63
				Aulophorus superterrenus	5	78.13

Effects on aquatic macroinvertebrate communities

The longest gradient provided by the DCA along the first axis (i.e. 1.82) corresponds to a low taxa turnover (inferior to 3.0), permitting us to conduct a linear type ordination (**Lepš & Šmilauer 2003**). Consequently, a redundancy analysis was computed for each spatial scale

and the explained variance was partitioned between variables from the aquatic habitat and from its surrounding terrestrial matrix (**Table 6.3c**). The amount of organic matter and the water volume held by the plant explained a significant amount of the taxa variance whatever the spatial scale (i.e. 10 m, 30 m, 50 m and 70 m). The size of the meta-habitat was significant only at the spatial scale of 10 m, while the distance to the nearest building was significant for the spatial scales of 10 m and 30 m, the surface area of buildings at 70 m, and that of ground cover at 50 m and 70 m (**Table 6.3b**).

Table 6.3 Results of redundancy analyses computed at each spatial scale permitting us to show what variables explain a significant amount of the taxa variance and separated into variance explained by the variables of the aquatic habitat alone, by the variables of the surrounding terrestrial habitat alone, and by the joint effect of both.

Spatial Scales	**10 meters**	**30 meters**	**50 meters**	**70 meters**
a. First two axes				
Total taxa variance	31.47 %	24.41 %	25.53 %	27.05 %
Taxa-environment variance	71.94 %	71.13 %	72.56 %	71.53 %
Eigen values Axis 1	4.32	3.46	3.67	3.76
Eigen values Axis 2	2.61	1.92	1.95	2.20
b. Variables explaining a significant amount of the taxa variance				
OM	P = 0.001	P = 0.001	P = 0.001	P = 0.002
WV	P = 0.002	P = 0.001	P = 0.001	P = 0.001
NW	NS	NS	NS	NS
PH	NS	NS	NS	NS
PW	NS	NS	NS	NS
IR	NS	NS	NS	NS
EG	NS	NS	NS	NS
mhs	P = 0.017	NS*	NS	NS
dist_build	P = 0.043	P = 0.048	NS*	NS*
dist_road	NS	NS	NS	NS
surf_build	NS	NS	NS*	P = 0.046
surf_ground	NS	NS	P = 0.040	P = 0.030
surf_road	NS	NS	NS	NS*
surf_veget	NS	NS	NS	NS

c. Results of the partial redundancy analysis

	Variance	Percentage	Variance	Percentage	Variance	Percentage	Variance	Percentage
Aquatic	4.7794	39.75 %	5.2487	52.85 %	4.9822	47.82 %	4.9173	46.40 %
Terrestrial	6.3974	53.20 %	4.3028	43.33 %	4.7909	45.98 %	4.9697	46.90 %
Joint effect	0.8483	7.05 %	0.3791	3.82 %	0.6459	6.20 %	0.7105	6.70 %
Total	12.0251	100 %	9.9306	100 %	10.419	100 %	10.5975	100 %

We found a positive and significant correlation between the volume of water held by the plant and the species richness of the local communities (Estimate = 1.705 ±0.749; t = 2.274; P

= 0.03). At the 10-m scale, a negative, but not significant correlation was found between the size of the meta-habitat and the species richness of the local communities (Estimate = -0.595 ±0.305; t = -1.95; P = 0.06). At larger scales, no correlation was found between the size of the meta-habitat and the species richness of the local communities (results not shown).

Effects on the abundance of mosquito species

The relative importance of each predictor at each spatial scale is presented in **Figures 6.2 and 6.3** for the two most abundant mosquito species. Because of the very low abundance and occurrence of *Ae.* (*Stg.*) *aegypti* immatures, we did not attempt to statistically explain their presence.

The results of the multimodel inference reveal that aquatic habitat size is the most important predictor of the abundance of *Cx.* (*Mcx.*) *pleuristriatus* at every scale (**Fig. 6.2**). At spatial scales of 10 m and 30 m, the aquatic meta-habitat size is equivalent to the size of the aquatic habitat ($w+(j) = 1.00$) and second in terms of relative importance ($w+(j) = 0.79$), respectively, revealing that this predictor has a strong probability of appearing in the most appropriate model at these scales (**Fig. 6.2**). Yet, its relative importance is much lower at spatial scales of 50 m and 70 m ($w+(j) = 0.53$ and $w+(j) = 0.62$, respectively). The values for aquatic habitat size and aquatic meta-habitat size reveal a positive influence on *Cx.* (*Mcx.*) *pleuristriatus*, while the surface area of the ground cover reveals a high negative influence on the abundance of *Cx.* (*Mcx.*) *pleuristriatus* for spatial scales of 30 m, 50 m and 70 m (**Fig. 6.2**).

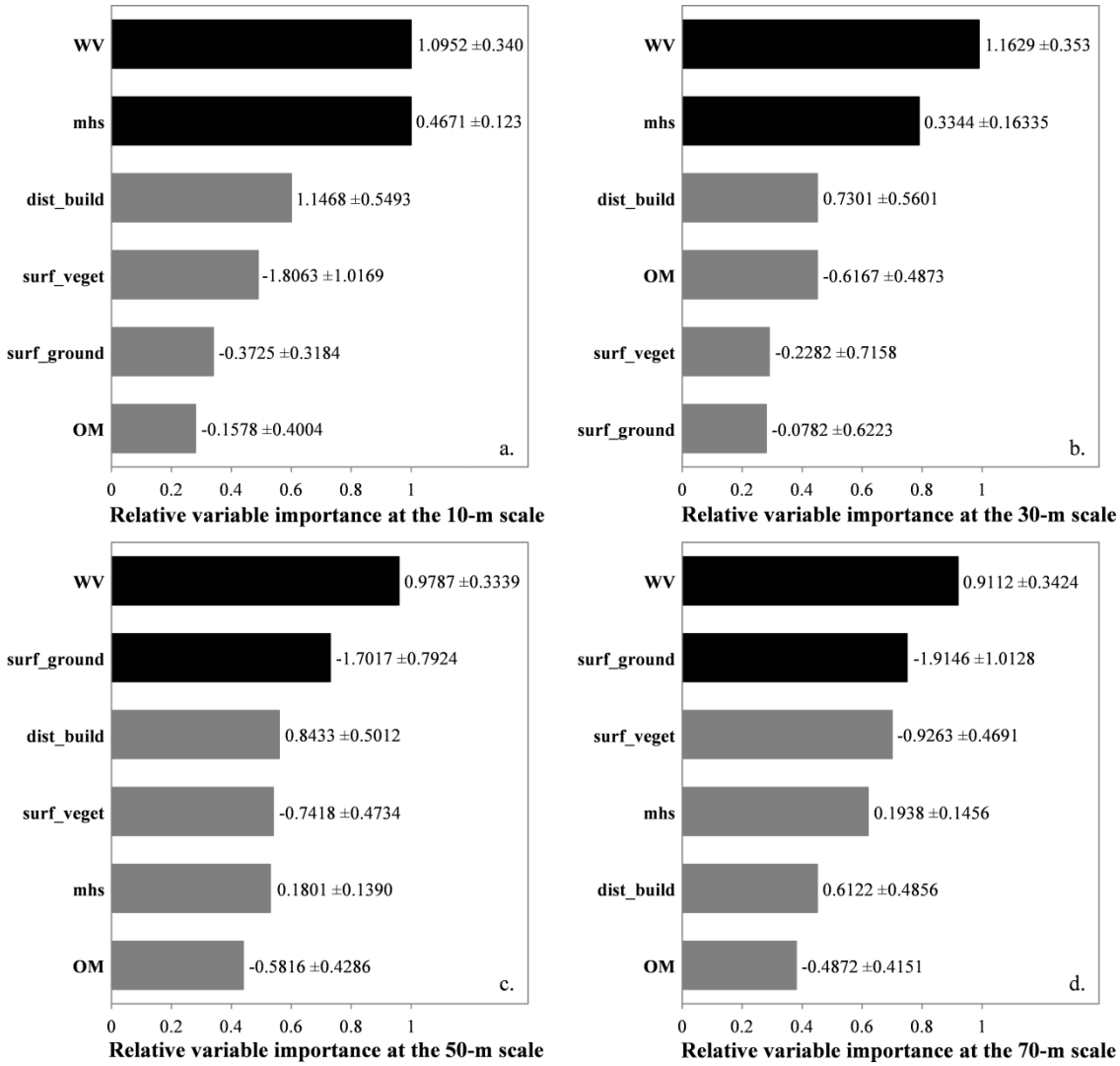

Figure 6.2 Relative importance of each variable explaining *Culex* (*Mcx.*) *pleuristriatus* abundance with landscape predictors calculated at (a.) 10 m, (b.) 30 m, (c.) 50 m and (d.) 70 m. Variables are ranked in increasing order based on the sum of their Akaike weights, which are the probabilities that the given variable will appear in the best-fitting model (lowest AIC value). Black bars indicate variables with a probability higher than 0.7 of appearing in the best-fitting model. Estimated parameter values and the SE for each variable are provided to the right of each bar.

Concerning *Wy.* (*Wyo.*) *pertinans* abundance, at spatial scales of 10 m and 30 m, the size of the aquatic meta-habitat is the most important predictor with the sum of the Akaike weights 0.89 and 0.66, respectively; at spatial scales of 50 m and 70 m, it is the amount of organic matter (**Fig. 6.3**). All of the other predictors have a low relative importance and are assumed to have a slight or no effect.

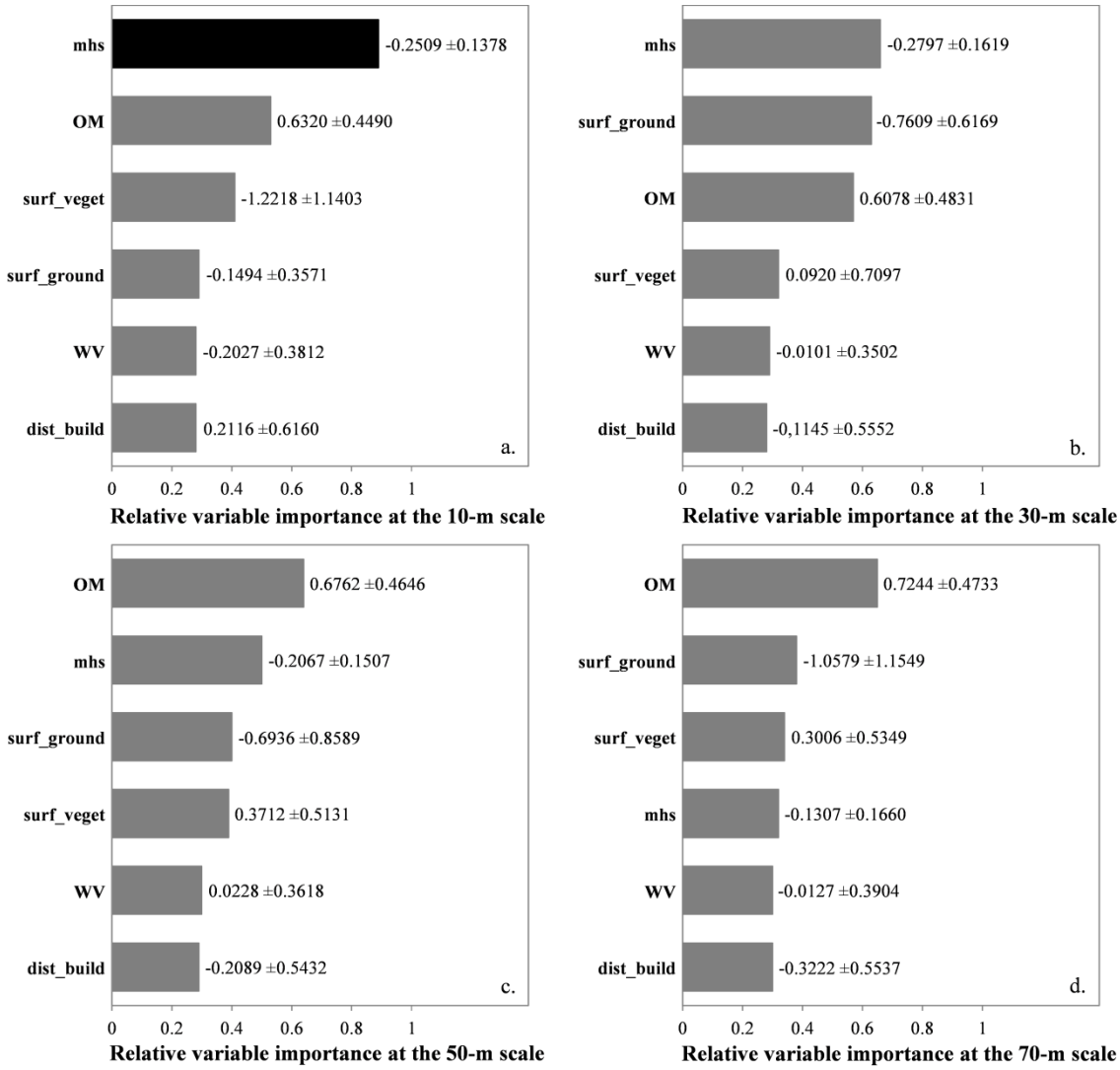

Figure 6.3 Relative importance of each variable in explaining the abundance of *Wyeomyia* (*Wyo.*) *pertinans* with landscape predictors calculated at (a.) 10 m, (b.) 30 m, (c.) 50 m and (d.) 70 m (see details in **Figure 6.2**).

The presence of *Tx.* (*Lyn.*) *haemorrhoidalis* is influenced positively by the surface area of the vegetation cover, the only important predictor at spatial scales of 50 m and 70 m ($w+(j)$ = 0.69 and $w+(j)$ = 0.80, respectively) (**Fig. 6.4c, d**), while all of the other predictors have a slight or no effect.

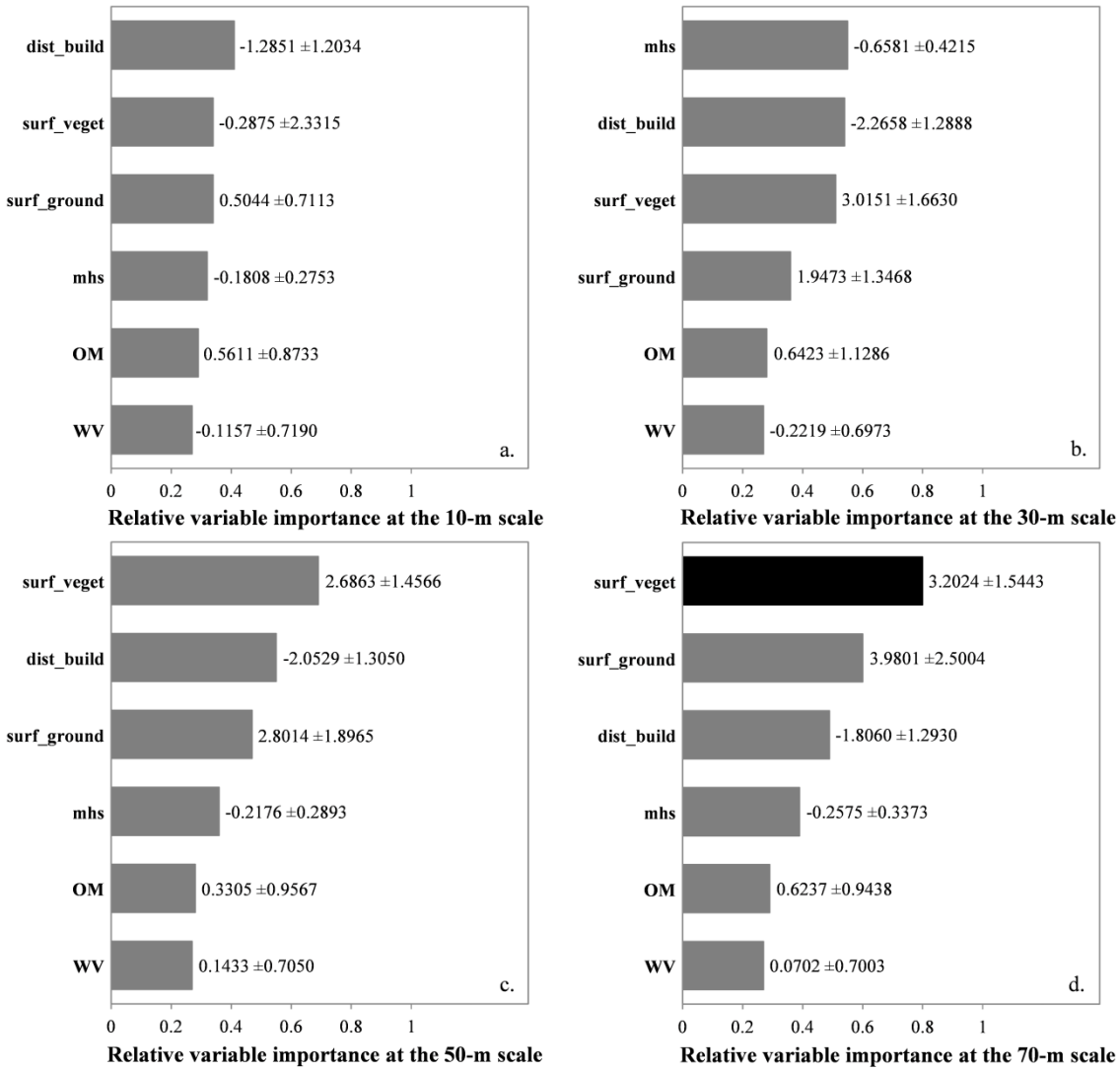

Figure 6.4 Relative importance of each variable in explaining the presence of Toxorhynchites haemorrhoidalis with landscape predictors calculated at (a.) 10 m, (b.) 30 m, (c.) 50 m and (d.) 70 m (see details in **Figure 6.2**).

DISCUSSION

The characteristics of aquatic habitats as well as the surrounding terrestrial matrix in which they are embedded drive the patterns of aquatic macroinvertebrate communities, including mosquitoes (**Yee & Yee 2007**). This study, conducted in a small Neotropical city, offers a good illustration of this as the aquatic macroinvertebrate communities developing in the tanks of *A. aquilega* depend on the characteristics of both these aquatic habitats and the surrounding terrestrial matrix.

Aquatic macroinvertebrate communities are generally a mixture of organisms displaying simple aquatic life cycles and others having complex life cycles. For the latter, the

dispersal and the mortality of flying adults are influenced by the terrestrial characteristics which indirectly shape the spatial distribution of their aquatic larvae (**LeCraw *et al.* 2014**). So, the proportion of these two types of life cycles has a great influence on the overall response of local aquatic communities to terrestrial characteristics. In the present study, only two Oligochaeta species have a simple life cycle, while all of the other taxa are insects with a complex life cycle, their great proportion explaining the strong overall response to the terrestrial variables we recorded. Also, quantifying the landscape heterogeneity within the same environment (a small city) at four spatial scales shows that characteristics from the terrestrial habitat explain a large proportion of the structure of the aquatic macroinvertebrate communities. At the smallest spatial scale (a radius of 10 m), they even explained more of the taxa variance than did the characteristics of the aquatic habitat (**Table 6.3c**).

The metacommunity theory predicts that the species richness of a local community will increase with habitat size and proximity to other, similar habitats (**Brown *et al.* 2011**). Here, habitat size corresponds to the volume of water held by each *A. aquilega* (WV) and the proximity to other conspecifics can be approximated by measuring the meta-habitat size (mhs). The relationship between species richness and habitat size was significant and positive (simple linear regressions; $P = 0.03$), confirming that larger aquatic habitats can sustain speciose communities (see **Richardson 1999**). Moreover, the local aquatic communities surrounded by a larger meta-habitat were not particularly species-rich, confirming that species richness is not related to meta-habitat size which is consistent with the relatively constant alpha diversity found by **LeCraw *et al.*** (**2014**) across metacommunities of different sizes.

Classically, the characteristics of the aquatic habitat do not vary with spatial scale, so that the size of the aquatic habitat and the amount of organic matter significantly explain the structure of the aquatic communities at all spatial scales (**Table 6.3b**) (see also **Richardson 1999; Dézerald *et al.* 2014**). On the contrary, terrestrial characteristics vary between spatial scales. At the 10-m scale, meta-habitat size and the distance to the nearest building explained a significant amount of taxa variance within local communities. These two variables lose their significance with an increasing spatial scale while building and ground cover become significant (**Table 6.3b**).

At the species level, water volume is determinant for *Cx.* (*Mcx.*) *pleuristriatus*, whereas it is not for *Wy.* (*Wyo.*) *pertinans* which seems more influenced by the amount of organic matter. This result is likely due to their distinct feeding modes; the larvae of the former are collector-filters which depend on the water column, and the latter are collector-gatherers that feed mainly on deposited particles (**Clements 1992**). Consequently, this suggests a niche

segregation which could facilitate species coexistence at both the local level (i.e. each bromeliad) and landscape scale (i.e. the level of the metacommunity). Concerning terrestrial characteristics, we noted a positive relationship between meta-habitat size and the abundance of *Cx.* (*Mcx.*) *pleuristriatus*. This suggests that oviposition and/or the survival of this species are high in tank bromeliads that are surrounded by a large aquatic meta-habitat. This is true at the 10-m and 30-m spatial scales, but becomes irrelevant at larger scales (**Fig. 6.2**) and is probably due to the limited dispersal of this species (see **Krawchuk & Taylor 2003**). Indeed, at the 50-m and 70-m spatial scales, ground cover is the most important landscape variable having a negative influence on the *Cx.* (*Mcx.*) *pleuristriatus* larval population, likely indicating a higher adult mortality associated with the reduction of suitable terrestrial habitats and, as a result, less oviposition.

Concerning *Wy.* (*Wyo.*) *pertinans*, the variables from the aquatic habitat and from its surrounding terrestrial matrix poorly explain larval abundance although the size of the aquatic meta-habitat influences larval abundance at the 10-m spatial scale; however, contrary to *Cx.* (*Mcx.*) *pleuristriatus*, the relationship is negative (**Fig. 6.3**). This counterintuitive pattern might be due to niche displacement because of the presence of a superior competitor, here *Cx.* (*Mcx.*) *pleuristriatus*, facilitating the coexistence of these species (see **Amarasekare 2003**). Scale dependency was also shown in a North American peatland system where the carnivorous plant *Sarracenia purpurea* is patchily distributed and the larvae of three dipteran species, including *Wyeomyia* (*Wyeomyia*) *smithii*, are able to develop in leaf-held water (**Krawchuk & Taylor 2003**).

The presence of *Tx.* (*Lyn.*) *haemorrhoidalis* in this system is favored by the surface area covered by vegetation at the 50-m and 70-m spatial scales. The destruction of vegetation within this urban area definitely impacts the presence of this top predator and likely reduces the top-down control on the aquatic macroinvertebrate communities.

Our field sampling was conducted during a short period of time and does not account for the population dynamics of the species composing the community. We can reasonably argue, however, that seasonal fluctuations in the size of the populations might change the hierarchy of the factors characterizing the aquatic habitat and its surrounding terrestrial matrix that explain the structure of the aquatic communities. For example, the processes underlying spatial competition might be lower when the size of the population is small, enhancing the roles of stochastic colonization and extinction events in structuring local communities. In this situation, the establishment of invasive species, like the dengue vector *Ae.* (*Stg.*) *aegypti*

found in a few cases in this study could be favored. This hypothesis deserves further investigation given the medical importance of this species worldwide.

Mosquito control in urban areas is usually based on integrated management targeting both immature and adults. Larval control is often dependent on discrete local action like the physical removal or chemical treatment of aquatic habitats, while adult control is conducted using the pulverization of an insecticide (the case in this study). Here, we provide empirical evidence that the size of the meta-habitat and landscape characteristics can have a strong influence on the structure of the aquatic communities in a tank bromeliad, as well as on mosquito larval abundance. These results open up perspectives for mosquito management since modifications conducted at the landscape scale could have negative consequences on both the terrestrial and the aquatic compartments of the ecosystem. So, we can dream of a world where mosquito control starts with urban planning.

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Chapitre 7: Impacts of biotic and abiotic factors on immature populations of *Aedes* (*Stegomyia*) *aegypti* (L.) along an urbanization gradient (Talaga *et al.*, en préparation)

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Abstract: 1. *Aedes (Stegomyia) aegypti* has invaded most urban areas throughout the Tropics. Due to its vector competence for chikungunya, dengue and zika, it causes major public health problems. Despite decades of research on the autoecology of this species, we still know little about its biotic interactions with recipient communities. In this study, we monitored twice a month during 1 year 54 aquatic macroinvertebrate communities found in four types of containers across three levels of urbanization in the city of Kourou, French Guiana. We assessed the variation in diversity and used a multimodel inference approach to examine the relative effects of abiotic and biotic predictors on the abundance of *Ae. (Stg.) aegypti* immatures between the three sites. Alpha diversity reached a peak at moderate-level urbanization in accordance with the intermediate perturbation hypothesis. The low-level urbanization site showed both the lowest alpha diversity and the highest beta diversity. The multimodel inference revealed that, in addition to abiotic predictors, the presence of controphic species (other than mosquitoes) aided the development of *Ae. (Stg.) aegypti*, suggesting a mechanism of facilitation through a chain of processes. We also detected a significant negative influence of native mosquitoes on the abundance of *Ae. (Stg.) aegypti* in the low-level urbanization site, indicating competitive reduction and displacement. In the other sites, predation by higher trophic levels was high at the scale of the community. Synthesis and applications. Our findings suggest that biotic interactions with the recipient community can have measurable impacts on the abundance and thus the reproduction of *Ae. (Stg.)*

aegypti. Competitive reduction and displacement as well as predation can be considered ecosystem services. This opens exciting perspectives in terms of mosquito management, including the conservation and/or the augmentation of natural enemies that can serve as biological control agents.

Keywords: Competitive reduction, Diversity, Mosquito management, Processing chain mutualism, Trophic interactions.

INTRODUCTION

Climatic factors and land use can strongly affect the spatio-temporal dynamics of mosquito populations (**Dufourd & Dumont 2012, 2013**). To some extent, they likely also influence the dynamics of immature mosquito vectors in the aquatic environment (**Honório *et al.* 2009**). Climatic variables can be modulated to a certain extent by anthropogenic perturbations such as deforestation or urbanization. In fact, urban areas are generally warmer (i.e. urban heat island effect) due to the re-emission of solar radiation by buildings and to the heat generated by human activity (**Rizwan *et al.* 2008**). The increase in temperatures may affect the survival, dispersal and fecundity of adult mosquitoes (**Honório *et al.* 2003; Delatte *et al.* 2009**), while it might reduce larval development time, consequently allowing the production of more offspring during the transmission period (**Rueda *et al.* 1990**). Under similar precipitation regimes, urban areas are also expected to be drier as a consequence of less surface area covered by vegetation and more impervious surface area, respectively limiting evapotranspiration and evaporation (**Landsberg & Maisel 1972**). These drier conditions have been associated with the lower survival and fecundity rates of adult mosquitoes and egg viability (**Canyon *et al.* 1999; Luz *et al.* 2008**).

The development of pre-imaginal stages also depends on the suitability of the aquatic habitat and adults are expected to choose the most favorable habitats for the survival of their progeny (**Clements 1999**). Parameters of water quality such as pH, concentration of total dissolved solids (TDS, often approximated with a measure of conductivity) and salinity have proven to be important determinants for certain mosquito species (**Clark *et al.* 2004; Burke *et al.* 2010**). Immature mosquitoes are often embedded within aquatic communities organized in food webs implying multiple trophic interactions (**Juliano 2009**). These interactions can be very diverse and their outcomes range from negative to positive for the targeted species

(reviewed in **Blaustein & Chase 2007**). For example, immature mosquitoes can be negatively influenced by predation by upper trophic levels and/or by competitive interactions with controphic species exploiting the same resource (**Juliano 2009**). Interaction outcomes can also be beneficial, for example, when two controphic species share a common predator (apparent mutualism) or when the exploitation of a resource by one species enhances access to another resource for the other species (indirect mutualism) for example by processing chains (**Daugherty & Juliano 2003**).

Because there are still no specific treatments against several mosquito-borne diseases (e.g. malaria, dengue, chikungunya and zika), their prevention mostly relies on controlling vector populations (**Becker *et al.* 2010**). Understanding mosquito ecology is thus essential to effective cost management and to avoid actions that might trigger trophic cascades of ecological effects that could lead to enhanced vector development and disease transmission (**Pace *et al.* 1999**). We still know little about the mechanisms that drive mosquito population dynamics, especially about the importance of biotic interactions relative to abiotic fluctuations. The principles of community ecology should be applied to mosquitoes and particularly to their larval habitats where interactions with predators, pathogens, and controphic species can be important (**Blaustein & Chase 2007**).

In this study, we investigated the roles of both biotic and abiotic environmental determinants on the larval dynamics of *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762), the main vector of dengue and chikungunya worldwide and, together with *Culex* (*Culex*) *quinquefasciatus* Say 1823, a major vector of zika. We studied biotic interactions, microclimatic variables and water container characteristics along an urbanization gradient in a dengue epidemic urban area situated in French Guiana to characterize the most productive mosquito larval locations and breeding sites. We hypothesized that a higher level of urbanization will negatively affect the diversity of aquatic macroinvertebrate communities as a result of warmer/drier microclimatic conditions related to greater human-mediated perturbation. Consequently, we predicted that biotic interactions involving *Ae.* (*Stg.*) *aegypti* will be lower the greater the level of urbanization, thereby giving more relative importance to abiotic fluctuations in explaining its larval abundance. We also predicted that predation and intraguild competition for food resources would influence negatively *Ae.* (*Stg.*) *aegypti*, while interguild interactions with controphic species would favor *Ae.* (*Stg.*) *aegypti* through processing chains and/or apparent mutualism.

MATERIALS AND METHODS

Study area

This study was conducted in French Guiana between October 2013 and October 2014 within the city limits of Kourou (5°10'N, 52°39'W). The region is characterized by an equatorial monsoon climate corresponding to an average of 2,500 mm of yearly rainfall distributed over 210 days (**Peel *et al.* 2007**). There is a major drop in rainfall from mid-July to mid-November (dry season) and a shorter and more irregular dry period in March. Minimum and maximum monthly mean temperatures, relatively stable, vary between 25.2°C and 30.6°C.

Three experimental sites with increasing levels of urbanization were selected. The first site was located in a *ca*. 5 ha fragment of secondary forest remaining within the city (hereafter 'low-level urbanization') situated *ca.* 100 meters from the nearest building and had the lowest level of urbanization (**Fig. 7.1a**). The second site, situated *ca.* 30 meters from the nearest building, was located in a residential area with gardens and patches of small trees and shrubs (**Fig. 7.1b**; hereafter 'moderate-level urbanization'). The third site was located in town in the middle of buildings with some isolated trees (**Fig. 7.1c**; hereafter 'high-level urbanization').

For each site, different microclimatic variables were recorded (see **Table 7.1**). The percentage of incident radiation was quantified using hemispherical photography (see **Leroy *et al*. 2009** for more details). Air temperature and relative humidity were recorded every hour with data loggers (iLog, Escort, New Zealand) installed at 1.5 meter in height under a protective shelter at each site. We were unable to measure the amount of precipitation within each site given the large amount of daily precipitation during the rainy season. Instead, daily precipitation records were obtained from a meteorological station situated in the city of Kourou. Mean temperature, relative humidity and precipitation were calculated with a time lag of one (Tm7, RHm7 and Prm7, respectively; **Fig. 7.2**) and two weeks (Tm15, RHm15 and Prm15, respectively) before each sampling date.


a.
N
0
50 m
b.
N
0
50 m
c.
N
0
50 m

Figure 7.1 High resolution orthophoto of the the low-level urbanization (a.), the moderate-level urbanization (b.) and the high-level urbanization (c.) experimental sites within Kourou, French Guiana. The three sites are buffered by a radius of 50 meters.

Table 7.1 Climatic characteristics for each site and water volume and chemistry for each of the four types of water containers between the three levels of urbanization. Significant effect of the level of urbanization was tested using a one-way ANOVA. Small letters indicate pairwise significance between sites at $P < 0.05$ (P adjusted for multiple comparisons).

	Low-level urbanization (N = 486)	**Moderate-level urbanization (N = 486)**	**High-level urbanization (N = 486)**	**P**
Temperature (°C)	^{a}26.4 ±0.15	^{b}27.12 ±0.15	^{b}27.22 ±0.18	< 0.001
Relative humidity (in %)	^{a}97.65 ±0.39	^{b}94.64 ±0.74	^{c}93.34 ±0.58	< 0.001
Daily precipitation (in mm)	*5.52 ±0.33	*5.52 ±0.33	*5.52 ±0.33	-
Incident radiation (in %)	^{a}15.78 ±0.22	^{a}15.66 ±0.23	^{b}22.15 ±0.46	< 0.001
Water volume (in mL)				
Bromeliad	^{a}213.83 ±13.04	^{a}192.49 ±15.95	^{b}552.74 ±38.22	< 0.001
Bamboo	^{a}332.60 ±20.73	^{b}261.44 ±24.20	^{b}304.78 ±24.93	< 0.001
Ovitrap	244.49 ±13.12	215.99 ±13.78	205.42 ±16.53	NS
Tire	^{a}1269.66 ±89.50	^{a}1233.39 ±87.83	^{b}903.26 ±78.15	< 0.001
pH				
Bromeliad	^{a}5.93 ±0.05	^{b}5.71 ±0.06	^{a}5.79 ±0.04	< 0.01
Bamboo	^{a}5.65 ±0.12	^{b}6.48 ±0.11	^{b}6.54 ±0.08	< 0.001
Ovitrap	^{a}6.41 ±0.05	^{b}6.73 ±0.06	^{b}6.81 ±0.05	< 0.001
Tire	^{a}6.87 ±0.05	^{b}6.62 ±0.05	^{a}7.04 ±0.05	< 0.01
Conductivity (in µS)				
Bromeliad	^{a}189.63 ±26.64	^{b}313.79 ±37.44	^{a}129.01 ±17.51	< 0.001
Bamboo	^{a}374.39 ±35.36	^{b}1225.43 ±206.71	^{a}456.49 ±53.33	< 0.001
Ovitrap	^{a}96.51 ±9.00	^{b}301.48 ±35.19	^{a}155.16 ±15.06	< 0.001
Tire	^{a}176.96 ±22.50	^{b}449.09 ±87.98	^{a}173.255 ±26.57	< 0.001

*Data obtained from the same meteorological station.

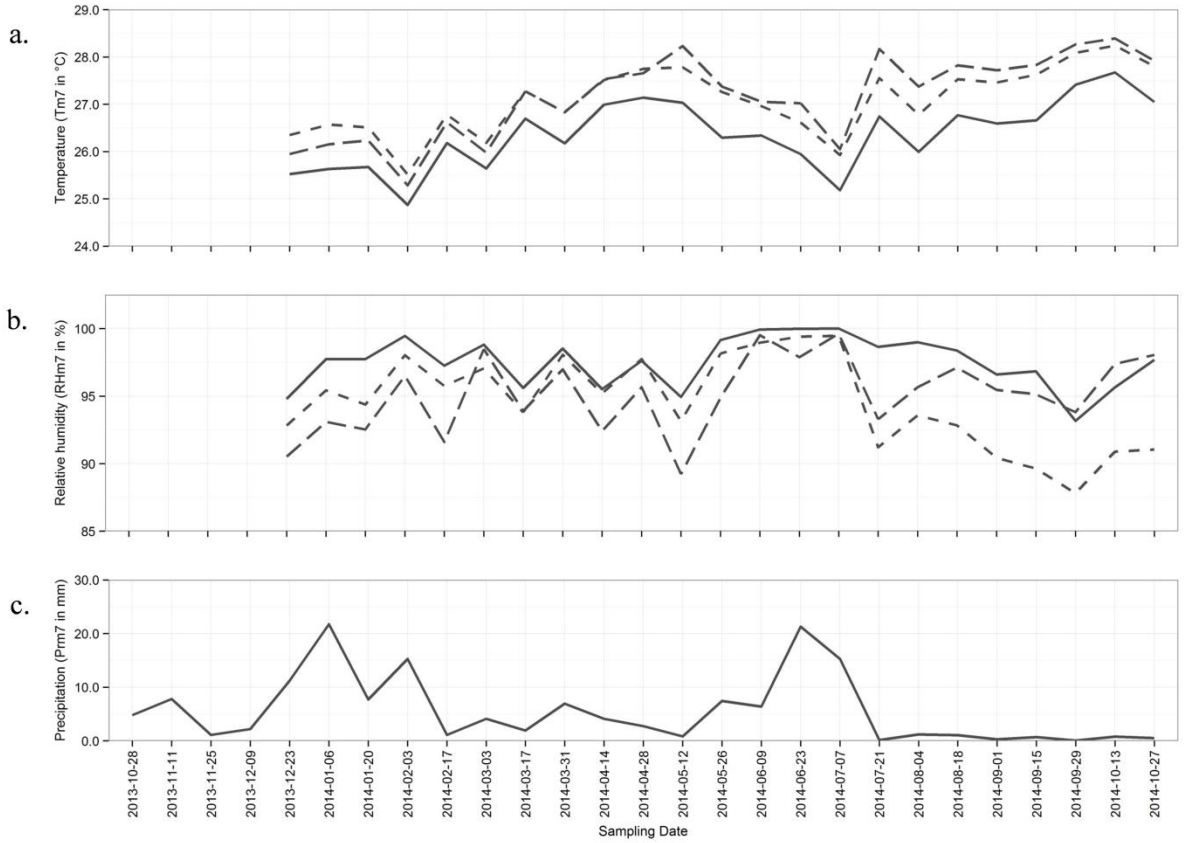

Figure 7.2 Mean temperature (a.), relative humidity (b.) and daily precipitation (c.) calculated at a one week interval before each sampling date (Tm7, RHm7 and Prm7, respectively). Temperature and relative humidity are indicated for the low-level urbanization (solid lines), the moderate-level urbanization (long dashed lines) and the high-level urbanization (short dashed lines) sites (a. and b.). Precipitation, obtained from the meteorological station in Kourou, are common for all sites.

Set up

A set of artificial and natural water containers known as *Ae.* (*Stg.*) *aegypti* breeding sites were used. Natural water containers were composed of potted tank bromeliads (BR; *Aechmea aquilega*) and dry stumps of bamboo (BA; *Bambusa vulgaris*). Artificial water containers were composed of CDC ovitraps (OV; black 500 mL plastic cups) and car tires of the same dimension (TI). Ten examples of each container type were installed within each site, with the exception of tires which were replicated only six times. At the beginning of the experiment in mid-October 2013 all of these containers were filled with 250 mL of rain water.

Sampling

The sampling began two weeks after the experiment was set up. At each sampling date, the water held by the containers was poured out and filtered through a 150 µm mesh. The residue containing organic matter and aquatic organisms was preserved in a formaldehyde

solution at 4 %. Then, the volume of water was assessed (in milliliters) using a graduated cylinder and the values for pH and conductivity (Cond; in microsiemens) were measured with a portable multimeter (Multi 3410, WTW GmbH, Germany). Finally, the filtered water was returned in its entirety to its container. Every two weeks we sampled one half of the example of each container type within each site. The second half was sampled two weeks later and so forth during one year. Therefore, the water in each container type was poured out every month, thus permitting us to mitigate the priority effect relative to the colonization of such habitats and to eliminate temporal dependency between sampling dates (**Alford & Wilbur 1985**).

In the laboratory, all aquatic and semi-aquatic macroinvertebrate organisms were extracted from the organic material under a stereomicroscope at 10X constant magnification. The individuals collected were separated into species or morphospecies, enumerated and preserved in 70 % alcohol. Mosquitoes were identified to species level using the **Lane** (**1953**) keys and individuals belonging to other families were identified using the **Merritt and Cummins** larval keys (**2008**). For the sake of convenience, both morphospecies and species are regrouped under the term 'taxa' in the rest of the text. Macroinvertebrates were classified into three functional groups (see **Céréghino *et al.* 2011**): (1) controphic taxa to *Ae.* (*Stg.*) *aegypti* sharing the same feeding mode (i.e. filter-feeder; hereafter, 'primary competitors'; CompI), (2) controphic taxa that do not have a filter-feeding mode (e.g. shredder, deposit-feeder; hereafter, 'secondary competitors'; CompII), and (3) taxa from a higher trophic level able to prey upon *Ae.* (*Stg.*) *aegypti* immatures ('predators'; Pred).

Statistical analyses

We first conducted Non-metric MultiDimensional Scaling (NMDS) ordination to determine the structural differences among aquatic macroinvertebrates communities between the different sites and types of container habitat. Then PERMANOVAs were used to test the effect on community structure between sites and between container habitat types when controlled for site variation. Pairwise comparisons between the different container habitats were also performed within each site and in these cases significance levels were adjusted using the Bonferroni correction.

We also calculated community diversity and partitioned each site into alpha, beta and gamma diversity based on **Marcon *et al.*** (**2014**). The alpha diversity is defined as the average local community diversity, gamma diversity corresponds to the diversity of the meta-community composed of all communities within each site, and beta diversity is understood as

the diversity between local communities (or the divergence between each community and the meta-community). Differences in alpha diversity between sites for each order q of diversity were tested using one-way ANOVAs with Tukey's *post-hoc* multiple comparisons tests.

To explain the abundance of *Ae.* (*Stg.*) *aegypti* immatures we used zero-inflated negative binomial (ZINB) models to take into consideration the excess number of zero counts (**Cheung 2002**). Full models were constructed with nine explanatory variables, three were related to climatic variations (i.e. Tm, RHm and Prm), three were related to the characteristics of the container habitat (i.e. WV, pH and Cond), three were related to the different functional groups of taxa (i.e. CompI, CompII and Pred), and the type of water container (i.e. TWC) was added as a three-level factor. Because the containers were consecutively sampled every month, we also added the container identity as a random factor in all the models. Due to the strong collinearity between climatic variables calculated with a time lag of one and two weeks, distinct models were computed for both time lags and compared using the Akaike information criterion (AIC). In addition, all explanatory variables were tested *a posteriori* for multicollinearity using the Variance Inflation Factor (VIF) for each site. Since the variables were computed for each site, we considered three different data sets, each including the nine above-cited variables.

Because tank bromeliads are highly compartmented contrary to the other three types of container habitats we considered (i.e. bamboo stump, ovitrap, tire), the effects of biotic interactions are likely lower. To avoid misinterpretation we created a model to test the effects of our predictors on the presence of *Ae.* (*Stg.*) *aegypti* immatures in this natural container. This model was constructed with a binomial distribution and the same explanatory variables as the previous, but we replaced the type of container by the type of site as a three-level factor.

We used a multimodel inference approach to examine the relative effects of the predictors on the abundance or presence of *Ae.* (*Stg.*) *aegypti* immatures. For each data set, all possible models were ranked using the AIC, and the Akaike weights (w_i) were computed for all models. Since the Akaike weights are probabilities, we were able to estimate the relative importance of a given variable by summing up the Akaike weights (noted $w+(j)$ for variable j) across all models where this variable occurred (**Burnham & Anderson 2002**). So, $w+(j)$ is the probability that the variable j will appear in the most appropriate model. The larger $w+(j)$, the more important variable j is relative to the other variables.

Statistical analyses were conducted in R (R software; **R Development Core Team 2013**) using 'car', 'entropart', 'glmmADMB', 'MuMIn' and 'vegan' packages.

RESULTS

A total of 174,840 aquatic and semi-aquatic macroinvertebrate individuals belonging to 25 taxa were sorted out from the 54 container habitats (five tank bromeliads, bamboo stumps, and ovitraps, and three car tires per site) sampled twice monthly all year round (**Table 7.2**). Most of the individuals were immature (larvae and pupae) Diptera; a few Coleoptera, Hemiptera and Oligochaeta specimens were also found. Overall, more than a half of all of the individuals (54.43 %) belonged to the Culicidae family and 30.97 % were *Ae.* (*Stg.*) *aegypti*.

Table 7.2 List of the aquatic and semi-aquatic macroinvertebrate species or morphospecies (hereafter, 'taxa') occurring in water containers in Kourou, French Guiana. The taxa were sampled from natural (tank bromeliads and bamboo stumps) and artificial (ovitraps and tires) water containers and are grouped as follows. Controphic taxa to *Aedes* (*Stegomyia*) *aegypti* sharing the same feeding mode (CompI), controphic taxa that do not share the same feeding mode (CompII), and taxa from higher trophic levels able to prey upon *Ae.* (*Stg.*) *aegypti* (Pred). The percentage of occurrence and the rank number (the first two in bold for each site) of a taxon's relative abundance are indicated for each site.

Class	Order	Family	Subfamily	Morphospecies/species	Group	Low-level urbanization		Moderate-level urbanization		High-level urbanization	
						% of occur.	No. of rank	% of occur.	No. of rank	% of occur.	No. of rank
Insecta	Coleoptera			Coleoptera sp.	CompII	1.06	18	3.95	20	1.33	13
	Diptera			Brachycera spp.	CompII	46.92	3	45.83	4	28.44	5
				Bezzia sp.1	CompII	2.55	12	25.44	8	8.89	12
				Bezzia sp.2	CompII	1.27	15	1.32	16	2.67	10
		Ceratopogonidae	Ceratopogoninae	Ceratopogoninae sp.2	CompII	1.91	16	2.19	18	0.44	18
				Dasyhelea sp.	CompII	-	-	15.13	7	18.67	7
			Forcipomyiinae	Forcipomyiinae sp.2	CompII	3.18	9	2.19	17	24.22	3
				Forcipomyiinae sp.3	CompII	-	-	-	-	0.22	15
		Chironomidae	Chironominae	Chironominae sp.	CompII	20.81	6	35.31	**2**	26.67	**2**
			Tanypodinae	Tanypodinae sp.	Pred	-	-	-	-	0.89	9
		Culicidae	Culicinae	*Aedes* (*Stg.*) *aegypti*	-	15.29	5	57.89	**1**	57.33	**1**
				Culex sp.1	CompI	-	-	0.66	15	-	-
				Culex sp.2	CompI	-	-	0.88	14	-	-
				Culex (*Car.*) *bonnei*	CompI	0.85	14	-	-	-	-
				Culex (*Cux.*) *mollis*	CompI	2.55	7	5.70	6	0.22	17
				Culex (*Cux.*) *quinquefasciatus*	CompI	0.42	11	7.24	5	2.22	8
				Culex (*Mcx.*) *pleuristriatus*	CompI	0.21	20	3.73	13	20.44	6
				Limatus durhamii	CompI	42.89	**1**	5.92	10	0.67	14
				Toxorhynchites (*Lyn.*) *haemorrhoidalis*	Pred	7.64	13	21.71	12	0.44	16
				Trichoprosopon digitatum	CompI	0.64	10	-	-	-	-
				Wyeomyia (*Wyo.*) *aporonoma*	CompI	7.22	8	0.44	21	-	-
				Wyeomyia (*Wyo.*) *pertinans*	CompI	16.77	4	7.89	11	-	-
		Psychodidae	Psychodinae	*Telmatoscopus* spp.	CompII	31.42	**2**	46.05	3	24.44	4
	Hemiptera	Veliidae		Veliidae sp.	Pred	1.06	19	9.87	9	7.11	11.00
Oligochaeta				Oligochaeta sp.	CompII	0.21	17	1.32	19	-	-

The composition of the aquatic macroinvertebrate communities were significantly different between the three urban sites (PERMANOVA; N = 820; F = 38.73; R^2 = 0.09; P < 0.001; **Fig. 7.3a**) and the type of container habitat also had a significant effect (PERMANOVA; N = 820; F = 69.99; R^2 = 0.20; P < 0.001; **Fig. 7.3b, c, d**). Pairwise comparisons of container habitat types within each site also showed significant differences (results not shown) with the exception of bamboo and ovitrap communities in the high-level urbanization site (PERMANOVA; N = 130; F = 2.30; R^2 = 0.02; P.adj = 0.18; **Fig. 7.3d**).

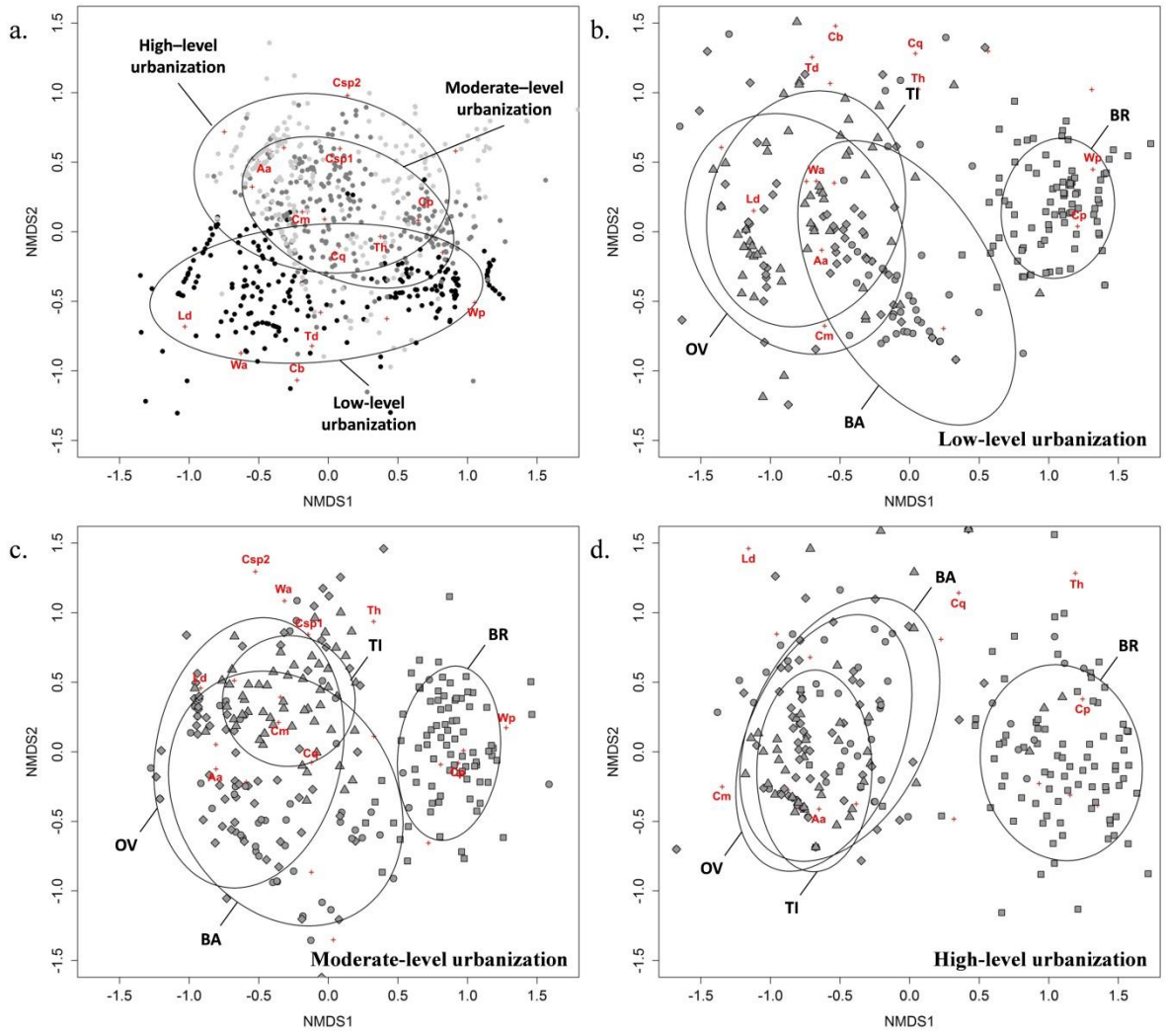

Figure 7.3 Non-metric MultiDimensional Scaling (NMDS) ordinations based on the Bray-Curtis distance showing the degree of dissimilarity of aquatic macroinvertebrate communities between the low-level urbanization, the moderate-level urbanization and the high-level urbanization sites (a.), and between types of containers within each site (b., c. and d.). Ellipses are drawn around each group with a level of confidence of 95 %. BR: tank bromeliads, BA: bamboo stumps, OV: ovitraps, TI: tires. Red crosses correspond to taxa projected in the same ordination space. For the sake of clarity only culicid taxa are indicated, abbreviated as in **Appendix 6**.

The comparison of partitioned alpha, beta and gamma diversity between the low-, moderate- and high-level urbanization sites is presented in **Figure 7.4**. In theory, a community is considered more diverse when its profile is above the others compared. Diversity profiles revealed that for each order of diversity, local alpha diversities were higher in the moderate-level urbanization site than in the high- and low-level urbanization sites, the latter showing the lowest values for alpha diversity (significant differences for the alpha diversity of order q = 0, q = 1 and q = 2; ANOVA: $F_{2,820}$; $P < 0.001$; **Fig. 7.4**). The beta diversity was clearly lower in the high-level urbanization meta-community than in the low- and moderate-level urbanization meta-communities (**Fig. 7.4**). The low-level urbanization meta-community showed higher beta diversity for orders of diversity between 0 and 1 relative to the moderate-level urbanization meta-community and this tendency was inversed for orders of diversity greater than 1 (**Fig. 7.4**). Overall, the variation of gamma diversity between sites did not show clear patterns (**Fig. 7.4**).

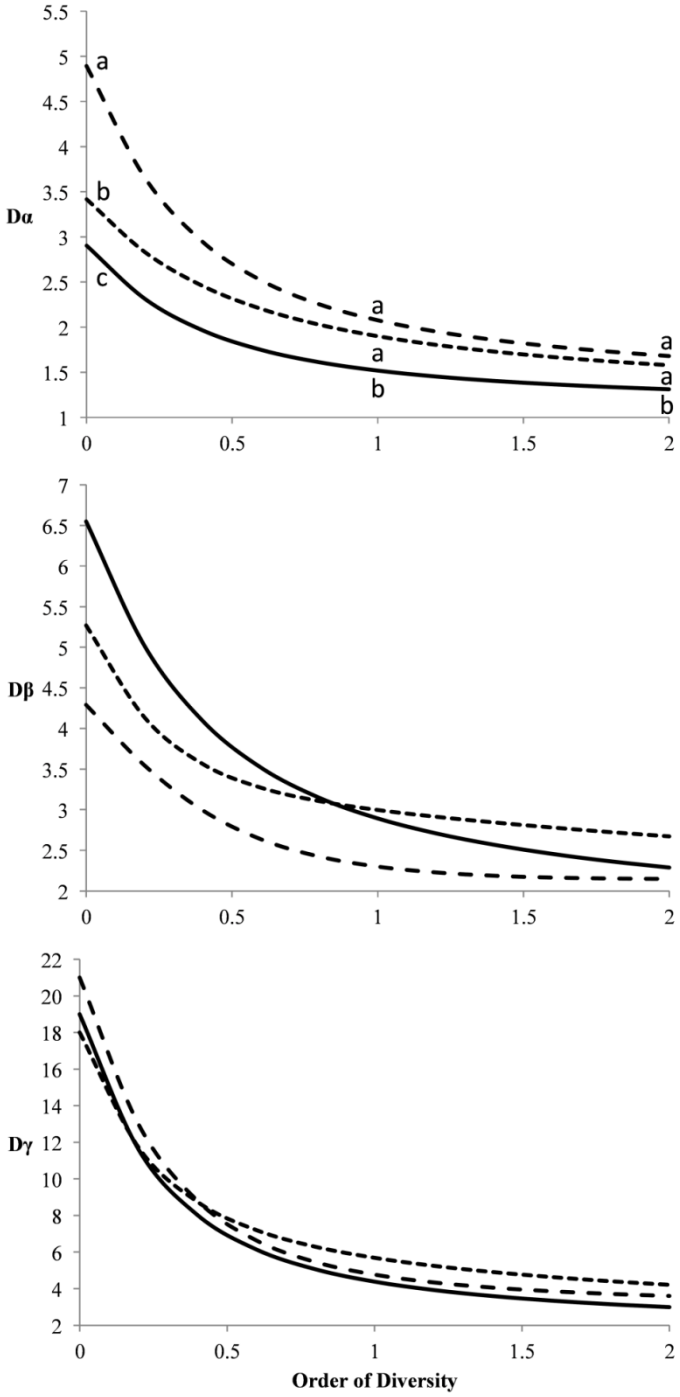

Figure 7.4 Profiles of alpha, beta and gamma diversity of the order q computed for the aquatic macroinvertebrate meta-communities of the low-level urbanization (solid lines), the moderate-level urbanization (long dashed lines) and the high-level urbanization (short dashed lines) sites. Small letters indicate a significant difference ($P < 0.01$) between sites for orders of diversity $q = 0$, 1 and 2.

During this 1-year-long experiment we sorted out 54,142 *Ae.* (*Stg.*) *aegypti* immature unequally distributed between the four types of water containers and the three urban sites

(**Tables 7.2, 7.3**). Regardless of the site, *Ae.* (*Stg.*) *aegypti* were always more abundant in artificial containers than in natural ones (**Table 7.3**).

Table 7.3 Descriptive statistic relative to *Aedes* (*Stegomyia*) *aegypti* between three levels of urbanization. The significant effect of the level of urbanization was tested using a one way ANOVA or Chi2 when proportions were tested. Exponential letters indicate pairwise significance between site at P < 0.05 (P adjusted for multiple comparisons).

	Low-level urbanization (N = 486)	**Moderate-level urbanization (N = 486)**	**High-level urbanization (N = 486)**	**P**
No. *Ae.* (*Stg.*) *aegypti*	**[a]2028**	**[b]31597**	**[c]20517**	**< 0.001**
Bromeliad (*N* = 405)	[a]2	[b]242	[b]396	< 0.001
Bamboo (*N* = 405)	[a]85	[b]2312	[c]1396	< 0.001
Ovitrap (*N* = 405)	[a]245	[b]4144	[c]2189	< 0.001
Tire (*N* = 243)	[a]1696	[b]24899	[b]16536	< 0.001
***Ae.* (*Stg.*) *aegypti* density (ind. L^{-1})**	**[a]6.75**	**[b]165.57**	**[b]137.02**	< 0.001
Bromeliad	[a]0.05	[b]10.89	[b]6.11	< 0.001
Bamboo	[a]2.25	[b]127.04	[c]75.1	< 0.001
Ovitrap	[a]11.54	[b]220.58	[b]224.48	< 0.001
Tire	[a]17.56	[b]378.86	[b]357.61	< 0.001
% of positive container*	**[a]18.32 (*N* = 393)**	**[b]73.61 (*N* = 360)**	**[b]74.64 (*N* = 347)**	< 0.001
Bromeliad	[a]1.67	[b]36.04	[c]52.10	< 0.001
Bamboo	[a]11.76	[b]89.16	[b]85.00	< 0.001
Ovitrap	[a]23.71	[b]85.26	[b]83.52	< 0.001
Tire	[a]47.30	[b]98.59	[c]92.98	< 0.001
% of co-occurrence with CompI	**[a]80.56 (*N* = 72)**	**[b]33.58 (*N* = 265)**	**[c]25.10 (*N* = 259)**	< 0.001
Bromeliad	50.00	55.00	75.81	NS
Bamboo	50.00	10.81	8.82	NA
Ovitrap	91.30	17.28	1.32	NA
Tire	[a]85.71	[b]64.29	[c]20.75	< 0.001
% of co-occurrence with CompII	**[a]77.78**	**[b]92.83**	**[a,b]87.26**	< 0.01
Bromeliad	100.00	100.00	96.77	NS
Bamboo	[a]100.00	[b]89.19	[a,b]85.29	< 0.05
Ovitrap	[a]60.87	[b]86.42	[b]80.26	< 0.01
Tire	[a]80.00	[b]100.00	[a]88.68	< 0.01
% of co-occurrence with Pred	**[a]5.56**	**[b]23.02**	**[a]1.93**	< 0.001
Bromeliad	0.00	32.50	1.61	NA
Bamboo	0.00	12.16	0.00	NA
Ovitrap	0.00	11.11	0.00	NA
Tire	[a]11.43	[b]42.86	[a]7.55	< 0.001

*Corresponds to the percentage of occurrence of *Ae.* (*Stg.*) *aegypti* without dry containers.

In the moderate- and high-level urbanization sites, *Aedes* (*Stg.*) *aegypti* was the most frequent and abundant taxon, while it was ranked fifth and sixth in terms of abundance and

occurrence, respectively, in the low-level urbanization site (**Tables 7.2, 7.3**). Also, its abundance, density and the percentage of containers positive to *Ae.* (*Stg.*) *aegypti* were significantly higher in the moderate- and high-level urbanization sites than in the low-level urbanization site, and overall their abundance was significantly higher in the moderate-level urbanization site (**Table 7.3**). Finally, the abundance of *Ae.* (*Stg.*) *aegypti* and other culicids all year round showed seasonal peaks (**Appendix 6**).

The percentages of co-occurrence of *Ae.* (*Stg.*) *aegypti* with other mosquito species were significantly different between sites and decreased with greater levels of urbanization ranging from 80.66 % in the low-level urbanization site, to 33.58 % and 25.10 % in the moderate- and high-level urbanization sites, respectively (**Table 7.3**). *Aedes* (*Stg.*) *aegypti* also co-occurred with secondary competitors and predators, and, in both cases, the highest percentages were found in the moderate-urbanization site (**Table 7.3**). In addition, regardless of the site, the percentage of co-occurrence of *Ae.* (*Stg.*) *aegypti* with competitors and predators was higher in water-filled tires compared to the other containers (**Table 7.3**).

Models with climatic predictors calculated at one or two week intervals yielded similar results. Because the former always had the lowest AIC values, only models with climatic predictors calculated at a one week interval are presented (**Fig. 7.5**). The multimodel inference reveals that the type of container (TWC) is an important predictor of the larval abundance of *Ae.* (*Stg.*) *aegypti* whatever the sites considered (**Fig. 7.5a, b, c**). Moreover, for the moderate- and high-level urbanization sites the size of the aquatic habitat (WV; $w+(j) = 0.80$ and $w+(j) = 1$, respectively) and the amount of precipitation (Prm7; $w+(j) = 0.99$ and $w+(j) = 0.89$, respectively) was important, both positively influencing the larval abundance of *Ae.* (*Stg.*) *aegypti*. On the contrary, for both sites, predators negatively influenced the larval abundance of *Ae.* (*Stg.*) *aegypti* with a relative importance of 0.94 and 0.81, respectively (**Fig. 7.5b, c**). In addition, for the low-level urbanization site the pH and the abundance of secondary competitors (CompII) were also important (both $w+(j) = 0.79$) and positively influenced the abundance of *Ae.* (*Stg.*) *aegypti* immatures. For the low-level urbanization site, the relative importance of temperature and humidity were high ($w+(j) = 1$ and $w+(j) = 0.99$, respectively) and positively influenced the abundance of *Ae.* (*Stg.*) *aegypti* immature (**Fig. 7.5a**). Furthermore, the abundance of primary competitors was also detected as an important predictor (CompI; $w+(j) = 0.87$) for this site and showed a negative influence on the abundance of *Ae.* (*Stg.*) *aegypti* immatures (**Fig. 7.5a**).

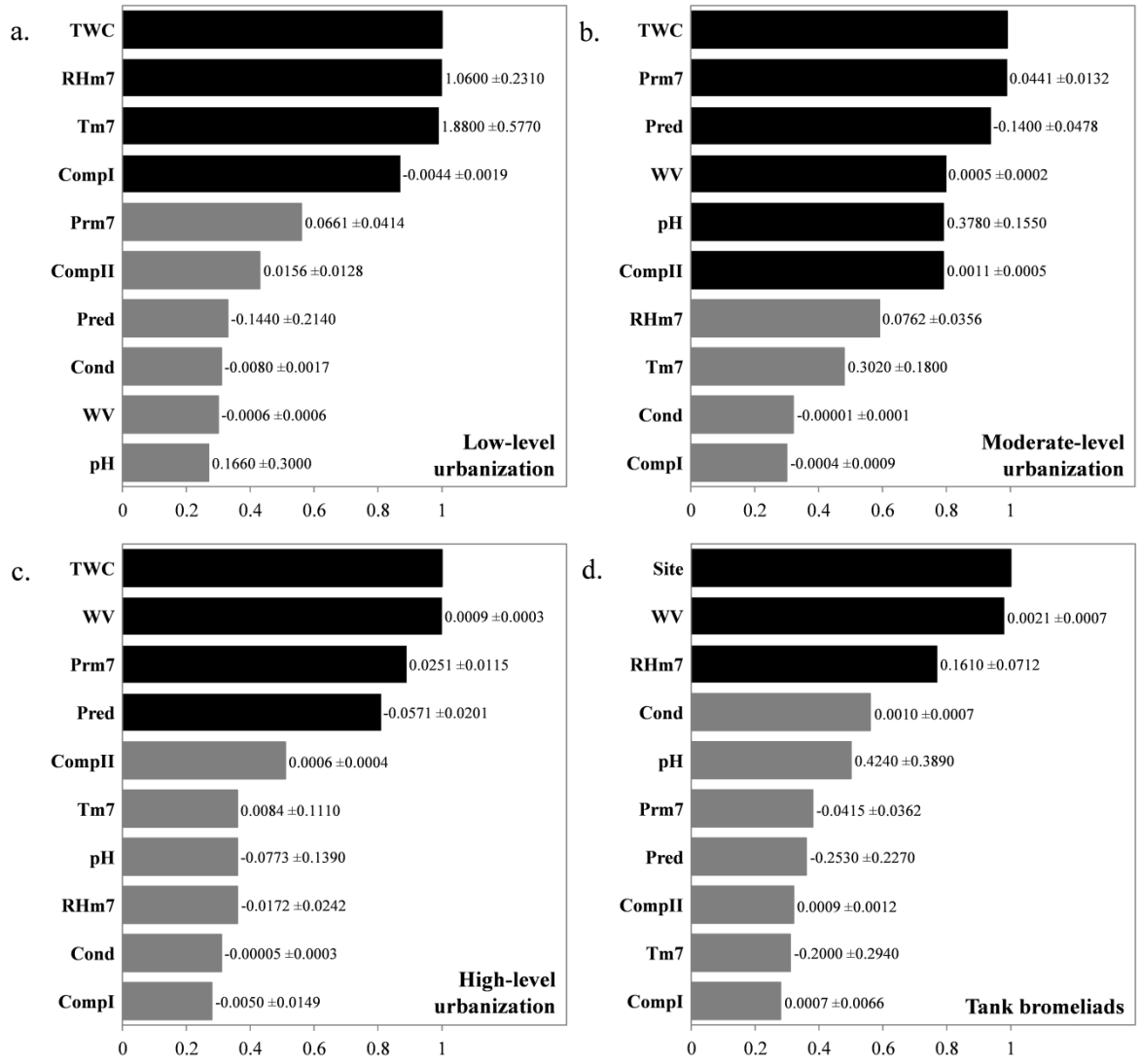

Figure 7.5 Relative importance of each variable explaining *Aedes* (*Stegomyia*) *aegypti* larval abundance in the low-level urbanization (a.), the moderate-level urbanization (b.) and the high-level urbanization (c.) sites, and presence in tank bromeliads at those sites (d.). Variables are ranked in increasing order of the sum of their Akaike weights, which are the probabilities that the given variable will appear in the best fitting model (lowest AIC value). Black bars indicate variables with a probability higher than 0.7 of appearing in the best-fitting model. Estimated parameter values and their SE for each variable are given to the right of each bar.

The presence of *Ae.* (*Stg.*) *aegypti* in tank bromeliads was influenced by the level of urbanization (Site; $w+(j) = 1$) and positively influenced by the size of the aquatic habitat (WV; $w+(j) = 0.98$) and the percentage of relative humidity (RHm7; $w+(j) = 0.77$) (**Fig. 7.5d**). All the other predictors had a low relative importance and are assumed to have a slight or no effect.

DISCUSSION

The microclimatic characteristics of our experimental sites were in line with our expectations because average temperatures were higher with greater levels of urbanization while average relative humidity was lower. Nevertheless, contrary to our first hypothesis, the alpha diversity was not lower with greater levels of urbanization but instead reached a peak at the moderate-level of urbanization site and, surprisingly, the low-level urbanization site showed the lowest level of diversity whatever the order of diversity considered. These results fit well with the intermediate disturbance hypothesis assuming that the highest level of diversity is maintained at intermediate scales of disturbance (**Connell 1978**). Another possible explanation might be related to a greater productivity in these sites due to higher average temperature, consequently allowing them to sustain a greater diversity (**Chase & Leibold 2002**). In parallel, *Ae.* (*Stg.*) *aegypti* dominated the two most urbanized sites, being the most frequent and abundant taxon, reflecting other studies conducted on this species worldwide (**Christophers 1960**) and confirming its domestic and invasive status in French Guiana (**Juliano & Lounibos 2005**). The percentage of containers with *Ae.* (*Stg.*) *aegypti* was higher with greater levels of urbanization, but, interestingly, their abundance and density reached a peak at the intermediate level of urbanization similarly to the alpha diversity.

In the low-level urbanization site interactions with other culicid species were detrimental to *Ae.* (*Stg.*) *aegypti* larval populations. This negative impact, which is in accordance with our predictions, can be attributed to the dominant native mosquito species in the area: *Limatus durhamii* Theobald 1901 (**Appendix 6**). This result confirms the observations and assumptions made by **Honório *et al.*** (**2006**) from a larval survey conducted in Rio de Janeiro, Brazil. Also, the low-level urbanization site is the only location where *Ae.* (*Stg.*) *aegypti* was not found all year long (**Appendix 6**). *Limatus durhamii* likely prevents the long-term establishment of *Ae.* (*Stg.*) *aegypti*, suggesting a mechanism of competitive exclusion (but see also **Chapter 8**). Because the abundance of *Ae.* (*Stg.*) *aegypti* in this site is aided by higher temperature and relative humidity; it can be supposed that its presence is also permitted by suitable climatic conditions. In the moderate- and high-level urbanization sites, the abundance of *Ae.* (*Stg.*) *aegypti* was negatively impacted when it co-occurred with the native predator mosquito species *Tx.* (*Lyn.*) *haemorrhoidalis*, a potential biocontrol agent of container-breeding mosquitoes (**Collins & Blackwell 2000**) and predator chironomid species of the subfamily Tanypodinae. These two species definitely play a role in the lower abundance of *Ae.* (*Stg.*) *aegypti* at the scale of the community; however, their relative low

occurrence at the scale of the meta-community likely reduces their impact on the overall population dynamics of this vector. On the contrary, the presence of *Ae.* (*Stg.*) *aegypti* might favor these predator species by providing abundant prey all year long. All interactions with native communities negatively impacting *Ae.* (*Stg.*) *aegypti* populations can be assimilated to a form of ecosystem services (**Millennium Ecosystem Assessment 2005**).

Furthermore, we provide evidence from the moderate-level urbanization site that the co-occurrence of *Ae.* (*Stg.*) *aegypti* with controphic species that do not share the same feeding mode (secondary competitors) enhanced the former species. Two non-mutually exclusive hypotheses can be put forward to explain this phenomenon. First, the presence of secondary competitors might reduce the predation pressure exerted on *Ae.* (*Stg.*) *aegypti* immatures by higher tropic levels, a mechanism known as an apparent mutualism (**Blaustein & Chase 2007**). Second, the presence of these secondary competitors might allow a greater amount of available food resources *via* processing chain (**Heard 1994**). Indeed, by processing coarse particulate organic matter, secondary competitors increase the amount of fine particulate organic matter (e.g. feces and/or uningested matter) beneficial to filtering mosquito larvae (**Daugherty & Juliano 2003**). This processing chain commensalism might be one of the mechanisms explaining why the more diverse communities also have the highest abundance and density of *Ae.* (*Stg.*) *aegypti* (**Juliano 2009**). Chironomids were the most frequent and abundant secondary competitor that we found in this moderate-level urbanization site, and they likely play an important role in the positive impact of secondary competitors on the abundance of *Ae.* (*Stg.*) *aegypti*. The co-occurrence of *Ae.* (*Stg.*) *aegypti* with non-culicid species has rarely been reported (but see **Chen *et al.* 2006; Martínez *et al.* 2012**). Nonetheless, it is difficult to know if this is due to the real absence of these taxa or to the fact that these taxa are simply overlooked. Yet, our observations indicate that these interactions are common in urban environments and they could potentially have important consequences on the production of vector species. This is particularly true in water-filled tires that appeared to be far more productive for *Ae.* (*Stg.*) *aegypti* than were natural containers (see also **Yee 2008**) and at the same time were a frequently used habitat for many culicids and non-culicid species (this study).

On the contrary, tank bromeliads sheltered structurally distinct communities and represented the least productive container habitat for *Ae.* (*Stg.*) *aegypti* compared to the other containers. This result is in accordance with other studies conducted in Brazil which concluded the marginal role of native tank bromeliads in the production of this vector (e.g. **Maciel-de-Freitas *et al.* 2007**). Yet, because tank bromeliads can be abundant in Neotropical

cities, it is still important to understand their role in the population dynamics of *Ae.* (*Stg.*) *aegypti.* In Florida, interactions with native *Wyeomyia* species have shown to restrict the distribution of *Ae.* (*Stg.*) *albopictus* in tank bromeliads (**Lounibos *et al.* 2003**). In French Guiana, it has been hypothesized that interactions with native mosquitoes can also explain the presence of *Ae.* (*Stg.*) *aegypti* in this phytotelmata (**Chapter 5**). In the present study, our results indicate that interactions with native fauna do not play an important role in explaining the presence of *Ae.* (*Stg.*) *aegypti* in tank bromeliads. Yet, their presence is positively influenced by the level of urbanization, a phenomenon also reported in Brazil (**Cunha *et al.* 2002**). In addition, the volume of water held by the plant and the relative humidity favored the presence of *Ae.* (*Stg.*) *aegypti*.

In summary, in natural conditions *Ae.* (*Stg.*) *aegypti* immatures are subjected to multiple biotic and abiotic environmental conditions varying in their relative importance between containers and along an urbanization gradient. We have shown that artificial water containers in the moderate-level urbanization site can ensure some optimal *Ae.* (*Stg.*) *aegypti* larval development. We also demonstrate that the presence of culicid and non-culicid aquatic organisms can have antagonistic effects (e.g. competition, predation) on *Ae.* (*Stg.*) *aegypti* larval populations showing that biotic interactions need to be better examined in future studies. Overall, these data can be used to produce a regional prioritization of site and container types for larval-vector control strategies.

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Chapitre 8: Larval interference with a native Neotropical mosquito species increases *Aedes* (*Stegomyia*) *aegypti*'s fitness (Talaga *et al.*, soumis à *Journal of Medical Entomology*)

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Abstract: Interspecific competition with native species plays a major role during biological invasions and can sometimes limit alien expansion. We aimed to determine the potential ecological effects of *Limatus durhamii* Theobald 1901, a native Neotropical mosquito (Diptera: Culicidae) species on the invasive species *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) that breeds in the same artificial water containers. Development time and adult dry mass were measured in three rearing conditions: control (a single larva), intraspecific competition (two conspecific larvae), and interspecific competition (two heterospecific larvae). Food was provided *ad libitum* to eliminate exploitative competition. For *Ae.* (*Stg.*) *aegypti*, development time was not affected by interspecific interference competition and the adult dry mass was higher, meaning that individual fitness likely increased. Nevertheless, previous studies showed longer development time and lighter adults during competition with other invasive mosquitoes. These results indicate that this species can express a different phenotype depending on the competing species. A similar pattern was found for *Li. durhamii* females, explaining in part why this species can compete with *Ae.* (*Stg.*) *aegypti*.

Keywords: Aedes, Culicidae, Interference competition, Limatus, Phenotypic plasticity.

INTRODUCTION

Biological invasions, which are on the rise due to the unprecedented explosion in human transport worldwide, can be described as a graded phenomenon consisting of the introduction, establishment and spread of species outside their native range. The success of invasive species in their introduced range depends on several factors, including the species' characteristics as well as the abiotic (e.g. temperatures, chemical properties) and biotic (e.g. predation, competition) conditions and their interaction (**Lockwood *et al.* 2013**). In some cases, the introduced species may be a superior competitor causing the displacement and sometimes the extinction of native populations. In other cases, however, the expansion of introduced species can be contained by biotic interactions with native pathogens, predators and, particularly, competitors (**Lockwood *et al.* 2013**).

Competition between species may be considered exploitative when one species depletes a resource (generally food) which then is not available for the other, while in interference competition agonistic behavioral interactions occur (**Blaustein & Chase 2007**). For instance, competition can affect survival and performance in mosquito larvae (Diptera: Culicidae) within an aquatic habitat and therefore influence which species will emerge as adults from a given habitat. Understanding the outcome of such competitive interactions is crucial, especially when we consider vector species of human diseases (**Alto *et al.* 2008**).

The aquatic conditions in which the larvae develop have an important impact on the fitness of the adults produced. Indeed, in mosquitoes of the genus *Aedes*, the dry mass of adults, a proxy of their body size, is related to their alimentation during larval life that has consequences for their survival and fecundity (**Ponlawat & Harrington 2007**). For instance, during intraspecific competition, the development time necessary for female *Aedes* (*Stegomyia*) *aegypti* (Linnaeus 1762) larvae is longer than for males, whereas adult males have lower dry masses, shorter wing length and less longevity (**Bedhomme *et al.* 2003**; **Couret *et al.* 2014**). When in interspecific competition with *Aedes* (*Stegomyia*) *albopictus* (Skuse 1894), the development time of *Ae.* (*Stg.*) *aegypti* larvae is longer and the adult dry mass is lower (**Daugherty *et al.* 2000; Lounibos *et al.* 2002; Murrell & Juliano 2008**).

The mosquito *Ae.* (*Stg.*) *aegypti* has been introduced into numerous regions worldwide where it then spread and potentially transmitted several viruses, including chikungunya, dengue, yellow fever and zika. In the Neotropics, its presence overlaps with that of the native mosquito *Limatus durhamii* Theobald 1901 that extends from Mexico to northern Argentina (**Harbach 2015**). Also, larval populations of *Li. durhamii* have been observed to outcompete

those of *Ae.* (*Stg.*) *aegypti* in artificial water containers in Brazil (**Honório *et al.* 2006**). In French Guiana, we observed that seasonal peaks in populations of *Li. durhamii* were correlated with the disappearance of *Ae.* (*Stg.*) *aegypti* larvae, suggesting the competitive displacement of the latter species (**Chapter 7**).

We therefore hypothesized that *Li. durhamii* larvae can be good competitors *vis-à-vis* those of *Ae.* (*Stg.*) *aegypti*. To test this hypothesis, we conducted laboratory competition experiments wherein we measured the larval development time and dry mass, both known to be related to fitness in mosquitoes, of the adults produced in the absence of competition and in situations of both intra- and interspecific competition. Food was provided *ad libitum* to eliminate potential exploitative competition in order to study the effects of interference competition between the two species.

MATERIALS AND METHODS

This study was conducted between January and June 2015 in the laboratory on the *Campus Agronomique* in Kourou, French Guiana. We used *Ae.* (*Stg.*) *aegypti* eggs from a strain sampled from tires left for this purpose in a remnant forest patch on the grounds of the *Campus Agronomique* and bred in the Unit of Medical Entomology at the *Institut Pasteur* of Cayenne, French Guiana. Thanks to their resistance to desiccation, these eggs can be dry stored to be used each time larvae are necessary. First instar *Li. durhamii* larvae were gathered from the same breeding site of *Ae.* (*Stg.*) *aegypti* on the *Campus Agronomique*. We followed an optimal food regime set up for *Ae.* (*Stg.*) *aegypti* consisting of flake fish food (Tetra®) which was diluted in mineral water at a concentration of 20 mg/ml to facilitate its distribution: 0.08 mg the first day, 0.16 mg the second day, 0.32 mg the third day and 0.64 mg per larva from then on (**Bedhomme *et al.* 2003**). This procedure was possible for a small number of individuals per treatment, and so enabled us to conduct numerous replicates. On the first day of the experiment, 24-h old *Ae.* (*Stg.*) *aegypti* larvae and wild-collected first instar *Li. durhamii* larvae were transferred into 40 ml tubes containing 5 ml of mineral water (Volvic®) at 28°C. We set up an experimental protocol with two control lots (one *Ae.* (*Stg.*) *aegypti* or one *Li. durhamii* larva per tube), two intraspecific competition treatments (two conspecific larvae per tube) and one interspecific competition treatment (one larva from each species per tube).

The tubes were inserted into 24-place test tube racks; we randomized their position to avoid the edge effect related to luminosity (i.e. the tubes situated along the sides were exposed

to slightly more light than those situated at the center). The racks were then put into a climatic chamber (VB 0714, Bio Line, Vötsch Industrietechnik, Germany) where typical climatic conditions from French Guiana were reproduced (12h:12h photoperiod; 28°C diurnally and 26°C nightly). This temperature range should not alter, according to **Lounibos *et al.*** (**2002**), the outcome of larval competition.

During the experiment, the tubes were controlled twice daily to note the mortality and the period of nymphosis. Pupae were isolated in 5 ml tubes containing 3 ml of mineral water and returned to the climatic chamber where they were again controlled twice daily to note the emergence of the adults. After emergence, the adults were transferred to dry tubes which were placed into a freezer. These freeze-killed adults were then put into a drying oven at 60°C during 48h. Dried adults were weighed to an accuracy of 1 µg using a microbalance (MX5, Mettler Toledo, Switzerland). The sex of the individuals was determined from the following adult morphological criteria. *Aedes* (*Stg.*) *aegypti* males have many antennal flagella and *Li. durhamii* males have a curved proboscis covered with blue scales on the ventral surface.

The mortality rate after the first few days of experimentation was too low and biased for *Li. durhamii* (because the larvae were collected in the field) to conduct any statistical analyses on the impact of competition. Thus, the development time (prior to emergence) and the dry mass of the adults, a proxy of body size, were used to test intra- and interspecific competition for the two sexes. Statistical analyses were conducted only when no larvae died. For *Ae.* (*Stg.*) *aegypti*, this resulted in 36 cases (20 males and 16 females) for the control lots, 62 cases (32 males and 30 females) for intraspecific competition and 57 cases (32 males and 25 females) for interspecific competition, while for *Li. durhamii* this resulted in 20 cases (8 males and 12 females) for the control lots, 26 cases (11 males and 15 females) for intraspecific competition and 32 cases (17 males and 14 females) for interspecific competition. For interspecific competition, the number of adults obtained differed from one species to the other because some of the isolated *Li. durhamii* pupae died, whereas their *Ae.* (*Stg.*) *aegypti* counterparts became adults. Because the tested variables met the assumptions of normality and homoscedasticity, a two-way ANOVA with a Tukey's *post-hoc* multiple comparisons test was conducted for *Ae.* (*Stg.*) *aegypti*. Because the number of adult control *Li. durhamii* females was low, pairwise exact non-parametric tests were conducted; corrections for simultaneous comparisons were made using the false discovery rate adjustment, BH correction (**Pike 2011**). The statistical analyses were conducted in R (R software; **R Development Core Team**) and the associated 'stats' package and evaluated under a 95 % confidence level. The results are presented as means ±SE throughout.

RESULTS AND DISCUSSION

In the absence of competition, *Ae.* (*Stg.*) *aegypti* males emerge *ca*. 11 hours earlier than do females (8.15 ±0.14 days and 8.60 ±0.17 days, respectively; **Fig. 8.1a**) which is in the same range of other studies (see **Bedhomme *et al.* 2003**). This sexual bimaturism is accompanied by sexual dimorphism wherein males are smaller than females (367.33 ±9.22 µg for males; 568.93 ±19.04 µg for females; **Fig. 8.1c**). These intersexual differences in development time and adult body mass were also observed in other studies (see **Bedhomme *et al.* 2003; Wormington & Juliano 2014**). Sexual bimaturism is selected when the early maturation of males is advantageous, when there is first-male sperm precedence, when the first emerging females are more fecund, or, as for *Ae. (Stg.) aegypti*, when females mate only once (**Morbey & Ydenberg 2001**). Although we did not record sexual bimaturism in *Li. durhamii* (**Fig. 8.1b**), we did note the existence of sexual dimorphism (260.83 ±12.99 µg for males; 386.75 ±21.90 µg for females; **Fig. 8.1d**).

In optimal food and temperature conditions, intra- and interspecific interference competition did not significantly modify the development time for either sex of either species compared to the control lots (**Fig. 8.1a, b**). Yet, other experimental studies showed that intraspecific competition delayed the period of emergence in *Ae. (Stg.) aegypti* (**Bedhomme *et al.* 2003; Couret *et al.* 2014**), while interspecific competition between the latter species and *Ae*. (*Stg*.) *albopictus* resulted in a longer development time (**Daugherty *et al.* 2000; Lounibos *et al.* 2002; Murrell & Juliano 2008**). For *Li. durhamii*, this can be at least partially due to the possible differences in age of the first instar larvae gathered from the field at the beginning of the experiments.

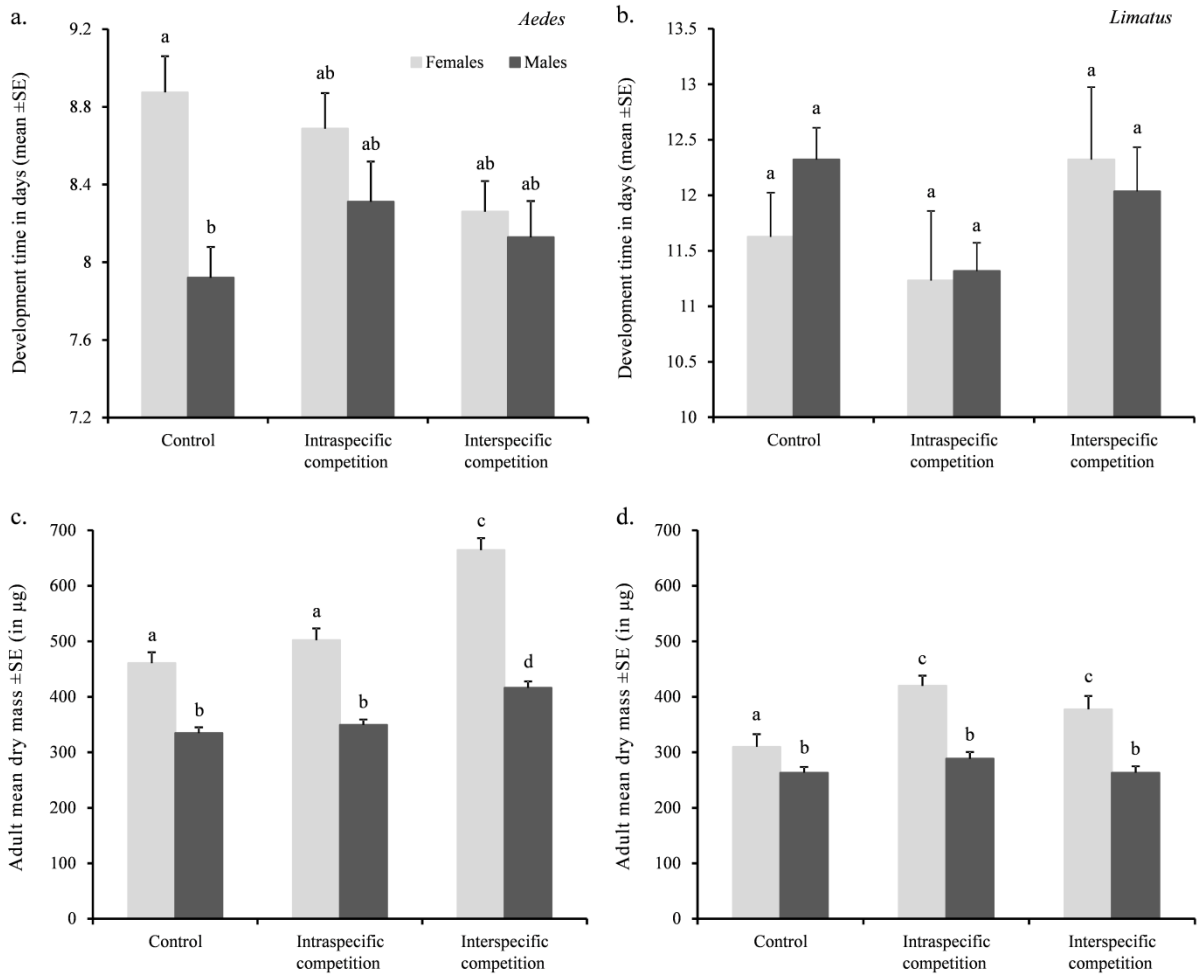

Figure 8.1 Impact of larval interference competition (control, intra- and interspecific competition) on (a. and b.) the development time (in days) and (c. and d.) the adult mean dry mass (in µg) of *Aedes* (*Stegomyia*) *aegypti* and *Limatus durhamii* larvae. Statistical comparisons; for *Ae.* (*Stg.*) *aegypti*, two-way ANOVAs and Tukey's *post-hoc* test; for *Li. durhamii*, pairwise exact non-parametric tests and false discovery rate adjustement (BH correction). Different letters indicate significant differences at $P < 0.01$.

Concerning the dry body mass, intraspecific larval interference competition involving *Ae.* (*Stg.*) *aegypti* resulted in non-significant differences with the control lots for both the male and female adults produced (**Fig. 8.1c**), confirming that food was not a limiting factor for either sex of this species. Yet, during experiments conducted at a feeble density, the *Ae.* (*Stg.*) *aegypti* adults produced were lighter than were control individuals (**Bedhomme *et al.* 2003; Couret *et al.* 2014**). One can deduce that the number of individuals involved in intraspecific competition plays a role as do limited food conditions.

On the contrary, as concerns interspecific larval interference competition with *Li. durhamii*, *Ae.* (*Stg.*) *aegypti* adult dry masses were significantly higher than were those of control individuals (significant differences corresponding to an augmentation of 81.14 ±12.91 µg for males and 241.31 ±21.83 µg for females; **Fig. 8.1c**). Because larger body size is related to fecundity and survival in *Ae.* (*Stg.*) *aegypti* females (**Bedhomme *et al.* 2003**), those involved in competition with *Li. durhamii* likely have better fitness. The same is true for males for which body size is related to survival and spermatozoid quality (**Ponlawat & Harrington 2007**). For *Li. durhamii*, the female dry masses were significantly higher compared to those of the control lots for both intra- and interspecific larval interference competition, but this was not the case for the males whose dry mass did not vary significantly regardless of the situation (**Fig. 8.1d**). In any case, the males were not lighter than when a mosquito species is confronted with a superior competitor (**Daugherty *et al.* 2000; Murrell & Juliano 2008**).

We show in this study that, under controlled experimental conditions, interspecific larval interference competition enhances the fitness of both interacting species. First, these results indicate that native *Li. durhamii* larvae can be potentially good competitors *vis-à-vis Ae. (Stg.) aegypti* larvae of a similar size. Second, when in interference competition, individuals of these two species react by increasing their mass (or, at the very least, *Li. durhamii* males were not lighter) by increasing their rate of filtration that might be stimulated by interspecific chemical interference, something needing to be demonstrated in further studies. In this situation, small changes in abiotic conditions will favor one or the other species, explaining the observed seasonal dominance of *Li. durhamii* over *Ae.* (*Stg.*) *aegypti* larvae in water containers (**Chapter 7; Honório *et al.* 2006**) which triggered this study. Third, we also point out that larval interference with a native mosquito species increases *Ae.* (*Stg.*) *aegypti*'s fitness through higher adult masses.

This result was unexpected because an inverse relationship between larval density and adult body size was reported in numerous studies where the competitor species was *Ae.* (*Stg.*) *albopictus*, another invasive vector species (**Daugherty *et al.* 2000; Lounibos *et al.* 2002; Murrell & Juliano 2008**). Such differences in adult body sizes depending on the larval competitor likely result from phenotypic plasticity which is related to the species' genotype (see also **Bedhomme *et al.* 2003**). Phenotypic plasticity does not obligatorily provide an advantage to a given species. When it does (as in a case of adaptive plasticity), the reactions

of the benefiting species are tailored to the abiotic and/or biotic conditions, but we lack enough information to assert that this is the case for *Ae*. (*Stg*.) *aegypti*.

Yet, in mosquitoes another factor, vector competence, is of importance because it can be influenced by plastic responses in life history traits induced by larval competition (**Alto *et al*. 2008**). Indeed, according to the competitive-susceptibility hypothesis, vector competence is inversely correlated to body size: small females develop and transmit viruses more readily than do large ones (**Juliano *et al*. 2014**). Because in the present study *Ae*. (*Stg*.) *aegypti* adult females are larger after larval interference competition with *Li. durhamii*, this interaction might reduce *Ae*. (*Stg*.) *aegypti*'s susceptibility to viral infection. On the other hand, according to the longevity-susceptibility hypothesis, this interaction might increase their longevity and indirectly increase their capacity to transmit viruses (**Juliano *et al*. 2014**). Nevertheless, because in this study we had optimal food and temperature conditions for *Ae*. (*Stg*.) *aegypti* but (possibly) not for *Li. durhamii*, further experiments with different food conditions (i.e. quality and/or quantity) would be helpful in better understanding the outcomes of such competitive interaction.

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DISCUSSION

L'humanité est en train de transformer les paysages de la planète à une échelle et à des taux encore inégalés (**McKinney 2002**). Les paysages sont altérés par l'urbanisation, l'extraction des ressources, la pratique de l'agriculture et le développement des industries. Les invasions biologiques sont l'une des conséquences – le plus souvent accidentelles - de ces altérations qui impactent l'ensemble des écosystèmes sur Terre (**Vitousek *et al.* 1997**). Lorsque les espèces introduites sont vectrices de pathogènes chez l'Homme, leur expansion peut devenir un enjeu majeur pour la santé publique et le développement économique (**Gubler 1998**).

Nos travaux ont analysé les interactions biologiques qu'entretient *Ae.* (*Stg.*) *aegypti* avec les communautés résidentes et plus précisément avec les moustiques autochtones. Malgré une diversité taxonomique très importante en Guyane, l'impact de ces interactions apparait relativement limité dans l'espace et dans le temps. Dans les paragraphes suivants, une synthèse de nos différents résultats est présentée et une hiérarchisation des processus écologiques et évolutifs pouvant expliquer ce phénomène est proposée.

I Homogénéisation biotique et urbanisation

La tendance avec laquelle en milieu urbain un petit nombre d'espèces remplace un grand nombre d'espèces se répète dans de nombreuses régions du monde est connue sous le terme d'homogénéisation biotique (**McKinney & Lockwood 1999**). La formation de communautés uniformes en milieu urbain est causée par la transformation des paysages en milieux urbains et par la création de structures écologiques similaires dans ces différentes régions (**Kark *et al.* 2007**). Ce phénomène est dû au remplacement des espèces autochtones, souvent mal adaptées (*urban avoiders*), par un cortège d'espèces pré-adaptées composé d'*urban adapters* et d'*urban exploiters* (**Blair 2001**). Les *urban exploiters* profitent de la libération de la niche engendrée par l'anachronisme évolutif dont la plupart des *urban avoiders* sont victimes. En Guyane, seuls les moustiques *Ae.* (*Stg.*) *aegypti* et *Cx.* (*Cux.*) *quinquefasciatus* peuvent être rangés dans cette catégorie d'*urban exploiters*. Si nous excluons les espèces de passage qui ne se trouvent qu'au stade adulte en milieu urbain, la plupart des espèces de moustiques autochtones en Guyane peuvent être classées dans la catégorie des *urban avoiders*. En effet, sur les 108 espèces de moustique des réservoirs sur le

territoire (**Appendix 2**), seulement une douzaine d'espèces ont été retrouvées au stade larvaire en milieu urbain (**Chapitre 7**).

Les *urban adapters* sont plus rares et correspondent aux espèces capables de s'adapter aux conditions environnementales imposées par les milieux urbains et périurbains. La majorité d'entre elles partagent une caractéristique commune, celle de pouvoir utiliser les réservoirs artificiels comme type d'habitat aquatique. Dans cette catégorie, nous pouvons citer : *Culex* (*Car.*) *bonnei*, *Culex* (*Cux.*) *mollis*, *Limatus durhamii*, *Toxorhynchites* (*Lyn.*) *haemorrhoidalis*, *Trichoprosopon digitatum* et *Wyeomyia* (*Triamyia*) *aporonoma* que nous avons retrouvés dans des pneus dans la ville de Kourou (**Chapitre 7**). En dehors des villes, d'autres espèces ont également été collectées dans divers réservoirs artificiels. Parmi elles nous pouvons citer : *Aedes* (*Gec.*) *fluviatilis*, *Culex* (*Car.*) *infoliatus*, *Culex* (*Car.*) *urichii*, *Culex* (*Cux.*) *coronator*, *Lutzia* (*Lut.*) *allostigma* et *Limatus flavisetosus* (**Chapitre 3**). Pour être exhaustifs, il faut également ajouter *Culex* (*Cux.*) *bonneae*, *Culex* (*Cux.*) *declarator*, *Culex* (*Cux.*) *surinamensis*, *Culex* (*Phc.*) *corniger* et quelques espèces de *Culex* du sous-genre *Melanoconion* qui ont été collectées dans divers réservoirs artificiels par **Floch et Abonnenc** (**1947b**). Ces dernières espèces, suffisamment généralistes pour utiliser des réservoirs artificiels, peuvent être considérées comme de potentiels *urban adapters*.

Par ailleurs, certaines espèces endémiques des phytotelmes ont également été retrouvées en milieu urbain. C'est le cas de *Culex* (*Mcx.*) *pleuristriatus* et de *Wyeomyia* (*Wyo.*) *pertinans* que nous avons retrouvés dans les *A. aquilega* dans les villes de Kourou et de Sinnamary (**Chapitres 5-7**). Il est intéressant de noter que ces deux espèces présentent une certaine plasticité dans l'utilisation des différents types de phytotelmes utilisés. En effet, nous avons pu retrouver *Culex* (*Mcx.*) *pleuristriatus* dans pas moins de quatre types de phytotelmes différents : les bractées d'*Heliconia bihai*, différentes espèces de broméliacées à réservoir, les entrenœuds de *Bambusa vulgaris*, et à la base des palmes de palmiers-bâche (i.e. *Mauritia flexuosa*). On notera que *Wy.* (*Wyo.*) *pertinans* a été retrouvé dans différentes espèces de broméliacées à réservoir, les entrenœuds de bambous et à la base des palmes de palmiers-bâches, et ce depuis le niveau de la mer jusqu'aux plus hauts sommets de Guyane (e.g. Mont Itoupé et Mont Galbao). Cette stratégie généraliste vis-à-vis de l'utilisation de ces différents types de phytotelmes pourrait être un avantage en milieu urbain où la densité de phytotelmes est souvent plus faible et leur distribution plus fragmentée.

Malgré le nombre restreint de villes que nous avons pu étudier durant cette thèse, il est intéressant de noter que les assemblages de Culicidae que nous avons observés dans les

réservoirs artificiels présentent de nombreuses similarités avec ceux rapportés pour d'autres villes Néotropicales. Du Nord vers le Sud, nous pouvons citer les études réalisées au Mexique (**Baak-Baak *et al.* 2014**), au Costa Rica (**Calderón-Arguedas *et al.* 2004, 2009**), en Colombie (**Olano & Tinke 1993; Carvajal *et al.* 2009**), au Brésil à Manaus (**Fé *et al.* 2003; Barbosa *et al.* 2009**) et à Rio de Janeiro (**Honório & Lourenço-de-Oliveira 2001; Lourenço-de-Oliveira *et al.* 2004; Honório *et al.* 2006**) et en Argentine (**Lestani *et al.* 2002**).

Les conséquences de l'urbanisation étant analogues à toutes les latitudes, ce filtre environnemental sélectionne de la même manière les différentes espèces. À l'instar d'autres groupes taxonomiques tels que les oiseaux ou les papillons (**Blair 2001**), l'urbanisation semble également provoquer une homogénéisation des assemblages de Culicidae sous les Néotropiques. Compte tenu du fort pouvoir prédictif de ce phénomène à large échelle, cette question mériterait une révision bibliographique complète et des analyses plus poussées.

II Influence de l'urbanisation sur *Aedes* (*Stegomyia*) *aegypti*

Contrairement aux communautés autochtones qui sont globalement négativement influencées par le processus d'urbanisation, *Ae.* (*Stg.*) *aegypti* est au contraire fortement associé à ces milieux perturbés. Il est indéniable que la présence de l'Homme conditionne la présence d'*Ae.* (*Stg.*) *aegypti* à tel point que cette espèce peut être considérée comme un commensal ou un parasite de l'Homme selon les cas (**Brown *et al.* 2014**). Ce lien étroit peut être perçu comme une forme de spécialisation et est vraisemblablement l'héritage de la domestication de cette espèce qui a débuté il y a plusieurs milliers d'années (**Powell & Tabachnick 2013**). Nos observations en Guyane entre 2013 et 2015 ne contredisent pas ce fait établi, notamment nous n'avons pas trouvé d'immatures d'*Ae.* (*Stg.*) *aegypti* à plus de 150 mètres de l'habitation la plus proche, ce qui est en accord avec des observations faites à Rio de Janeiro au Brésil (**Lourenço-de-Oliveira *et al.* 2004**).

Toutefois, des populations ayant effectué un retour à l'état sauvage, dites férales, et se développant dans des dépressions rocheuses ont été notées dans plusieurs îles des caraïbes (**Weinbren & O'Gower 1966; Parker *et al.* 1983**) et au Brésil (**Forattini 1965**). À Anguilla les populations férales ont montré des caractéristiques morphologiques et génétiques différentes de la souche domestique (**Wallis & Tabachnick 1990; Verna & Munstermann 2011**). En Guyane, des larves et des nymphes d'*Ae.* (*Stg.*) *aegypti* ont été collectées lors d'une mission sur le lac de Petit-Saut (Sinnamary) dans des broméliacées épiphytes poussant sur les

arbres de la forêt inondée en amont du barrage (**Fouque & Carinci 1996**). Le caractère unique de ce signalement, ainsi que l'absence de spécimens de références, rendent ces prélèvements particulièrement douteux. L'un des auteurs de cette étude n'exclut pas que ces prélèvements aient pu être contaminés au laboratoire (**Romuald Carinci**, communication personnelle). À notre connaissance, aucune autre collecte d'adultes ou bien d'immatures n'a pu être réalisée à de telles distances de zones habitées, de surcroit dans des réservoirs naturels.

La diversité génétique est souvent associée avec un meilleur succès des espèces introduites. Les populations d'Amérique du Sud et notamment de Guyane ont montré un faible niveau de variabilité génétique (**Failloux *et al.* 2002**). Cette faible diversité génétique actuelle ne permettra peut-être jamais aux populations actuelles de s'adapter aux milieux naturels en Guyane. Cependant, il faut garder à l'esprit que des réintroductions sont hautement probables et sont donc à surveiller pour éviter l'introduction de nouvelles souches disposant d'une plus grande plasticité écologique.

III Résistance biotique des communautés résidentes

À notre connaissance, seul **Russell (1986)** s'est intéressé, en Australie aux effets des interactions qu'entretient *Ae.* (*Stg.*) *aegypti* avec une espèce de Culicidae autochtone (i.e. *Aedes notoscriptus* (Skuse 1889)) et à fortiori avec l'ensemble de la communauté résidente.

Depuis la formulation de l'hypothèse diversité-invasibilité par **Elton (1958)**, il faut bien admettre que les résultats théoriques et empiriques ont conduit à des avis partagés (**Levine & D'Antonio 1999**). Certains auteurs ont montré que ce paradoxe était lié, au moins en partie, au choix de l'échelle d'étude (**Fridley *et al.* 2007**). À une échelle fine la relation a souvent été mise en évidence (**Levin 1992**). Que ce soit à l'échelle de la communauté ou de la méta-communauté, aucun de nos résultats en condition naturelle indique que la présence et/ou l'abondance d'*Ae.* (*Stg.*) *aegypti* peut être diminuée par la diversité des communautés résidentes. Par exemple, dans la ville de Sinnamary la plus forte abondance d'*Ae.* (*Stg.*) *aegypti* dans les *A. aquilega* a été notée à une période de l'année où la méta-communauté était la plus diversifiée (**Fig. D.1**).

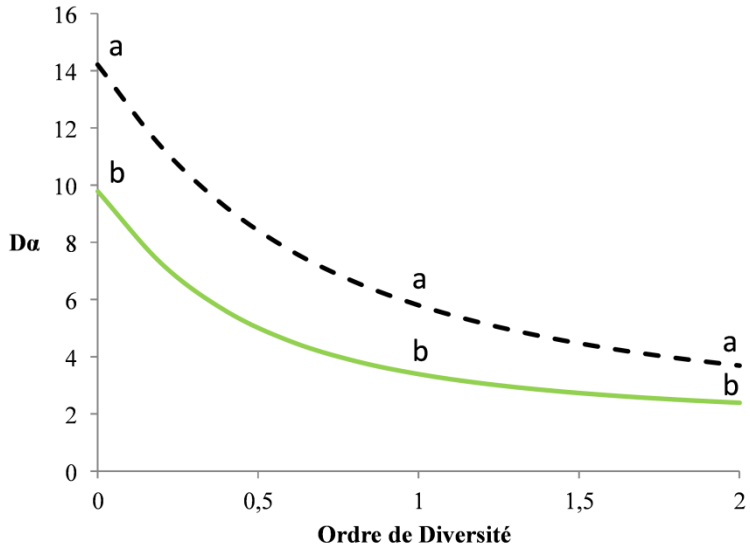

Figure D.1 Profils de diversité alpha d'ordre q des méta-communautés de macro-invertébrés aquatiques hébergées par *Aechmea aquilega* dans la ville de Sinnamary en 'saison sèche' (juillet 2011, en noir) et 'petite saison sèche' (mars 2013, en vert). Les lettres en minuscule indiquent une différence significative ($P < 0,01$) entre ces deux périodes pour les ordres de diversité q = 0, 1 et 2. Voir les **Chapitres 5 et 6** pour plus de détails.

À fortiori, le suivi temporel réalisé à Kourou donne des résultats similaires, les méta-communautés les plus diversifiées sont celles où *Ae.* (*Stg.*) *aegypti* est le plus abondant (**Chapitre 7**). En ce sens ces résultats vont à l'encontre de la théorie d'Elton. Il est possible que la diversité soit tellement réduite en milieu urbain que son domaine de variation ne permet pas de détecter une quelconque réponse. Cette hypothèse pourrait être testée expérimentalement en créant artificiellement des communautés avec un domaine de variation plus important que ce que nous avons pu observer dans des conditions naturelles (**Dézerald 2015**).

Interactions biologiques à issue négative

À Kourou, nos résultats indiquent que les populations de *Li. durhamii* excluent de manière saisonnière les populations larvaires d'*Ae.* (*Stg.*) *aegypti*. Ces observations rejoignent celles faites à Rio de Janeiro qui sous-entendaient que les abondances d'*Ae.* (*Stg.*) *aegypti* et d'*Ae.* (*Stg.*) *albopictus* étaient plus faibles qu'attendues au moment où les abondances de *Li. durhamii* étaient les plus fortes (**Honório *et al.* 2006**).

Plusieurs mécanismes ont été identifiés chez les insectes pour expliquer ce phénomène d'exclusion compétitive (**Reitz & Trumble 2002**). Parmi eux nous pouvons citer la compétition par exploitation, la compétition par interférence et la prédation intraguilde. Dans le **Chapitre 8** nous avons précisé quels pouvaient être les mécanismes responsables de

l'exclusion d'*Ae.* (*Stg.*) *aegypti* par *Li. durhamii*. Nos expérimentations au laboratoire ont permis d'écarter l'hypothèse selon laquelle la compétition par interférence serait le mécanisme à l'origine de l'exclusion compétitive observée en condition naturelle. Néanmoins, nous pouvons suggérer au moins deux autres mécanismes potentiellement responsable de ce phénomène.

L'étude de la compétition interspécifique entre *Ae.* (*Stg.*) *aegypti* et *Ae.* (*Stg.*) *albopictus* a permis de mettre en évidence que les conditions de l'environnement pouvaient changer l'issue de la compétition (**Juliano 2009**). Notamment, *Ae.* (*Stg.*) *albopictus* est systématiquement un meilleur compétiteur vis-à-vis d'*Ae.* (*Stg.*) *aegypti* sur une ressource alimentaire à base de litière végétale (**Juliano 1998; Murrell & Juliano 2008**). De manière analogue, il est plausible que l'exclusion d'*Ae.* (*Stg.*) *aegypti* de notre site forestier à Kourou soit liée à une meilleure exploitation de la litière végétale comme ressource alimentaire par *Li. durhamii*.

Limatus durhamii possède également l'avantage face à *Ae.* (*Stg.*) *aegypti* d'être capable de prédation intraguilde (**Fig. D.1**) et de cannibalisme sur des individus de taille similaire (observation personnelle). Ce comportement est assez mal connu chez cette espèce et a été parfois interprété à tort comme de la prédation classique (**Lopes 1999**). Nous avons observé à Kourou que ce comportement de prédation pouvait être déclenché par de brusques augmentations de densité de la population (observation personnelle). Il est possible que cette adaptation comportementale puisse créer un déséquilibre compétitif entre les deux espèces lorsque les ressources alimentaires sont limitées (**Sherratt & Church 1994**).

Il serait relativement aisé de tester ces hypothèses en laboratoire en adaptant le protocole présenté dans le **Chapitre 8**, avec par exemple l'utilisation de deux types de ressource alimentaire (artificielle *versus* naturelle) et en se plaçant dans des conditions de ressource limitante.

Figure D.2 Scène *in vivo* de prédation intraguilde entre *Runchomyia* (*Ctenogoeldia*) *magna* et *Wyeomyia* (Uncertain) *occulta* agrandie environs six fois (Crédit photo : **Hadrien Lalagüe**).

IV Spécialisation biotique et invasions biologiques

La spécialisation biotique est considérée comme une réaction évolutive à un environnement stable dans l'espace et dans le temps, alors que les stratégies généralistes sont plus susceptibles d'être favorisées dans un environnement hétérogène et perturbé (**Futuyma & Moreno 1988**). En d'autres termes, la spécialisation biotique est plus susceptible d'apparaître dans des environnements relativement stables plutôt que dans ceux soumis à des changements fréquents.

La spécialisation a pour conséquence de réduire la taille de la niche fondamentale des espèces, ce qui tendrait au sein d'une communauté à diminuer le rôle de l'environnement biotique par rapport à l'environnement abiotique dans la structuration de celle-ci (**Clavel *et al.***

2010). Idéalement, la spécialisation devrait être mesurée comme la dimension de l'hyper-volume de la niche écologique de l'espèce considérée (**Julliard *et al.* 2006**). Concrètement, elle est le plus souvent quantifiée comme une variable discrète en terme de diversité d'hôtes chez des organismes tels que les pollinisateurs, les phytophages ou les parasites (**Tripet *et al.* 2002; Dyer *et al.* 2007; Forister *et al.* 2015**).

Sous les tropiques, les organismes sont souvent considérés comme globalement plus spécialisés que leurs équivalents tempérés (**Clavel *et al.* 2010**). Bien que quelques contre-exemples existent, la plupart des études empiriques ont permis de vérifier que la spécialisation biotique augmentait vers les tropiques (**Schleuning *et al.* 2012; Forister *et al.* 2015**). En Guyane, l'étude de la diversité d'hôtes chez les moustiques utilisant les phytotelmes nous a permis de mettre en évidence qu'un fort degré de spécialisation existait au sein de ce système (**Chapitre 4**). Bien que nous n'ayons pas eu l'occasion de comparer ce degré de spécialisation avec des écosystèmes tempérés, ce résultat corrobore avec la théorie. De plus, la compétition pour la ressource aquatique est certainement à l'origine de la forte partition de niche que nous avons pu observer chez ces moustiques (**Chapitre 4**). À travers cette spécialisation, l'évolution progressive sous les tropiques suggère une tendance à favoriser les associations plutôt que les interactions (**Dobzhansky 1950**).

La forte spécialisation biotique sous les tropiques pourrait avoir au moins deux conséquences dans le cadre des invasions biologiques.

a) La spécialisation d'un organisme a un coût, celui d'une dépendance accrue à la ou aux ressources auxquelles il se spécialise, le rendant d'autant plus vulnérable aux perturbations du milieu (**McKinney 1997**). Dans notre cas la fragmentation et/ou la destruction des habitats aquatiques liées à l'urbanisation est certainement la principale cause de la disparition d'une grande majorité des espèces. La spécialisation pour d'autres ressources pourrait également rentrer en ligne de compte, notamment la préférence d'hôtes vertébrés lors des repas de sang, certaines espèces se nourrissant préférentiellement sur des singes, des oiseaux, ou encore des amphibiens, autant de groupes taxonomiques potentiellement impactés par l'urbanisation (**McKinney 2008**).

b) Pour les espèces introduites, la spécialisation des organismes de l'écosystème receveur le rendrait d'autant plus difficile à investir (**Sax *et al.* 2007**). Ce phénomène pourrait permettre d'expliquer pourquoi les écosystèmes tropicaux continentaux sont considérés

comme étant plus résistants aux invasions biologiques que les écosystèmes tropicaux insulaires ou bien que les écosystèmes tempérés (**Delnatte & Meyer 2012**).

L'importance de l'évolution dans le processus d'invasion biologique se réduit souvent à l'étude de la génétique des populations des espèces invasives (**Brown *et al.* 2011**). Pourtant, l'importance de l'histoire évolutive de l'écosystème receveur lors du phénomène d'invasion biologique doit être soulignée. La spécialisation des communautés autochtones expliquerait à la fois pourquoi si peu d'espèces autochtones arrivent à s'adapter aux milieux urbains et pourquoi si peu d'espèces invasives arrivent à s'affranchir de ces mêmes milieux. Cette hypothèse spécialisation-urbanisation-invasion mériterait d'être testée le long d'un gradient latitudinal. Nous pourrions nous attendre à ce que le renouvellement d'espèces (i.e. la beta diversité) entre les communautés urbaines et adjacentes soit relativement moins important dans les écosystèmes tempérés que dans les écosystèmes tropicaux. Les moustiques associés aux phytotelmes ne seraient pas nécessairement le modèle d'étude le plus approprié en raison de la faible abondance des phytotelmes en régions tempérées.

V *Aedes* (*Stg.*) *albopictus* : prédictions et plan d'action

Le moustique tigre *Aedes* (*Stegomyia*) *albopictus* (Skuse 1894) poursuit inexorablement son expansion géographique et partage maintenant son aire de répartition avec *Ae.* (*Stg.*) *aegypti* sur une grande partie de la zone pantropicale (**Kraemer *et al.* 2015**). Comme *Ae.* (*Stg.*) *aegypti*, cette espèce est également compétente pour la transmission de nombreux pathogènes chez l'Homme dont le chikungunya, la dengue et le zika (**Turell *et al.* 1992; Alto *et al.* 2008; Dupont-Rouzeyrol *et al.* 2016)**. La Guyane a jusqu'à présent été épargnée par l'introduction de cette espèce (ou du moins sa naturalisation) mais la colonisation de l'Amérique du Sud semble toucher à sa fin (**Benedict *et al.* 2007**). À l'Est comme à l'Ouest du territoire guyanais *Ae.* (*Stg.*) *albopictus* gagne du terrain et la question n'est plus de savoir si cette espèce finira par arriver en Guyane, mais quand va-t-elle arriver (**Carvalho *et al.* 2014; Rubio-Palis *et al.* 2015**). Même s'il est impossible de prédire son arrivée avec précision, il est encore plus difficile de prédire les lieux de sa future introduction tant les possibilités sont nombreuses (**Navarro *et al.* 2013**). Les secteurs sensibles sont bien évidemment les zones de transit pour l'homme et les marchandises avec des régions déjà investies par *Ae.* (*Stg.*) *albopictus* telles que les principaux ports (i.e. Cayenne, Kourou et Saint-Laurent-du-Maroni) et l'aéroport international Félix Eboué. Les frontières naturelles

formées par les fleuves Oyapock à l'Est et Maroni à l'Ouest, respectivement avec la région de l'Amapa brésilienne et le Suriname, constituent également des secteurs d'arrivées possibles. Les zones portuaires et aéroportuaires sont actuellement suivies avec des ovitraps par le Service Départemental de Désinfection (SDD) afin de détecter au plus tôt l'arrivée de cette espèce (**Romain Girod**, communication personnelle). Ces dispositifs de suivi doivent absolument être maintenus et si possible renforcés et étendus aux principales zones d'échanges transfrontaliers, afin de détecter au plus tôt l'arrivée de cette espèce.

Dans l'hypothèse de l'introduction d'*Ae.* (*Stg.*) *albopictus* en Guyane, les nouvelles populations devront faire face aux communautés résidentes. Contrairement à *Ae.* (*Stg.*) *aegypti*, le moustique tigre s'établit plus volontiers dans les milieux ruraux et les réservoirs naturels (**Lounibos *et al.* 2003; Reiskind & Lounibos 2012**). En conséquence, il est probable que les interactions biologiques avec les communautés résidentes jouent un rôle plus important dans l'établissement de cette espèce que dans le cas d'*Ae.* (*Stg.*) *aegypti*. L'invasion d'*Ae.* (*Stg.*) *albopictus* en Amérique du Nord est surement l'exemple d'exclusion compétitive en conditions naturelles le mieux documenté (**Lounibos 2007**). En Floride, l'arrivée d'*Ae.* (*Stg.*) *albopictus* a progressivement conduit à l'exclusion des populations d'*Ae.* (*Stg.*) *aegypti* des milieux ruraux, de sorte que sa distribution actuelle est limitée aux milieux les plus urbanisés (**O'Meara *et al.* 1995**).

En Guyane un scénario similaire avec un établissement d'*Ae.* (*Stg.*) *albopictus* dans les milieux ruraux et périurbains est envisageable. Dans cette situation, les rôles seraient en quelque sorte inversés et *Ae.* (*Stg.*) *aegypti* pourrait alors jouer le rôle de barrière biologique à la naturalisation dans les milieux les plus urbanisés. À la marge des villes et dans les milieux naturels les communautés autochtones prendraient le relai et leur présence pourrait avoir une toute autre importance que dans le cas d'*Ae.* (*Stg.*) *aegypti*. En Floride, la présence de *Wyeomyia* spp. dans les broméliacées à réservoirs a permis d'expliquer à l'échelle régionale l'absence d'*Ae.* (*Stg.*) *albopictus* dans ce phytotelme (**Lounibos *et al.* 2003**). On peut également imaginer un impact écologique plus grand sur les communautés autochtones de Guyane, incluant le déplacement compétitif de certaines populations.

Nous avons rarement un état des lieux précis avant une invasion (**Lockwood *et al.* 2013**). En Guyane, seul un court rapport relate l'introduction d'*Ae.* (*Stg.*) *aegypti* dans un village isolé de l'intérieur (Saül) entre 1944 et 1946 (**Floch & Abonnenc 1951**). Potentiellement, notre travail pourra servir d'état initial pour les futures études liées à l'introduction probable d'*Ae.* (*Stg.*) *albopictus* en Guyane.

VI Implications pour la lutte anti-vectorielle

Ce travail de thèse permet de mieux comprendre l'écologie des Culicidae en Guyane française et peut être utilisé afin d'orienter les méthodes de lutte anti-vectorielle. Nos résultats permettent en effet d'envisager de nombreuses pistes, développées et proposées ci-dessous. À l'heure actuelle, le contrôle d'*Ae.* (*Stg.*) *aegypti* en Guyane repose sur une lutte intégrant à la fois l'élimination physique des gîtes larvaires, la pulvérisation ULV (*Ultra Low Volume*) inter-domiciliaire d'agent chimiques (e.g. Temephos, Malathion, Deltamethrine), et la sensibilisation des guyanais.

Nos travaux ont montré qu'*Ae.* (*Stg.*) *aegypti* utilise les broméliacées à réservoirs naturellement présentes en Guyane comme habitat aquatique en milieu urbain (**Chapitres 5, 7**). L'utilisation de cet habitat aquatique n'avait pas été documentée auparavant en Guyane, sûrement en raison du fait que les broméliacées poussent le plus souvent à plusieurs mètres au-dessus du sol (**Chapitre 6**). Cette situation rappelle le rôle des gouttières en Guadeloupe, systématiquement négligées en raison de leur accès difficile (**Gustave *et al.* 2012**). Cependant, les broméliacées à réservoirs ne peuvent pas être considérées comme très productives dans le cas d'*Ae.* (*Stg.*) *aegypti* en comparaison avec d'autres réservoirs artificiels (**Chapitre 7**). Cette faible productivité tient au fait d'un plus faible taux d'oviposition et des conditions physico chimiques imposées par la plante, notamment par l'acidification du milieu aquatique (**Lopez *et al.* 2011**). La présence de phytotelmes naturels et ornementaux pourrait poser problème durant la phase finale d'élimination de l'ensemble des gîtes larvaires localement. Leur suivi serait donc justifié, notamment dans les milieux les plus fortement urbanisés. Des moyens de gestion non destructifs seraient à favoriser afin de conserver l'aspect esthétique et patrimonial de ces plantes (**Da Silva & Gomes 2008**).

Du service écosystémique à la lutte biologique

À la suite de la campagne d'éradication de 1949 en Guyane, Floch rapporte l'utilisation d'un poisson guyanais (i.e. *Poecilia vivipara*) comme agent de lutte biologique contre les populations de *Cx.* (*Cux.*) *quinquefasciatus* résistantes au DDT (**Floch 1950**). Cette méthode est encore utilisée aujourd'hui dans certaines régions et l'emploi de poissons autochtones comme agents de lutte biologique devrait être encouragée (**Azevedo-Santos *et al.* 2016**). Néanmoins, l'utilisation de ces poissons se limite à la gestion des réservoirs les plus grands, ce qui restreint largement le champ d'action dans la lutte contre *Ae.* (*Stg.*) *aegypti*.

Nous avons mis en évidence l'existence de deux espèces de moustiques autochtones antagonistes d'*Ae.* (*Stg.*) *aegypti*, un compétiteur, *Li. durhamii*, et un prédateur, *Tx.* (*Lyn.*) *haemorrhoidalis*. En Guyane, ces deux espèces font partie des *urban adapters* capables d'utiliser aussi bien des réservoirs naturels qu'artificiels. Nos résultats indiquent qu'ils influencent négativement l'abondance d'*Ae.* (*Stg.*) *aegypti* en conditions naturelles (**Chapitre 7**). Ils constituent donc deux agents de lutte biologique crédibles.

Chez les moustiques du genre *Toxorhynchites*, les larves sont prédatrices (**Fig. D.2**) et les adultes non hématophages, se nourrissent exclusivement de nectar floral et extra-floral (**Collins & Blackwell 2000**). L'idée de les utiliser comme agents de lutte biologique est séduisante et a été formulée pour la première fois en 1911 (**Colledge 1911**). L'espèce *Tx.* (*Lyn.*) *haemorrhoidalis* présente plusieurs avantages. Le premier est qu'elle colonise une large gamme d'habitats aquatiques également utilisés par *Ae.* (*Stg.*) *aegypti*, qu'il s'agisse de réservoirs naturels ou artificiels (**Chapitre 7**). Le second est que cette espèce semble s'adapter dans une certaine mesure aux perturbations imposées par le milieu urbain. À Kourou, c'est d'ailleurs dans le site présentant le niveau intermédiaire d'urbanisation que nous avons retrouvé la plus grande abondance de *Tx.* (*Lyn.*) *haemorrhoidalis* (**Chapitre 7**). Dans la ville de Sinnamary, sa présence dans les broméliacées à réservoirs est positivement influencée par la surface couverte par la végétation formée par les arbres et les arbustes (**Chapitre 6**). En revanche, le site de forêt secondaire à Kourou n'est que faiblement investi par cette espèce, ce qui suggère que *Tx.* (*Lyn.*) *haemorrhoidalis* favorise les écotones plutôt que des milieux fermés.

Figure D.3 Scène de prédation *in vivo* entre *Toxorhynchites* (*Lynchiella*) *guadeloupensis* et *Aedes* (*Stegomyia*) *aegypti* agrandie environs six fois (Crédit photo : **Hadrien Lalagüe**).

Nous avons observé qu'en conditions naturelles les pics d'abondances de *Li. durhamii* en saison des pluies conduisait à l'exclusion compétitive d'*Ae.* (*Stg.*) *aegypti* dans les sites les moins perturbés. *Limatus durhamii* colonise aussi bien les réservoirs naturels qu'artificiels. Bien que cette espèce soit d'une faible importance médicale, elle n'en demeure pas moins une espèce hématophage connue pour piquer occasionnellement l'Homme (**Harbach 2015**).

Il serait souhaitable de conserver ces populations en réduisant au maximum notre impact au risque de perdre ce service écosystémique (**Millennium Ecosystem Assessment 2005**). À notre connaissance, il n'existe pas d'étude quantifiant l'impact des pulvérisations ULV sur les communautés résidentes. Compte tenu de la forte résistance des populations d'*Ae.* (*Stg.*) *aegypti* à la plupart des insecticides utilisés (**Dusfour *et al.* 2011**), nous sommes en droit de nous demander si le recours à cette méthode est toujours pertinent. Il faut aussi

souligner les risques encourus par les guyanais suite à l'exposition à ces agents chimiques de manière chronique et prolongée.

Deux approches pourraient être envisagées, dans un premier temps il faudrait réduire le filtre contraignant l'installation de ces espèces cibles. Comme suggéré dans le **Chapitre 6**, la modification de certaines composantes du paysage pourrait moduler l'intensité du filtre créé par l'environnement urbain. Dans un second temps, des lâchers d'adultes et/ou des introductions de larves pourraient être envisagés dans l'optique de renforcer artificiellement certaines populations. En effet, il serait illusoire de vouloir relâcher des individus de *Li. durhamii* ou des *Tx.* (*Lyn.*) *haemorrhoidalis* dans des quartiers fortement urbanisés en espérant que ceux-ci arrivent à s'établir de manière durable. Ceci implique de connaitre et de pouvoir agir sur les composantes du filtre urbain susceptibles d'empêcher l'établissement de ces espèces dans un premier temps, et de maitriser l'élevage *ex situ* de ces espèces dans un second temps.

Ces dernières années nous avons assisté à l'apparition de nouvelles méthodes de lutte anti-vectorielle basées sur la libération de mâles génétiquement modifiés. Deux approches existent. La première vise à supprimer les populations existantes, l'autre à les remplacer par des populations résistantes au pathogène ciblé (**Gantz *et al.* 2015; Hammond *et al.* 2016**). L'utilisation de mâles génétiquement modifiés est actuellement en cours au Brésil dans le but d'éradiquer certaines populations d'*Ae.* (*Stg.*) *aegypti* (**Carvalho *et al.* 2015**). Chacune des deux approches présente ses avantages et ses inconvénients. L'argument souvent avancé pour justifier le remplacement des populations plutôt que leur suppression tient au fait qu'une fois vide, la niche serait plus facilement investie par d'autres espèces ou bien réinvestie par la même espèce. Il est indéniable que la niche serait plus facilement colonisée en absence d'*Ae.* (*Stg.*) *aegypti*, en revanche les remplaçants potentiels ne sont pas nombreux, en particulier parmi les espèces autochtones.

Nous sommes encore loin de la mise en place d'une lutte biologique efficace et opérationnelle contre *Ae.* (*Stg.*) *aegypti*, et il est donc souhaitable de poursuivre les recherches dans ce sens. L'utilisation de ces agents de lutte biologique passera par une meilleure compréhension du fonctionnement du filtre urbain sur ces espèces autochtones. Cette approche pourrait s'intégrer dans les plans de lutte mis en place à l'heure actuelle et aurait l'énorme avantage d'être plus facilement acceptée par les guyanais que d'éventuelles méthodes faisant intervenir des organismes génétiquement modifiés (**Schreiber & Jones 1994**).

Les interactions biologiques qu'entretient *Ae.* (*Stg.*) *aegypti* avec les communautés résidentes en Guyane sont relativement limitées et varient dans l'espace et dans le temps le long de gradients environnementaux. La marginalité de ces interactions tient à la concomitance de trois phénomènes principaux : i) l'anthropisation des écosystèmes, en particulier l'urbanisation, qui tend à éroder et à homogénéiser la biodiversité, ii) la spécialisation des communautés autochtones qui tend à accentuer les effets de l'urbanisation et iii) l'anthropophilie d'*Ae.* (*Stg.*) *aegypti* qui participe à limiter la dispersion de cette espèce en dehors des milieux urbains où elle serait susceptible de rencontrer une plus grande résistance biotique.

Sous les tropiques, la grande diversité taxonomique est causée par un plus fort taux de diversification (**Cardillo 1999**) lié à une baisse du taux d'extinction et/ou une augmentation du taux de spéciation et/ou d'immigration (**Jablonsky *et al.* 2006**). En outre, les oscillations climatiques liées aux cycles de Milankovitch aux conséquences moins dramatiques sous ces latitudes expliqueraient notamment la plus forte spécialisation des organismes et des communautés (**Dynesius & Lansson 2000**). En plus de la relative stabilité climatique, l'hétérogénéité des habitats terrestres en Guyane a surement participé au développement et à la persistance de la diversité de Culicidae que l'on observe aujourd'hui (**Guitet *et al.* 2015**).

Paradoxalement, la biodiversité est certainement à la fois la plus grande force et la plus grande faiblesse des écosystèmes tropicaux face aux invasions biologiques.

La plus grande force, car les niveaux de spécialisation atteints par les organismes autochtones n'ont aucune chance d'être approchés par les espèces nouvellement introduites. Dans ce sens les communautés autochtones constituent une formidable barrière face à l'invasion.

La plus grande faiblesse car ces niveaux de spécialisation atteints par les organismes autochtones les rendent d'autant plus vulnérables aux perturbations d'origine anthropique telles que l'urbanisation.

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APPENDIX

APPENDIX 1. List of native monocotyledon plant species forming (or potentially forming) phytotelmata in French Guiana. Species are ranked alphabetically by family, genus and species. The occurrence in French Guiana as well the validity of species names is based on **Funk *et al.*** (**2007**). Type of phytotelm structures have been divided into leaf axil (LA), flower bract (FB) and hollow stem (HS), and indicated for each species. Phytotelm family, genus and species in which we have observed mosquito immature during this thesis are highlighted in light blue.

Family	Genus	Species	Author	Type of phytotelm
ARACEAE	*Alocasia*	*macrorrhiza*	(L.) G.Don	LA
	Anthurium	*clavigerum*	Poepp. & Endl.	LA
		eminens	Schott	LA
		pentaphyllum	(Aubl.) G.Don	LA
		rubrinervium	(Link) G.Don	LA
	Caladium	*bicolor*	(Aiton) Ventenat	LA
		picturatum	K.Koch & Bouche	LA
		schomburgkii	Schott	LA
	Colocasia	*esculenta*	(L.) Schott	LA
	Dieffenbachia	*elegans*	Jonker & Jonker	LA
		humilis	Poepp.	LA
		maculata	(Lodd.) G.Don	LA
		paludicola	N.E.Brown ex Gleason	LA
		seguine	(Jacq.) Schott	LA
	Homalomena	*picturata*	(Linden & Andre) Regel	LA
	Monstera	*adansonii*	Schott	LA
		obliqua	Miq.	LA
		spruceana	(Schott) Engl.	LA
	Montrichardia	*arborescens*	(L.) Schott	LA
		linifera	(Arruda) Schott	LA
	Philodendron	*cremersii*	Croat & Graynum	LA
		duckei	Croat & Graynum	LA
		exile	Bunting	LA
		guianense	Croat & Graynum	LA
		ornatum	Schott	LA
		placidum	Schott	LA
		rudgeanum	Schott	LA
	Rhodospatha	*latifolia*	Poepp.	LA
		oblongata	Poepp.	LA
		venosa	Gleason	LA
	Schismatoglottis	*americana*	Jonker & Jonker	LA
	Spathiphyllum	*humboltii*	Schott	LA
	Stenospermation	*multivulatum*	(Engl.) N.E.Brown	LA
	Syngonium	*hastifolium*	Engl.	LA
		podophyllum	(Schott) Croat	LA
	Urospatha	*sagittifolia*	(Rudge) Schott	LA
	Xanthosoma	*belophyllum*	(Willd.) Schott	LA
		conspurcatum	Schott	LA
		cordatum	Schott	LA
		granvillei	Croat & Thompson	LA

		striatipes	(Kunth) Madison	LA
		striolatum	Mart. ex Schott	LA
		undipes	(K. Koch) K.Koch	LA
		violaceum	Schott	LA
ARECACEAE	*Mauritia*	*flexuosa*	L.f.	LA
BROMELIACEAE	*Aechmea*	*angustifolia*	Poeppig & Endlicher	LA
		aquilega	(Salisbery) Grisebach	LA
		bromeliifolia	(Rudge) Baker	LA
		egleriana	L.B.Smith	LA
		lingulata	(L.) Baker	LA
		longifolia	(Rudge) Baker	LA
		melinonii	Hooker	LA
		mertensii	(Meyer) J.H.Schultes	LA
		moonenii	Gouda	LA
		nudicaulis	(L.) Grisebach	LA
		poitaei	(Baker) L.B.Smith & M.A.Spencer	LA
		politii	L.B.Smith	LA
		polyantha	E.Pereira & Reitz	LA
		rodriguesiana	(L.B.Smith) L.B.Smith	LA
		setigera	Martius ex J.H.Schultes	LA
		tocantina	Baker	LA
		vallerandii	(Carrière) Erhardt, Götz & Seybold	LA
	Ananas	*comosus*	(L.) Merrill	LA
	Araeococcus	*flagellifolius*	Harms	LA
		goeldianus	L.B.Smith	LA
		micranthus	Brongniart	LA
	Billbergia	*pyramidalis*	(Sims) Lindley	LA
		rosea	hort. ex Beer	LA
		violacea	Beer	LA
	Bromelia	*agavifolia*	Brongniart ex Houllett	LA
		alta	L.B.Smith	LA
		fosteriana	L.B.Smith	LA
		granvillei	L.B.Smith & Gouda	LA
		plumieri	(E.Morren) L.B.Smith	LA
		serra	Grisebach	LA
	Catopsis	*berteroniana*	(J.H.Schultes) Mez	LA
		sessiliflora	(Ruiz & Pavon) Mez	LA
	Disteganthus	*basilateralis*	Lem	LA
		lateralis	(L.B.Smith) Gouda	LA
	Guzmania	*altsonii*	L.B.Smith	LA
		lingulata	(L.) Mez	LA
		melinonis	Regel	LA
		plumieri	(Grisebach) Mez	LA
	Mezobromelia	*pleiosticha*	(Grisebach) J.Utley & H.Luther	LA
	Pitcairnia	*caricifolia*	Martius ex J.H.Schultes	LA
		cremersii	Gouda	LA
		geyskesii	L.B.Smith	LA
		pusilla	Mez	LA
		rubiginosa	(Brongniart) Baker	LA
		sastrei	L.B.Smith & R.W.Read	LA
		saxosa	Gouda	LA
		semijuncta	Baker	LA
		sprucei	Baker	LA
	Racinaea	*spiculosa*	(Grisebach) M.A.Spencer & L.B.Smith	LA

	Tillandsia	*adpressiflora*	Mez	LA	
		anceps	Loddiges	LA	
		fasciculata	Swartz	LA	
		flexuosa	Swartz	LA	
		kegeliana	Mez	LA	
		monadelpha	(E.Morren) Baker	LA	
	Vriesea	*heliconioides*	(Kunth) Hooker ex Walpers	LA	
		jonghei	(Koch) E.Morren	LA	
		procera	(Martius ex J.H.Schultes) Wittmack	LA	
		splendens	(Brongniart) Lemaire	LA	
	Werauhia	*gigantea*	(Martius ex Schultes f.) J.R.Grant	LA	
		gladioliflora	(Wendland) J.R.Grant	LA	
COSTACEAE	*Costus*	*arabicus*	L.	FB	
		claviger	Benoist	LA	FB
		curcumoides	Maas	FB	
		erythrothyrsus	Loes.	FB	
		scaber	Ruiz & Pav.	FB	
		spiralis	(Jacq.) Roscoe	FB	
CYCLANTHACEAE	*Asplundia*	*brachyphylla*	Harling	LA	
		glandulosa	(Gleason) Harling	LA	
		heteranthera	Harling	LA	
	Cyclanthus	*bipartitus*	Poit.	LA	
	Dicranopygium	*pygmaeum*	(Gleason)	LA	
	Evodianthus	*funifer*	(Poit.)	LA	
	Ludovia	*lancifolia*	Brongn.	LA	
	Thoracocarpus	*bissectus*	(Vell.) Harling	LA	
HELICONIACEAE	*Heliconia*	*acuminata*	L.C. Rich.	LA	FB
		aemygdiana	Burle-Marx	LA	FB
		bihai	(L.) L.	LA	FB
		chartacea	Lane ex Barreiros	LA	
		dasyantha	Koch & Bouche	LA	
		densiflora	B.Verl.	LA	FB
		hirsuta	L.f.	LA	FB
		lourteigiae	Mello & E. Santos	LA	FB
		pendula	Wawra	LA	
		psittacorum	L.f.	LA	FB
		richardiana	Miq.	LA	FB
		spathocircinata	Aristeguieta	LA	FB
MARANTACEAE	*Calathea*	*altissima*	(Poepp. & Endl.) Korn.	LA	FB
		cylindrica	(Roscoe) K.Schum.	LA	FB
		dilabens	L.Anderson & H.Kennedy	LA	
		grandis	Petersen	LA	
		granvillei	L.Andersson & H.Kennedy	LA	
		legrelleana	(Linden) Regel	LA	
		lutea	(Aubl.) Schult.	LA	FB
		maasiorum	H. Kennedy	LA	FB
		mansonis	Korn.	LA	
		micans	(Mathieu) Korn.	LA	FB
		microcephala	(Poepp. & Endl.) Korn.	LA	FB
		propinqua	(Poepp. & Endl.) Korn.	LA	FB
		splendida	(Verschaff. ex Lem.) Regel	LA	
		squarrosa	L.Andersson & H.Kennedy	LA	
		villosa	Lindl.	LA	
		zingiberina	Korn.	LA	

	Hylaeanthe	*hexantha*	(Poepp. & Endl.) Jonker & Jonker	LA		
		unilateralis	(Poepp. & Endl.) Jonker & Jonker	LA		
	Ischnosiphon	*arouma*	(Aubl.) Korn.	LA		
		centricifolius	L.Andersson	LA		
		enigmaticus	L.Andersson	LA		
		gracilis	(Rudge) Korn.	LA		
		leucophaeus	(Poepp. & Endl.) Korn.	LA		
		martianus	Eicchl. ex Petersen	LA		
		obliquus	(Rudge) Korn.	LA		
		petiolatus	(Rudge) L.Andersson	LA		
		puberulus	(Petersen) L.Andersson	LA		
		ursinus	L.Andersson	LA		
	Monotagma	*contractum*	Huber	LA		
		exile	Hagberg.	LA		
		juruanum	Loes.	LA		
		laxum	(Poepp. & Endl.) K.Schum.	LA		
		plurispicatum	(Korn.) K.Schum.	LA		
		spicatum	(Aubl.) Macbr.	LA		
		ulei	Schum. ex Loes.	LA		
		vaginatum	Hagberg.	LA		
	Myrosma	*cannifolia*	L.f.	LA		
	Stromanthe	*tonckat*	(Aubl.) Eichl.	LA		
	Thalia	*geniculata*	L.	LA		
POACEAE	*Guadua*	*glomerata*	Munro			HS
		latifolia	(Humb. & Bonpl.) Kunth			HS
		macrostachya	Rupr.			HS
	Lasiacis	*anomala*	Hitchc.			HS
		ligulata	Hitchc. & Chase			HS
		sorghoidea	(Desv. ex Ham.) Hitchc. & Chase			HS
		hexandra	Sw.			HS
STRELITZIACEAE	*Phenakospermum*	*guyannense*	(L.C.Rich.) Endl. ex Miq.	LA	FB	
TYPHACEAE	*Typha*	*domingensis*	Pers.	LA		

APPENDIX 2. Table of the Mosquitoes of French Guiana summarizing the known species distribution across the Neotropics, the type locality and the location of the type. Distribution is based on the **WRBU** (**2015**) and is defined as follows: French Guiana (FG), the Guiana Shield (GS), South America (SA) and South and Central America (SCA). Type localities and location of types are based on Knight and Stone (1977); otherwise, a reference is provided. Location of types are abbreviated as follows: Collection of the author of the species (A), Museo Argentino de Ciencias Naturales, Buenos Aires (BA), British Museum, London (BM), Faculdade de Saude Publica, Sao Paulo (BH), Faculté de Médecine, Paris (FMP), Faculdade de Medicina, Sao Paulo (FMSP), Magyar Nemzeti Muzeum, Budapest (HNM), Instituto Nacional de Endemias Rurais, Belo Horizonte (INER), Instituto Nacional de Microbiologia, Buenos Aires (INM), Instituto Oswaldo Cruz, Rio de Janeiro (IOC), Instituut voor Tropische Hygiene en Geographische Pathologie, Amsterdam (ITH), State Museum of Natural History, Leyden (LM), Museo de Division de Malariologia, Caracas (MDM), Museum National d'Histoire Naturelle, Paris (MNHP), Museo Nacional, Rio de Janeiro (MNRJ), Location unknown (LU), Non-existent (NE), Naturhistorisches Museum, Vienna (NMW), Institut Pasteur, Cayenne, Guyane française (IPGF), Institut Pasteur, Paris (PIP), Natur Museum und Forschungs Institut, Frankfurt (SNG), United States National Museum, Washington (USNM), Universitetets Zoologiske Museum, Copenhagen (ZMC). New species records since 1980 are underlined, species reported from French Guiana for the first time are indicated by an asterisk, species believed to be originally described from French Guiana are in **bold**, and the 108 species known to breed in natural and/or artificial container are highlighted in light blue.

Checklist of the Mosquitoes of French Guiana	**Distribution**	**Type-locality**	**Type-specimen**	**References**
1- *An.* (*Ano.*) *costai* da Fonseca & da Silva Ramos 1939	SA	Sao Vicente, Sao Paulo, Brazil	FH	
2- *An.* (*Ano.*) *forattinii* Wilkerson & Sallum 1999	SA	Costa Marques, Rondonia, Brazil	USNM	**Wilkerson & Sallum 1999**
3- *An.* (*Ano.*) *intermedius* (Peryassú 1908)	SA	Rio de Janeiro and Xerem, Rio de Janeiro, Brazil	IOC?	
4- *An.* (*Ano.*) *maculipes* (Theobald 1903)	SA	Sao Paulo, Sao Paulo, Brazil	BM	
5- *An.* (*Ano.*) *minor* da Costa Lima 1929	SA	Estrelia, Rio de Janeiro, Brazil	IOC	
6- *An.* (*Ano.*) *peryassui* Dyar & Knab 1908	SA	Bicudos, Minas Gerais, Brazil	IOC	
7- *An.* (*Ano.*) *eiseni* Coquillett 1902	SCA	Aguna, Guatemala	USNM	
8- *An.* (*Ker.*) *neivai* Howard, Dyar & Knab 1913	SCA	Fort San Felipe, Porto Bello Bay, Panama	USNM	
9- *An.* (*Lph.*) *squamifemur* Antunes 1937	SCA	Vegagrande, Restrepo, Meta, Colombia	IOC	
10- *An.* (*Nys.*) *aquasalis* Curry 1932	SCA	Canal Zone, Panama	LU	
11- *An.* (*Nys.*) *ininii* Senevet & Abonnenc 1938	**FG**	**Mines de Saint-Elie, Saint-Elie, French Guiana**	**NE**	
12- *An.* (*Nys.*) *oswaldoi* s.l. (Peryassú 1922)	SCA	Valle do Rio Doce, Espirito Santo, Brazil	MNRJ	
13- *An.* (*Nys.*) *sanctielii* Senevet &Abonnenc 1938	**FG**	**Mines de Saint-Elie, Saint-Elie, French Guiana**	**NE**	
14- *An.* (*Nys.*) *nuneztovari* s.l. Gabaldón 1940	SA	San Carlos, Cojedes, Venezuela	MDM	
15- *An.* (*Nys.*) *triannulatus* s.l. (Neiva & Pinto 1922)	SCA	Fazenda Sao Joao, Mato Grosso, Brazil	LU	
16- *An.* (*Nys.*) *marajoara* Galvão & Damasceno 1942	SA	Cachoeira do Arari, Para, Brazil	FMSP	
17- *An.* (*Nys.*) *braziliensis* (Chagas 1907)	SA	Lassance, Minas Gerais, Brazil	IOC	

18- *An.* (*Nys.*) *darlingi* Root 1926	SCA	Caxiribu, Rio de Janeiro, Brazil	USNM	
19- *An.* (*Ste.*) *acanthotorynus* Komp 1937	SA	Iquitos, Loreto, Peru	USNM	
20- *An.* (*Ste.*) *canorii* Floch & Abonnenc 1945	**FG**	**Saut Canori, Haut Approuague, French Guiana**	**PIP**	
21- *An.* (*Ste.*) *kompi* Edwards 1930	SCA	Almirante, Bocas del Toro, Panama	USNM	
22- *An.* (*Ste.*) *nimbus* (Theobald 1902)	SA	Cabacaburi, Pomeroon River, Guyana	BM	
23- *Ch. bathana* (Dyar 1928)	SCA	Gatun, Canal Zone, Panama	USNM	
24- *Ch. bonneae* Root 1927	SA	Dam and Moengo, Suriname	USNM	
25- *Ad.* (*Ady.*) *squamipennis* (Lynch Arribálzaga 1878)	SCA	Buenos Aires, Argentina	NE	
26- *Ae.* (*Gec.*) *fluviatilis* (Lutz 1904)	SCA	Rio Grande, Sao Paulo, Brazil	BM	
27- *Ae.* (*How.*) *arborealis* Bonne-Wepster & Bonne 1920	SA	Dam, Suriname	ITH	
28- *Ae.* (*How.*) *fulvithorax* (Lutz 1904)	SA	Ponte Ipe Arcado, Goias, Brazil	NE	
29- *Ae.* (*Och.*) *eucephalaeus* Dyar 1918	GS	Suriname	USNM	
30- *Ae.* (*Och.*) *fulvus* (Wiedemann 1828)	SCA	Salvador, Bahia, Brazil	SNG	
31- *Ae.* (*Och.*) *hastatus* Dyar 1922	SCA	Paitilla, Canal Zone, Panama	USNM	
32- *Ae.* (*Och.*) *hortator* Dyar & Knab 1907	SCA	Trinidad	USNM	
33- *Ae.* (*Och.*) *martineti* Senevet 1937	**FG**	**Cayenne, French Guiana**	**NE**	**Belkin 1968**
34- *Ae.* (*Och.*) *nubilus* Theobald 1903	SCA	Pomeroon Mission River, Guyana	BM	
35- *Ae.* (*Och.*) *oligopistus* Dyar 1918	SCA	Trinidad	USNM	
36- *Ae.* (*Och.*) *perventor* Cerqueira & Costa 1946	SA	Mangaratiba, Rio de Janeiro, Brazil	INER	
37- *Ae.* (*Och.*) *scapularis* (Rondani 1848)	SCA	Vicinity of Belem, Para, Brazil	LU	
38- *Ae.* (*Och.*) *serratus* (Theobald 1901)	SCA	Rio de Janeiro, Brazil	BM	
39- *Ae.* (*Och.*) *taeniorhynchus* (Wiedemann 1821)	SCA	Mexico	NMW	
40- *Ae.* (*Pro.*) *argyrothorax* Bonne-Wepster & Bonne 1920	SA	Paramaribo, Suriname	ITH	
41- *Ae.* (*Pro.*) *braziliensis* Gordon & Evans 1922	GS	Macapa, Amazonas, Brazil	BM	
42- *Ae.* (*Pro.*) *terrens* (Walker 1856)	SCA	Guanabara, Rio de Janeiro, Brazil	BM	
43- *Ae.* (*Stg.*) *aegypti* (Linnaeus 1762)	SCA	Malaya, Kuala Lumpur, Selangor	BM	
44- *Hg.* (*Con.*) *leucocelaenus* (Dyar & Shannon 1924)	SA	Franca, Sao Paulo, Brazil	BM	
45- *Hg.* (*Hag.*) *albomaculatus* Theobald 1903	GS	Cara Cara, Demerara River, Guyana	BM	
46- *Hg.* (*Hag.*) *janthinomys* Dyar 1921	SCA	Trinidad	USNM	
47- *Ps.* (*Gra.*) *cingulata* (Leicester 1908)	**SCA**	**Cayenne, French Guiana**	**ZMC**	
48- *Ps.* (*Jan.*) *albipes* (Theobald 1907)	SCA	Santa, Aqua, Trinidad	BM	
49- *Ps.* (*Jan.*) *ferox* (von Humboldt 1819)	SCA	Borodon, Ecuador	NE	
50- *Ps.* (*Jan.*) *lutzii* (Theobald 1901)	SCA	Rio de Janeiro, Brazil	BM	
51- *Ps.* (*Pso.*) *cilipes* (Fabricius 1805)	**SCA**	**Cayenne, French Guiana**	**ZMC**	
52- *Ps.* (*Pso.*) *lineata* (von Humboldt 1819)	SCA	Magdalena River, Colombia	NE	

53- *Cx.* (*Ads.*) *accelerans* Root 1927	SCA	Porto das Caixas, Rio de Janeiro, Brazil	USNM	
54- *Cx.* (*Ads.*) *amazonensis* (Lutz 1905)	SCA	Manaus, Amazonas, Brazil	LU	
55- *Cx.* (*Ads.*) *clastrieri* Casal & Garcia 1968	SA	Belem, Para, Brazil	INM	
56- *Cx.* (*Ads.*) *guyanensis* Clastrier 1970	**FG**	**Cabassou Forest, Cayenne, French Guiana**	**MNHP**	**Berlin & Belkin 1980**
57- *Cx.* (*And.*) *belemensis* Duret & Damasceno 1955	SA	Belem, Para, Brazil	USNM	**Harbach *et al.* 1991**
58- *Cx.* (*And.*) *damascenoi* Duret 1969	GS	Joao Goulard, Amazonas, Brazil	USNM	**Harbach *et al.* 1991**
59- *Cx.* (*And.*) *originator* Gordon & Evans 1922	SA	Macapa, Amazonas, Brazil	BM	
60- *Cx.* (*Car.*) *infoliatus* Bonne-Wepster & Bonne 1920	SA	Dam, Suriname	ITH	
61- *Cx.* (*Car.*) *urichii* (Coquillett 1906)	SCA	Trinidad	USNM	
62- *Cx.* (*Car.*) *antunesi* Lane & Whitman 1943	SCA	Sao Joao de Petropolis, Espirito Santo, Brazil	INER	
63- *Cx.* (*Car.*) *bonnei* Dyar 1921	SA	Suriname	USNM	
64- *Cx.* (*Car.*) *insigniforceps* Clastrier & Claustre 1978	**FG**	**Gallion Forest, French Guiana**	**MNHP**	**Clastrier & Claustre 1978a**
65- *Cx.* (*Cux.*) *coronator* Dyar & Knab 1906	SCA	St. Joseph, Trinidad	USNM	
66- *Cx.* (*Cux.*) *bonneae* Dyar & Knab 1919	SCA	Compagnie des Mines d'Or, Lawa River, Suriname	USNM	
67- *Cx.* (*Cux.*) *mollis* Dyar & Knab 1906	SCA	Sangre Grande, Trinidad	USNM	
68- *Cx.* (*Cux.*) *nigripalpus* Theobald 1901	SCA	St. Lucia Island	NE	
69- *Cx.* (*Cux.*) *quinquefasciatus* Say 1823	SCA	Mississippi River, United States	USNM	**Sirivanakarn & White 1978**
70- *Cx.* (*Cux.*) *brevispinosus* Bonne-Wepster & Bonne 1920	SA	Kwakoegron, Saramacca, Suriname	ITH	
71- *Cx.* (*Cux.*) *declarator* Dyar & Knab 1906	SCA	Trinidad	USNM	
72- *Cx.* (*Cux.*) *surinamensis* Bruijning 1959	SA	Suriname	USNM	
73- *Cx.* (*Cux.*) *pseudojanthinosoma* Senevet & Abonnenc 1946	**FG**	**French Guiana**	**FMP**	
74- *Cx.* (*Mel.*) *commevynensis* Bonne-Wepster & Bonne 1920	SCA	Alkmaar, Commewijne, Suriname	ITH	
75- *Cx.* (*Mel.*) *dunni* Dyar 1918	SCA	Mandingo River, Canal Zone, Panama	USNM	
76- *Cx.* (*Mel.*) *ensiformis* Bonne-Wepster & Bonne 1920	SCA	Dam, Suriname	ITH	
77- *Cx.* (*Mel.*) *trigeminatus* Clastrier 1970	**SA**	**Gallion Forest, French Guiana**	**MNHP**	
78- *Cx.* (*Mel.*) *zeteki* Dyar 1918	SCA	Gatun, Canal Zone, Panama	USNM	
79- *Cx.* (*Mel.*) *bastagarius* Dyar & Knab 1906	SCA	Laventille, Trinidad	USNM	
80- *Cx.* (*Mel.*) *comatus* Senevet & Abonnenc 1939	**SA**	**Saut Tigre, Sinnamary River, French Guiana[1]**	**NE**	
81- *Cx.* (*Mel.*) *coppenamensis* Bonne-Wepster & Bonne 1920	SA	Kabelstation, Suriname	ITH	
82- *Cx.* (*Mel.*) *creole* Anduze 1949	SA	Caripito, Monagas, Venezuela	FH	
83- *Cx.* (*Mel.*) *tournieri* Senevet & Abonnenc 1939	**FG**	**Saut Tigre, Sinnamary River, French Guiana[1]**	**NE**	
84- *Cx.* (*Mel.*) *corentynensis* Dyar 1920	GS	Suriname	USNM	
85- *Cx.* (*Mel.*) *dolichophyllus* Clastrier 1970	**FG**	**Cabassou Forest, Cayenne, French Guiana**	**MNHP**	
86- *Cx.* (*Mel.*) *alcocki* Bonne-Wepster & Bonne 1920	GS	Zanderij, Suriname	ITH	
87- *Cx.* (*Mel.*) *comminutor* Dyar 1920	SCA	Suriname	USNM	

88- *Cx.* (*Mel.*) *distinguendus* Dyar 1928	SCA	Mojinga Swamp, Canal Zone, Panama	USNM	
89- *Cx.* (*Mel.*) *maxinocca* Dyar 1920	GS	Suriname	USNM	
90- *Cx.* (*Mel.*) *patientiae* Floch & Fauran 1955	**FG**	**Patience, Haute-Mana, French Guiana**	**IPGF**	
91- *Cx.* (*Mel.*) *productus* Senevet & Abonnenc 1939	**SA**	**Saint-Elie, French Guiana**	**NE**	**Belkin 1968**
92- *Cx.* (*Mel.*) *phlabistus* Dyar 1920	SA	Suriname	USNM	
93- *Cx.* (*Mel.*) *putumayensis* Matheson 1934	SA	Santo Antonio do Ica, Amazonas, Brazil	USNM	
94- *Cx.* (*Mel.*) *rorotaensis* Floch & Abonnenc 1946	**SA**	**Rorota, Remire-Montjoly, French Guiana**	**IPGF**	
95- *Cx.* (*Mel.*) *dyius* Root 1927	SA	Brazil	USNM	
96- *Cx.* (*Mel.*) *elevator* Dyar & Knab 1906	SCA	Port Limon, Costa Rica	USNM	
97- *Cx.* (*Mel.*) *cristovaoi* Duret 1968	GS	Caracarai, Roraima, Brazil	USNM	
98- *Cx.* (*Mel.*) *inadmirabilis* Dyar 1928	SCA	Sao Paulo, Brazil	USNM	
99- *Cx.* (*Mel.*) *theobaldi* (Lutz 1904)	SCA	Lagoa, Sao Paulo, Brazil	BM	
100- *Cx.* (*Mel.*) *vaxus* Dyar 1920	SA	Suriname	USNM	
101- *Cx.* (*Mel.*) *erraticus* (Dyar & Knab 1906)	SCA	Baton Rouge, Louisiana, United States	USNM	**Townsend *et al.* 1990**
102- *Cx.* (*Mel.*) *batesi* Rozeboom & Komp 1948	SCA	Villavicencio, Meta, Colombia	USNM	
103- *Cx.* (*Mel.*) *evansae* Root 1927	SCA	Mage, Rio de Janeiro, Brazil	USNM	
104- *Cx.* (*Mel.*) *caudatus* Clastrier 1970	**SA**	**Cabassou Forest, Cayenne, French Guiana**	**MNHP**	
105- *Cx.* (*Mel.*) *serratimarge* Root 1927	SCA	Rio de Janeiro, Brazil	USNM	
106- *Cx.* (*Mel.*) *abonnenci* Clastrier 1970	**FG**	**Gallion Forest, French Guiana**	**MNHP**	
107- *Cx.* (*Mel.*) *albinensis* Bonne-Wepster & Bonne 1920	SCA	Paramaribo, Suriname	ITH	
108- *Cx.* (*Mel.*) *contei* Duret 1968	SCA	Sao Miguel do Guama, Para, Brazil	USNM	**Harbach *et al.* 1991**
109- *Cx.* (*Mel.*) *flabellifer* Komp 1936	SCA	Santa Rosa, Colon, Panama	USNM	
110- *Cx.* (*Mel.*) *inhibitator* Dyar & Knab 1906	SCA	San Francisco Mts., Santo Domingo, Dom. Rep.	USNM	
111- *Cx.* (*Mel.*) *phlogistus* Dyar 1920	SCA	Suriname	USNM	
112- *Cx.* (*Mel.*) *plectoporpe* Root 1927	SCA	Bangu, Rio de Janeiro, Brazil	USNM	
113- *Cx.* (*Mel.*) *vidali* Floch & Fauran 1954	**FG**	**Moulin-de-Vidal, Cayenne, French Guiana**	**IPGF**	**Dégallier & Claustre 1980**
114- *Cx.* (*Mel.*) *eastor* Dyar 1920	SCA	Suriname	USNM	
115- *Cx.* (*Mel.*) *idottus* Dyar 1920	SCA	Suriname	USNM	
116- *Cx.* (*Mel.*) *equinoxialis* Floch & Abonnenc 1945	**SA**	**Camp Rochambeau, French Guiana**	**NE**	**Pecor *et al.* 1992**
117- *Cx.* (*Mel.*) *intrincatus* Brethés 1916	SA	San Isidro, Buenos Aires, Argentina	BA	**Harbach *et al.* 1984**
118- *Cx.* (*Mel.*) *rabanicola* Floch & Abonnenc 1946	**SA**	**Raban, French Guiana**	**PIP**	
119- *Cx.* (*Mel.*) *trisetosus* Fauran 1961	**FG**	**Conte River, St. Antoine, French Guiana**	**MNHP**	
120- *Cx.* (*Mel.*) *ybarmis* Dyar 1920	SA	Paramaribo, Suriname	USNM	
121- *Cx.* (*Mel.*) *alogistus* Dyar 1918	SCA	Suriname	USNM	
122- *Cx.* (*Mel.*) *caudelli* (Dyar & Knab 1906)	SCA	Arima, Trinidad	USNM	

123- *Cx.* (*Mel.*) *foliafer* Komp & Rozeboom 1951	SCA	Suriname	USNM	
124- *Cx.* (*Mel.*) *lacertosus* Komp & Rozeboom 1951	SCA	Almirante, Bocas del Toro, Panama	USNM	
125- *Cx.* (*Mel.*) *palaciosi* Duret 1968	GS	Boa Vista, Roraima, Brazil	USNM	**Harbach *et al.* 1991**
126- *Cx.* (*Mel.*) *innovator* Evans 1924	SA	Itacoatiara, Amazonas, Brazil	BM	
127- *Cx.* (*Mel.*) *pilosus* Lee 1946	SCA	Santa Lucrecia, Veracruz, Mexico	USNM	
128- *Cx.* (*Mel.*) *unicornis* Root 1928	SA	Maracay, Aragua, Venezuela	USNM	
129- *Cx.* (*Mel.*) *saramaccensis* Bonne-Wepster & Bonne 1920	SA	Kabelstation, Surinam River, Suriname	ITH	
130- *Cx.* (*Mel.*) *adamesi* Sirivanakarn & Galindo 1980	SCA	Canal Zone, Panama	USNM	**Sirivanakarn & Galindo 1980**
131- *Cx.* (*Mel.*) *epanastasis* Dyar 1922	SCA	Arenal River, Canal Zone, Panama	USNM	**Sirivanakarn & Belkin 1980**
132- *Cx.* (*Mel.*) *pedroi* Sirivanakarn & Belkin 1980	SCA	Juan Mina, Canal Zone, Panama	USNM	**Sirivanakarn & Belkin 1980**
133- *Cx.* (*Mel.*) *faurani* Duret 1968	SA	Manaos, Amazonas, Brazil	USNM	**Harbach *et al.* 1991**
134- *Cx.* (*Mel.*) *spissipes* (Theobald 1903)	SCA	Trinidad	BM	
135- *Cx.* (*Mel.*) *taeniopus* Dyar & Knab 1907	SCA	Bluefields, Nicaragua	USNM	**Sirivanakarn & Belkin 1980**
136- *Cx.* (*Mel.*) *portesi* Senevet & Abonnenc 1941	**SA**	**French Guiana**	**NE**	**Belkin 1968**
137- *Cx.* (*Mel.*) *vomerifer* Komp 1932	SCA	Almirante, Bocas del Toro, Panama	USNM	
138- *Cx.* (*Mcx.*) *chryselatus* Dyar & Knab 1919	SCA	Compagnie des Mines d'Or, Lawa River, Suriname	USNM	
139- *Cx.* (*Mcx.*) *imitator* Theobald 1903	SA	Sao Paulo, Sao Paulo, Brazil	BM	
140- *Cx.* (*Mcx.*) *pleuristriatus* Theobald 1903	SA	Sao Paulo, Brazil	BM	
141- *Cx.* (*Mcx.*) *reginae* Floch & Fauran 1955	**FG**	**Regina, Approuague, French Guiana**	**IPGF**	
142- *Cx.* (*Mcx.*) *stonei* Lane & Whitman 1943	SA	Trinidad	USNM	
143- *Cx.* (*Phc.*) *corniger* Theobald 1903	SCA	Para, Brazil	BM	
144- *Cx.* (*Tin.*) *breviculus* Senevet & Abonnenc 1939	**SA**	**Saut Tigre, Sinnamary River, French Guiana**[1]	**FMP**	
145- *Cx.* (*Tin.*) *cauchensis* Floch & Abonnenc 1945	**SA**	**Kaw, French Guiana**	**NE**	
146- *Cx. flochi* Duret 1969	SA	Belem, Para, Brazil	USNM	**Harbach *et al.* 1991**
147- *Cx. nigrimacula* Lane & Whitman 1943	SA	Guanabara, Rio de Janeiro, Brazil	INER	
148- *Cx. ocellatus* Theobald 1903	SA	Sao Paulo, Brazil	LU	**Townsend *et al.* 1990**
149- *Cx. punctiscapularis* Floch & Abonnenc 1946	**FG**	**Crique Anguille, Montsinery, French Guiana**	**PIP**	
150- *De. magnus* (Theobald 1901)	SA	St. Lucia Island, Lesser Antilles	NE	
151- *Lt.* (*Lut.*) *allostigma* Howard, Dyar & Knab 1915	SCA	Las Cascadas, Canal Zone, Panama	USNM	
152- *Cq.* (*Rhy.*) *albicosta* (Peryassú 1908)	SA	Serra da Cantareira, Sao Paulo, Brazil	IOC	
153- *Cq.* (*Rhy.*) *arribalzagae* (Theobald 1903)	SCA	Para, Brazil	BM	
154- *Cq.* (*Rhy.*) *fasciolata* (Lynch Arribálzaga 1891)	SCA	Navarro, Buenos Aires, Argentina	BM	
155- *Cq.* (*Rhy.*) *lynchi* (Shannon 1931)	SA	Para, Brazil	USNM	
156- *Cq.* (*Rhy.*) *venezuelensis* (Theobald 1912)	SCA	Cano de la Viuda, Venezuela	MNHP	
157- *Ma.* (*Man.*) *humeralis* Dyar & Knab 1916	SCA	Georgetown, Demerara, Guyana	USNM	

158- *Ma.* (*Man.*) *pseudotitillans* (Theobald 1901)	SCA	Lower Amazon, Brazil	BM	
159- *Ma.* (*Man.*) *titillans* (Walker 1848)	SCA	Belem, Para, Brazil	BM	
160- *Or. fascipes* (Coquillett 1906)	SCA	Rio Aranjuez, Puntarenas, Costa Rica	USNM	
161- *Jb. longipes* (Fabricius 1805)	**SCA**	**French Guiana**	**ZMC**	
162- *Jb. ulopus* (Dyar & Knab 1906)	SCA	Bluefields, Nicaragua	USNM	
163- *Li. asulleptus* (Theobald 1903)	SCA	Demerara River, Guyana	BM	
164- *Li. durhamii* Theobald 1901	SCA	Para, Brazil	BM	
165- *Li. flavisetosus* de Oliveira Castro 1935	SCA	Cubatao, Sao Paulo, Brazil	LU	
166- *Li. martiali* Senevet & Abonnenc 1939	**FG**	**Saut Tigre, Sinnamary River, French Guiana**[1]	**FMP**	**Clastrier & Claustre 1978b**
167- *Li. pseudomethysticus* (Bonne-Wepster & Bonne 1920)	GS	Suriname	ITH	
168- *Onirion sp. cf. **Harbach & Peyton (2000)**	SCA	-	-	
169- *Ru. (Cte.) magna (Theobald 1905)	SCA	San Antonio, Bolivia	HNM	
170- *Sa. (Pey.) hadrognathus Harbach 1995	SCA	Finca La Selva, Puerto Viejo, Costa Rica	USNM	**Harbach 1995**
171- *Sa. (Pey.) paradoxus Harbach 2002	SCA	Darien, Panama	USNM	**Harbach & Howard 2002**
172- *Sa. (Pey.) soperi Lane & Cerqueira 1942	SA	Piraja, Bahia, Brazil	IOC	
173- *Sa.* (*Pey.*) *undosus* (Coquillett 1906)	SCA	Trinidad	USNM	
174- *Sa.* (*Sab.*) *albiprivus* Theobald 1903	SA	Sao Paulo and Rio de Janeiro, Brazil	BM	
175- *Sa.* (*Sab.*) *belisarioi* Neiva 1908	SCA	Bicudos, Minas Gerais, Brazil	LU	
176- *Sa.* (*Sab.*) *bipartipes* Dyar & Knab 1906	SCA	Santo Domingo, Dominican Republic	USNM	
177- *Sa.* (*Sab.*) *cyaneus* (Fabricius 1805)	**SCA**	**Cayenne, French Guiana**	**ZMC**	
178- *Sa.* (*Sab.*) *purpureus* (Theobald 1901)	SA	Rio de Janeiro, Brazil	BM	
179- *Sa. (Sab.) quasicyaneus Peryassú 1922	SA	Matta do Utinga, Para, Brazil	LU	
180- *Sa.* (*Sab.*) *tarsopus* Dyar & Knab 1908	SCA	Bocas del Toro, Panama	USNM	**Harbach & Petersen 1992**
181- *Sa. (Sbn.) idiogenes Harbach 1994	SA	Pakitza, Rio Manu, Madre de Dios, Peru	USNM	**Harbach 1994**
182- *Sa.* (*Sbn.*) *intermedius* (Lutz 1904)	SCA	Sao Paulo, Brazil	BM	
183- *Sa.* (*Sbo.*) *chloropterus* (von Humboldt 1819)	SCA	Guayaquil River, Borodan, Ecuador	NE	
184- *Sh. fluviatilis* (Theobald 1903)	SCA	Sao Paulo, Brazil	BM	
185- *Sh. schedocyclia* (Dyar and Knab 1908)	SCA	Bluefields, Nicaragua	USNM	
186- *Tr. compressum* Lutz 1905	SCA	Sao Paulo, Brazil	IOC	
187- *Tr. digitatum* (Rondani 1848)	SCA	Guanabara, Rio de Janeiro, Brazil	LU	
188- *Tr. pallidiventer* (Lutz 1905)	SCA	Brazil	BM	**Townsend *et al.* 1990**
189- *Tr. soaresi* Lane & Cerqueira 1942	SA	Sao Joao de Petropolis, Espirito Santo, Brazil	IOC	
190- *Wy. (Cae.) sp. cf. **Harbach & Peyton (1990)**	SCA	-	-	
191- *Wy.* (*Cru.*) *forattinii* Clastrier 1974	**FG**	**Matoury, French Guiana**	**A**	
192- *Wy.* (*Dec.*) *pseudopecten* Dyar & Knab 1906	SCA	Trinidad	USNM	

193- *Wy.* (*Dec.*) *ulocoma* (Theobald 1903)	SCA	Demerara River, Guyana	BM	
194- *Wy.* (*Den.*) *complosa* (Dyar 1928)	SCA	San Juan de Pequini, Panama	USNM	
195- *Wy.* (*Den.*) *luteoventralis* Theobald 1901	SA	Para, Brazil	BM	
196- *Wy.* (*Den.*) *testei* Senevet & Abonnenc 1939	**GS**	**Saut Tigre, Sinnamary River, French Guiana[1]**	**FMP**	
197- *Wy.* (*Den.*) *trifurcata* Clastrier 1973	**FG**	**Montsinery, French Guiana**	**A**	
198- *Wy. (Den.) ypsipola* Dyar 1922	SCA	Comacho, Canal Zone, Panama	USNM	
199- *Wy.* (*Dod.*) *aphobema* Dyar 1918	SA	Lawa River, Suriname	USNM	
200- *Wy. (Hys.) lamellata* (Bonne-Wepster & Bonne 1920)	GS	Lawa River, Suriname	ITH	
201-*Wy. (Miamyia) oblita* (Lutz 1904)	SA	Sao Paulo and Ponte Ipe Arcado, Goias, Brazil	IOC	
202- *Wy.* (*Pho.*) *splendida* Bonne-Wepster & Bonne 1919	SA	Lawa River, Sarah Creek, Suriname	ITH	
203- *Wy.* (*Spi.*) *bourrouli* (Lutz 1905)	SA	Itaci, Sao Paulo, Brazil	NE	
204- *Wy.* (*Triamyia*) *aporonoma* Dyar & Knab 1906	SCA	Sonsonate, El Salvador	USNM	
205- *Wy.* (*Wyo.*) *arthrostigma* (Lutz 1905)	SCA	Brazil	IOC	
206- *Wy.* (*Wyo.*) *pertinans* (Williston 1896)	SCA	St. Vincent Island, Lesser Antilles	BM	
207- *Wy.* (*Wyo.*) *pseudorobusta* Pajot & Fauran 1975	**FG**	**Inini River, Maripasoula, French Guiana**	**IPGF**	
208- *Wy.* (*Wyo.*) *robusta* Senevet & Abonnenc 1939	**FG**	**Saut Tigre, Sinnamary River, French Guiana[1]**	**FMP**	
209- *Wy. albosquamata* Bonne-Wepster & Bonne 1919	GS	Lawa River, Suriname	ITH	
210- *Wy. argenteorostris* (Bonne-Wepster & Bonne 1920)	GS	Lawa River, Suriname	ITH	
211- *Wy. chalcocephala* Dyar & Knab 1906	SCA	Cacao Trece Aguas, Alta Vera Paz, Guatemala	USNM	
212- *Wy. clasoleuca* Dyar & Knab 1908	SCA	Caldera Island, Panama	USNM	
213- *Wy. compta* Senevet & Abonnenc 1939	**FG**	**Saut Tigre, Sinnamary River, French Guiana[1]**	**FMP**	
214- *Wy. ininicola* Fauran & Pajot 1974	**FG**	**Inini River, Maripasoula, French Guiana**	**IPGF**	
215- *Wy. melanocephala* Dyar & Knab 1906	SCA	Trinidad	USNM	
216- *Wy. nigricephala* Clastrier & Claustre 1978	**FG**	**Gallion Forest, French Guiana**	**MNHP**	**Clastrier & Claustre 1978b**
217- *Wy. occulta* Bonne-Wepster & Bonne 1919	SA	Suriname	ITH	
218- *Wy. rorotai* Senevet, Chabelard & Abonnenc 1942	**SA**	**Rorota, Remire-Montjoly, French Guiana**	**FMP**	
219- *Wy. surinamensis* Bruijning 1959	GS	Ornamibo, Suriname	LM	
220- *Tx.* (*Ank.*) *trichopygus* (Wiedemann 1828)	SA	Salvador, Bahia, Brazil	SNG	
221- *Tx. (Lyn.) guadeloupensis* (Dyar and Knab 1906)	SCA	Guadeloupe Island, Lesser Antilles	USNM	
222- *Tx.* (*Lyn.*) *haemorrhoidalis haemorrhoidalis* (Fabricius 1787)	**SCA**	**Cayenne, French Guiana**	**NE**	
223- *Tx.* (*Lyn.*) *haemorrhoidalis superbus* (Dyar & Knab 1906)	SCA	Trinidad	USNM	
224- *Tx. (Lyn.) moctezuma* (Dyar & Knab 1906)	SCA	Rio Aranjuez, Puntarenas, Costa Rica	USNM	**Zavortink & Chaverri 2009**
225- *Ur.* (*Ura.*) *apicalis* Theobald 1903	SCA	Antigua, Lesser Antilles	BM	
226- *Ur.* (*Ura.*) *calosomata* Dyar & Knab 1907	SCA	Tabernilla, Canal Zone, Panama	USNM	
227- *Ur.* (*Ura.*) *geometrica* Theobald 1901	SCA	Cubatao, Sao Paulo, Brazil	BM	

228- *Ur.* (*Ura.*) *hystera* Dyar & Knab 1913	SCA	Orinoco River, Manoa, Venezuela	USNM
229- *Ur.* (*Ura.*) *leucoptera* (Theobald 1907)	SCA	Stanley Town, New Amsterdam, Berbice, Guyana	BM
230- *Ur.* (*Ura.*) *lowii* Theobald 1901	SCA	St. Lucia Island, Lesser Antilles	BM
231- *Ur.* (*Ura.*) *mathesoni* Lane 1943	SA	Juquia, Sao Paulo, Brazil	FH
232- *Ur.* (*Ura.*) *nataliae* Lynch Arribálzaga 1891	SCA	Baradero, Buenos Aires, Argentina	BA
233- *Ur.* (*Ura.*) *pallidoventer* (Theobald 1907)	SCA	Para, Brazil	BM
234- *Ur.* (*Ura.*) *pulcherrima* Lynch Arribálzaga 1891	SCA	Las Conchas, Buenos Aires, Argentina	NE
235- *Ur.* (*Ura.*) *socialis* Theobald 1901	SCA	Kingston, Surrey, Jamaica	BM

[1]Note that the type locality of Saut Tigre, Saint-Elie, French Guiana no longer exist since the filling of the dam of Petit-Saut between 1994 and 1998.

APPENDIX 3. Biological traits and their modalities. Scores range from '0' (no affinity) to '3' (high affinity). *Taxa ID as in Table 1. BS, body size; AS, aquatic stage; RE, reproduction mode; DM, dispersal mode; RF, resistance form; RM, respiration mode LO, locomotion; FD, food; FG, feeding group.

Traits	Modality	Abbreviation	Taxa ID*																																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
BS	≤ 0.25 cm	BS1	0	0	0	0	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	> 0.25-0.5 cm	BS2	0	2	0	0	3	3	3	3	3	3	3	3	3	3	3	3	1	0	3	3	3	0	2	1	1	1	1	0	0	0	0	0	0	0	0	3
	> 0.5-1 cm	BS3	1	3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	3	1	2	0	0	1	3	3	3	3	3	0	2	2	2	0	2	2	0	0
	> 1-2 cm	BS4	2	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	3	3	3	2	3	3	3	0
	> 2-4 cm	BS5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	2	0
AS	Egg	AS1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2	3	3	3	3	3
	Larva	AS2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	2	2	3	3	3	2	2	3	3	3	3	3	3	3	2	2	2	3	3	3	3	3
	Pupa	AS3	2	2	3	3	1	1	1	1	1	1	1	1	1	1	2	2	3	3	3	2	2	3	3	3	3	3	3	3	0	2	2	0	0	0	0	0
	Adult	AS4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	3	3
RE	Ovoviviparity	RE1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
	Isolated eggs, free	RE2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	1	0	0	2	2	2	2	2
	Isolated eggs, fixed	RE3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	3	0	0	0	2	0	1	1	1	1	1	1	1
	Clutches, fixed	RE4	3	3	0	0	1	1	1	1	1	1	1	1	1	1	3	3	1	1	1	3	3	1	1	2	2	2	0	0	1	3	3	0	0	0	0	0
	Clutches, free	RE5	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0	0	3	3	0	3	3	3	0	0	0	0	0	0	0	0	0
	Clutches, terrestrial	RE6	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	Asexual reproduction	RE7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	3	3
DM	Aerial passive	DM1	1	1	2	2	3	3	3	3	3	3	3	3	3	3	0	0	3	3	3	0	0	3	3	0	2	2	2	2	3	1	1	3	3	3	3	3
	Aerial active	DM2	3	3	3	3	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	2	2	1	1	3	3	3	3	3	1	3	3	0	0	0	0	0
RF	Eggs	RF1	0	0	3	3	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	3	2	2	3	2	0	0	0	0	0	0	0	0
	Cocoons	RF2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	3	3
	Diapause/Dormancy	RF3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	None	RF4	3	3	0	0	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	0	0	0	0	0	3	3	3	0	0	0	0	0
RM	Tegument	RM1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	1	1	3	3	1	1	1	1	1	1	0	0	3	3	3	3	3
	Gill	RM2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	1	1	1	3	3	2	2	0	0	0	0	0	3	0	0	0	0	0	3	0
	Siphon/Spiracle	RM3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	0	0	0	0	0	0	0	0	0	3	3	3	3	3	3	3	3	0	0	0	0	0
LO	Surface swimmer	LO1	0	0	3	3	2	2	2	2	2	2	2	2	2	2	1	1	0	0	0	0	0	0	0	3	3	3	3	3	0	1	1	0	0	0	0	0
	Full water swimmer	LO2	0	0	2	2	3	3	3	3	3	3	3	3	3	3	3	3	1	1	1	0	0	1	3	2	2	2	2	2	0	0	0	2	2	2	2	2
	Crawler	LO3	0	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	3	3	3	2	0	0	0	0	0	3	2	2	0	0	0	0	0
	Burrower	LO4	2	3	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	0	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0

	Interstitial	LO5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1
FD	Microorganisms	FD1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	3	3	3	0	0	0	0	1	1	1	1	1
	Detritus (< 1 mm)	FD2	2	2	1	1	0	0	0	0	0	0	0	0	0	0	1	1	3	3	2	0	0	3	0	2	2	2	2	1	0	2	2	2	2	2	2	2
	Dead plant (litter)	FD3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	1	2	1	0	0	0	0	0	3	3	3	0	0	0	0	0
	Living microphytes	FD4	2	2	0	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	0	3	3	1	1	3	3	3	3	0	0	2	2	2	2	2	2	2
	Living leaf tissue	FD5	1	1	0	0	3	3	3	3	3	3	3	3	3	3	0	0	1	1	0	1	1	1	0	0	0	0	0	0	2	1	1	0	0	0	0	0
	Dead animal (> 1 mm)	FD6	2	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	0
	Microinvertebrates	FD7	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3	3	1	1	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0
	Macroinvertebrates	FD8	0	0	3	3	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0
FG	Gathering-collector	FG1	2	1	1	1	3	3	3	3	3	3	3	3	3	3	1	1	2	3	0	2	2	3	1	2	2	2	2	1	1	2	2	1	3	3	3	3
	Shredder	FG2	3	2	0	0	0	0	0	0	0	0	0	0	0	0	1	3	3	2	2	0	0	1	0	0	0	0	0	0	3	3	3	0	0	0	0	0
	Scraper	FG3	1	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1	3	3	3	2	0	0	0	0	0	0	0	1	1	0	0	0	1	0
	Filter-feeder	FG4	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	2	2	0	0	0	2	0	3	3	3	3	0	0	0	0	0	0	0	0	0
	Predator	FG5	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	3	0	0	0	0	3	0	0	0	3	0	0	0	0

APPENDIX 4. Updated Checklist of the Bromeliads (Bromeliaceae) of French Guiana.

INTRODUCTION

The last checklist of the bromeliads (Bromeliaceae) of the Guianas accounted for 68 species in French Guiana (**Gouda 1999**). However, this list included two doubtful records (i.e. *Bromelia oleveiriae* L.B. Smith and *Bromelia tubulosa* L.B. Smith), and two species only thought to be present in French Guiana (i.e. *Billbergia brachysiphon* L.B. Smith and *Bromelia morreniana* (Regel) Mez). Furthermore, since the checklist of 1999, a number of revisions concerning some groups of species were made (e.g. **Bartholomew *et al.* 2002; Gouda 2009**). These taxonomic studies have led to the discovery of new species, the better definition of some others, and the recognition of synonyms. In the present revision, we propose an updated checklist of the bromeliads of French Guiana to reflect the knowledge accumulated over the past 15 years. The list is voluntarily conservative to assure continuity with the previous studies conducted on bromeliads in French Guiana.

As a result of this update, seven species have been removed, four species have been added and six species have been synonymized. We also report the existence of three unidentified species which might constitute new country records. Species are listed alphabetically and ranked by subfamily and genus. The species considered to be present in French Guiana are numbered, while the species expected to be present in French Guiana, doubtful species records, and misidentifications are indicated but not numbered. Species names and authors follow the "The New Bromeliad Taxon List" (**Butcher & Gouda 2015**), and new species records since 1999 are highlighted with an asterisk. The "Notes" section includes useful explanations about the exclusion and the inclusion of species.

Today, it appears that 66 species of Bromeliaceae are known in French Guiana; they are distributed into three subfamilies and 14 genera:

BROMELIOIDEAE	PITCAIRNIOIDEAE	TILLANDSIOIDEAE
Aechmea (17 species)	*Pitcairnia* (9 species)	*Catopsis* (2 species)
Ananas (2 species)		*Guzmania* (4 species)
Araeococcus (3 species)		*Mezobromelia* (1 species)
Billbergia (3 species)		*Racinaea* (1 species)
Bromelia (6 species)		*Tillandsia* (10 species)
Disteganthus (2 species)		*Vriesea* (4 species)
		Werauhia (2 species)

THE BROMELIADS OF FRENCH GUIANA
SUBFAMILY BROMELIOIDEAE

Genus *Aechmea* Ruiz & Pavon

1- *Aechmea angustifolia* Poeppig & Endlicher
2- *Aechmea aquilega* (Salisbery) Grisebach
var. *aquilega*
3- *Aechmea bromeliifolia* (Rudge) Baker
- *Aechmea castelnavii* Baker (see Note 1)
- *Aechmea costantinii* (Mez) L.B.Smith (see Note 2)
4- *Aechmea egleriana* L.B.Smith
- *Aechmea fernandae* (E.Morren) (see Note 3)
- *Aechmea x lanjouwii* (L.B.Smith) Gouda & Moonen (see Note 4)
5- *Aechmea lingulata* (L.) Baker
6- *Aechmea longifolia* (Rudge) Baker [syn. *Streptocalyx longifolius*]
7- *Aechmea melinonii* Hooker
8- *Aechmea mertensii* (Meyer) J.H.Schultes
9- *Aechmea moonenii* Gouda
10- *Aechmea nudicaulis* (L.) Grisebach
var. *nudicaulis*
11- *Aechmea poitaei* (Baker) L.B.Smith & M.A.Spencer [syn. *Streptocalyx poitaei*]
12- *Aechmea politii* L.B.Smith
13- *Aechmea polyantha* E. Pereira & Reitz
14- *Aechmea rodriguesiana* (L.B.Smith) L.B.Smith
- *Aechmea rubiginosa* Mez (see Note 5)
15- *Aechmea setigera* Martius ex J.H.Schultes
- *Aechmea* sp.1 (see Note 6)
- *Aechmea* sp.2 (see Note 6)
16- *Aechmea tocantina* Baker
17- *Aechmea vallerandii* (Carrière) Erhardt, Götz & Seybold [syn. *Streptocalyx poeppigii*]

Genus *Ananas* Miller (see Note 7)
18- *Ananas ananassoides* (Baker) L.B.Smith
var. *nanus* L.B.Smith
- *Ananas* 'Comosus'
- *Ananas* 'Erectifolius'
19- *Ananas parguazensis* Camargo & L.B.Smith

Genus *Araeococcus* Brongniart
20- *Araeococcus flagellifolius* Harms
21- *Araeococcus goeldianus* L.B.Smith
22- *Araeococcus micranthus* Brongniart

Genus *Billbergia* Thunberg
- *Billbergia brachysiphon* L.B.Smith (see Note 8)
23- *Billbergia pyramidalis* (Sims) Lindley
24- **Billbergia rosea* hort. ex Beer (see Note 9)
25- *Billbergia violacea* Beer

Genus *Bromelia* L.
26- *Bromelia agavifolia* Brongniart ex Houllett
27- **Bromelia alta* L.B.Smith (see Note 10)
28- **Bromelia fosteriana* L.B.Smith (see Note 10)
29- *Bromelia granvillei* L.B.Smith & Gouda
- *Bromelia morreniana* (Regel) Mez (see Note 11)
- *Bromelia oleveiriae* L.B.Smith (see Note 12)
30- *Bromelia plumieri* (E.Morren) L.B.Smith
31- *Bromelia serra* Grisebach
- *Bromelia tubulosa* L.B.Smith (see Note 13)

Genus *Disteganthus* Lemaire
32- *Disteganthus basilateralis* Lemaire
33- *Disteganthus lateralis* (L.B.Smith) Gouda

SUBFAMILY PITCAIRNIOIDEAE

Genus *Pitcairnia* L'Héritier de Brutelle
34- *Pitcairnia caricifolia* Martius ex J.H.Schultes
35- **Pitcairnia cremersii* Gouda (see Note 14)
36- *Pitcairnia geyskesii* L.B.Smith
- *Pitcairnia patentiflora* L.B.Smith (see Note 15)
37- *Pitcairnia pusilla* Mez
38- *Pitcairnia rubiginosa* (Brongniart) Baker
var. *rubiginosa* [syn. *Pitcairnia leprieurii*]
39- *Pitcairnia sastrei* L.B.Smith & R.W.Read
40- **Pitcairnia saxosa* Gouda (see Note 14)
41- *Pitcairnia semijuncta* Baker [syn. *Pitcairnia incarnata*]
42- *Pitcairnia sprucei* Baker

SUBFAMILY TILLANDSIOIDEAE

Genus *Catopsis* Grisebach
43- *Catopsis berteroniana* (J.H.Schultes) Mez
44- *Catopsis sessiliflora* (Ruiz & Pavon) Mez

Genus *Guzmania* Ruiz & Pavon
45- *Guzmania altsonii* L.B.Smith
- *Guzmania erythrolepis* Brongniart ex Planchon (see Note 16)
46- *Guzmania lingulata* Mez
var. *lingulata*
47- *Guzmania melinonis* Regel
48- *Guzmania plumieri* (Grisebach) Mez (see Note 17)

Genus *Mezobromelia* L.B. Smith
49- *Mezobromelia pleiosticha* (Grisebach) J.Utley & H.Luther [syn. *Vriesea pleiosticha*]

Genus *Racinaea* M.A. Spencer & L.B. Smith
50- *Racinaea spiculosa* (Grisebach) M.A.Spencer & L.B.Smith
var. *spiculosa*

Genus *Tillandsia* L.
51- *Tillandsia adpressiflora* Mez
52- *Tillandsia anceps* Loddiges
53- *Tillandsia bulbosa* Hooker
54- *Tillandsia fasciculata* Swartz
var. *fasciculata*
55- *Tillandsia flexuosa* O.P.Swartz
56- *Tillandsia kegeliana* Mez
57- *Tillandsia monadelpha* (E.Morren) Baker
58- *Tillandsia paraensis* Mez
59- *Tillandsia tenuifolia* L.
var. *tenuifolia*
60- *Tillandsia usneoides* (L.) L.

Genus *Vriesea* Lindley
61- *Vriesea heliconioides* (Kunth) Hooker ex Walpers
62- *Vriesea jonghei* (Koch) E.Morren
63- *Vriesea procera* (Martius ex J.H.Schultes) Wittmack
64- *Vriesea splendens* (Brongniart) Lemaire
var. *splendens*
- *Vriesea* sp.1 (see Note 18)

Genus *Werauhia* J.R. Grant
65- *Werauhia gigantea* (Martius ex Schultes f.) J.R.Grant
66- *Werauhia gladioliflora* (Wendland) J.R.Grant

NOTES

1. According to Gouda, *Aechmea castelnavii* Baker should be found in French Guiana (**Boggan *et al.* 1992, 1997; Funk *et al.* 2007**). However, nothing indicates that this species is actually present on the Guianese territory. Therefore, *A. castelnavii* is not included here.

2. *Aechmea costantinii* (Mez) L.B.Smith was formerly listed as *Aechmea megalantha* Harms in the first two editions of the checklist of the plants of the Guianas (**Boggan *et al.* 1992, 1997**) but was always followed by the comment "probable misidentification of *Aechmea melinonii* Hooker according to Gouda". This species is no longer listed as either *A. megalantha* or *A. costantinii* in the last checklist of the plants of the Guiana Shield (**Funk *et al.* 2007**). Its presence in French Guiana should be interpreted as a misidentification and, thus, the species is not included here.

3. *Aechmea fernandae* (E.Morren) Baker was listed as "to be expected in French Guiana" in **Boggan *et al.*** (**1992, 1997**), but was not listed in **Funk *et al.*** (**2007**). Because there are no confirmed records of this species in French Guiana, *A. fernandae* is not included here.

4. A specimen identified by Gouda as *Aechmea lanjouwii* (L.B.Smith) L.B.Smith from the inselberg 'La Virginie' was deposited in the Herbarium of Cayenne, French Guiana. It appears that this taxon is a natural hybrid of *A. aquilega* and *A. moonenii* (**Gouda & Moonen 2002**). For that reason, this taxon is listed but is not included here.

5. *Aechmea rubiginosa* Mez was not listed in **Boggan *et al.*** (**1992, 1997**), but listed as "to be expected in French Guiana" in **Funk *et al.*** (**2007**). Because there are no confirmed records of this species in French Guiana, *A. rubiginosa* is not included here.

6. Two unidentified species of *Aechmea* (i.e. *Aechmea* sp.1 and sp.2) were collected by Aurélien Sambin in French Guiana from two unknown locations. These specimens might constitute new species records for the Guianese territory.

7. The nomenclature adopted here for the intricate genus *Ananas* follows the line of thinking of **Butcher and Gouda** (**2014**). *Ananas comosus* (L.) L. and *Ananas erectifolius* L.B.Smith, first known from French Guiana, have been reduced to the rank of variety. They are listed as *Ananas* 'Comosus' and *Ananas* 'Erectifolius'; because they no longer represent proper species, they have not been taken into account. Some evidence indicates that *Ananas ananassoides* var. *nanus* L.B.Smith, *Ananas* 'Bracteatus' and *Ananas* 'Tricolor' might be present in French Guiana. These records need to be confirmed and are thus not included here.

8. According to Gouda, *Billbergia brachysiphon* L.B.Smith should be found in French Guiana (**Boggan *et al.* 1992, 1997; Gouda 1999; Funk *et al.* 2007**). However, at this time, there are no confirmed records of this species in French Guiana; thus, *B. brachysiphon* is not included here.

9. *Billbergia rosea* hort. ex Beer appeared in the checklist by **Funk *et al.*** (**2007**) without further references. Nevertheless, we decided to include this species in the present list.

10. *Bromelia alta* L.B.Smith and *Bromelia fosteriana* L.B.Smith were collected by Olivier Tostain in 2011 and 2013, respectively. Voucher specimens of each species (ID4998 and ID6395, respectively) were deposited in the **Herbarium of Cayenne, French Guiana** (**2015**). They constitute confirmed records and are thus included here.

11. According to Gouda, *Bromelia morreniana* (Regel) Mez should be found in French Guiana (**Boggan *et al.* 1992, 1997; Gouda 1999; Funk *et al.* 2007**). However, at this time, there are no confirmed records of this species in French Guiana; thus, *B. morreniana* is not included here.

12. *Bromelia oleveiriae* L.B.Smith was listed in **Boggan *et al.*** (**1992**), its presence questioned in **Boggan *et al.*** (**1997**) and finally noted as "not expected in French Guiana" in **Funk *et al.*** (**2007**). A voucher specimen identified as *B. oleveiriae* (ID7112) collected by de Granville on Mont Belvédère in 1984 is deposited in the **Herbarium of Cayenne, French Guiana** (**2015**). However, this specimen needs to be reexamined before the species is included here.

13. The presence of *Bromelia tubulosa* L.B.Smith in French Guiana was questioned in **Boggan *et al.*** (**1992, 1997**) and **Funk *et al.*** (**2007**). Voucher specimens identified as *B. tubulosa* (ID7414 and ID10702) were deposited in the Herbarium of Cayenne, French Guiana (2015) collected respectively by Cremers at La Trinité in 1981, and by de Granville at the Monts Atachi Bakka in 1989. However, these specimens need to be reexamined before the species can be included here.

14. *Pitcairnia cremersii* Gouda and *Pitcairnia saxosa* Gouda were originally described from Guianese inselbergs in 2009. It is natural that these two species are included in the present list.

15. According to **Gouda** (**2009**), *Pitcairnia patentiflora* L.B.Smith "is not yet known from the Guianas, but from the neighboring Venezuela, Amazonas, Rio Negro, and Brazil (Pará)". Therefore, *P. patentiflora* is not included here.

16. *Guzmania erythrolepis* Brongniart ex Planchon was listed in French Guiana as a probable misidentification of *Guzmania melinonis* Regel in **Boggan *et al.*** (**1992, 1997**) and

Gouda (**1999**), and finally not listed in **Funk *et al.*** (**2007**). Its presence in French Guiana should be interpreted as a misidentification and, thus, the species is not included here.

17. *Guzmania plumieri* (Grisebach) Mez is abundant in the Lesser Antilles. This species has also been listed for French Guiana (**Boggan *et al.* 1992, 1997; Gouda 1999; Funk *et al.* 2007**). However, we failed to find any information on the location of this species in French Guiana. Nevertheless, we chose to keep this species in the present list until more information becomes available.

18. On November 2014, a mysterious specimen belonging to the genus *Vriesea* was collected by the first author growing on the ground on the western slopes (600 a.s.l.) of Mont Itoupé, Camopi, French Guiana. As regards to its vegetative characteristics (cf. herbarium specimen), the specimen was identified as *Vriesea vagans* (L.B.Smith) L.B.Smith. However, considering that the collected specimen was not in bloom, this record cannot be confirmed. DNA sequencing using matK and rbcL is underway.

APPENDIX 5a. Results of the global models for *Culex* (*Microculex*) *pleuristriatus*, *Wyeomyia* (*Wyeomyia*) *pertinans* and *Toxorhynchites* (*Lynchiella*) *haemorrhoidalis* at four spatial scales. Models include the volume of water (WV), the amount of organic matter (OM), the meta-habitat size (mhs), the distance to the nearest building (dist_build), the surface area of ground (surf_ground), and the surface area of vegetation (surf_veget). The Variance Inflation Factor (VIF) is indicated for each variable at each spatial scale. Level of significance: *: P < 0.05; **: P < 0.01; ***: P < 0.001.

Culex (*Mcx.*) *pleuristriatus*

Scales	10 m				30 m			
	Estimate ± SE	t-value	P-value	VIF	Estimate ± SE	t-value	P-value	VIF
WV	1.0952 ± 0.3400	3.222	0.0035**	1.60450	1.1626 ± 0.3533	3.291	0.0029**	1.27243
OM	-0.1578 ± 0.4004	-0.394	0.6968	1.49328	-0.6167 ± 0.4873	-1.266	0.2173	1.62408
mhs	0.4671 ± 0.1229	3.802	0.0008***	1.31364	0.3344 ± 0.1634	2.047	0.0512	1.10723
dist_build	1.1468 ± 0.5493	2.088	0.0471*	1.69267	0.7301 ± 0.5601	1.304	0.2042	1.29200
surf_ground	-0.3725 ± 0.3184	-1.17	0.2531	2.54508	-0.0782 ± 0.6223	-0.126	0.9010	1.66803
surf_veget	-1.8063 ± 1.0169	-1.776	0.0878	3.34617	-0.2282 ± 0.7158	-0.319	0.7524	1.89696
Scales	50 m				70 m			
	Estimate ± SE	t-value	P-value	VIF	Estimate ± SE	t-value	P-value	VIF
WV	0.9787 ± 0.3339	2.932	0.0071**	1.28436	0.9112 ± 0.3424	2.661	0.0134*	1.41797
OM	-0.5816 ± 0.4286	-1.357	0.1869	1.42006	-0.4872 ± 0.4151	-1.174	0.2516	1.39814
mhs	0.1801 ± 0.1390	1.295	0.2070	1.06598	0.1938 ± 0.1456	1.331	0.1953	1.22902
dist_build	0.8433 ± 0.5012	1.683	0.1049	1.16940	0.6122 ± 0.4856	1.261	0.2191	1.15246
surf_ground	-1.7017 ± 0.7924	-2.148	0.0416*	1.25972	-1.9146 ± 1.0128	-1.890	0.0703	1.41293
surf_veget	-0.7418 ± 0.4734	-1.567	0.1297	1.17331	-0.9263 ± 0.4691	-1.975	0.0594	1.14654

Wyeomyia (*Wyo.*) *pertinans*

Scales	10 m				30 m			
	Estimate ± SE	t-value	P-value	VIF	Estimate ± SE	t-value	P-value	VIF
WV	-0.2027 ± 0.3812	-0.532	0.5995	1.60450	-0.0101 ± 0.3502	-0.029	0.9773	1.27244
OM	0.6320 ± 0.4490	1.408	0.1716	1.49328	0.6078 ± 0.4831	1.258	0.2200	1.62408
mhs	-0.2509 ± 0.1378	-1.821	0.0806	1.31364	-0.2797 ± 0.1619	-1.727	0.0965	1.10724
dist_build	0.2116 ± 0.6160	0.343	0.7341	1.69267	-0.1145 ± 0.5552	-0.206	0.8382	1.29200
surf_ground	-0.1494 ± 0.3571	-0.418	0.6793	2.54508	-0.7609 ± 0.6169	-1.233	0.2289	1.66803
surf_veget	-1.2218 ± 1.1403	-1.071	0.2942	3.346178	0.0920 ± 0.7097	0.130	0.8979	1.89696
Scales	50 m				70 m			
	Estimate ± SE	t-value	P-value	VIF	Estimate ± SE	t-value	P-value	VIF
WV	0.0228 ± 0.3618	0.063	0.950	1.28436	-0.0127 ± 0.3904	-0.032	0.974	1.41797
OM	0.6762 ± 0.4646	1.455	0.158	1.42006	0.7244 ± 0.4733	1.530	0.139	1.39814
mhs	-0.2097 ± 0.1507	-1.391	0.176	1.06598	-0.1307 ± 0.1660	-0.787	0.439	1.22902
dist_build	-0.2089 ± 0.5432	-0.384	0.704	1.16940	-0.3222 ± 0.5537	-0.582	0.566	1.15246
surf_ground	-0.6936 ± 0.8589	-0.808	0.427	1.25972	-1.0579 ± 1.1549	-0.916	0.368	1.41293
surf_veget	0.3712 ± 0.5131	0.723	0.476	1.17331	0.3006 ± 0.5349	0.562	0.579	1.14654

Toxorynchites (*Lyn.*) *haemorrhoidalis*									
Scales	10 m					30 m			
	Estimate ± SE		z-value	P-value	VIF	Estimate ± SE		z-value	P-value	VIF
WV	-0.1157 ± 0.7190		-0.161	0.872	1.53776	-0.2219 ± 0.6973		-0.318	0.750	1.30965
OM	0.5611 ± 0.8733		0.643	0.521	1.55637	0.6423 ± 1.1286		0.569	0.569	1.80833
mhs	-0.1808 ± 0.2753		-0.657	0.511	1.37481	-0.6581 ± 0.4215		-1.561	0.119	1.50149
dist_build	-1.2851 ± 1.2034		-1.068	0.286	1.55404	-2.2658 ± 1.2888		-1.758	0.079	1.47226
surf_ground	0.5044 ± 0.7113		0.709	0.478	2.68359	1.9473 ± 1.3468		1.446	0.148	2.01632
surf_veget	0.2875 ± 2.3315		0.123	0.902	3.24467	3.0151 ± 1.6630		1.813	0.069.	2.62086
Scales	50 m					70 m			
	Estimate ± SE		z-value	P-value	VIF	Estimate ± SE		z-value	P-value	VIF
WV	0.1433 ± 0.7050		0.203	0.839	1.33987	0.0702 ± 0.7003		0.100	0.920	1.25940
OM	0.3305 ± 0.9567		0.346	0.730	1.38407	0.6237 ± 0.9438		0.661	0.509	1.26323
mhs	-0.2176 ± 0.2893		-0.752	0.452	1.05406	-0.2575 ± 0.3373		-0.763	0.445	1.12714
dist_build	-2.0529 ± 1.3050		-1.573	0.116	1.39639	-1.8060 ± 1.2930		-1.397	0.163	1.22080
surf_ground	2.8014 ± 1.8965		1.477	0.140	1.62929	3.9801 ± 2.5004		1.592	0.111	1.64332
surf_veget	2.6863 ± 1.4566		1.844	0.065	1.89666	3.2024 ± 1.5443		2.074	0.038*	1.62295

APPENDIX 5b. Result of the multimodel inferences for *Culex* (*Microculex*) *pleuristriatus*, *Wyeomyia* (*Wyomyia*) *pertinans* and *Toxorhynchites* (*Lynchiella*) *haemorrhoidalis* at four spatial scales. For each case, only the first eight best-fitting models are indicated and the predictors are abbreviated as follows: 1: the distance to the nearest building (dist_build), 2: the amount of organic matter (OM), 3: the surface area of vegetation (surf_veget), 4: the surface area of ground (surf_ground), 5: the meta-habitat size (mhs), and 6: the volume of water (WV).

Culex (*Mcx.*) *pleuristriatus*

Model at 10 m	*K*	log(L)	AIC	Δ_i	w_i	Model at 30 m	*K*	log(L)	AIC	Δ_i	w_i
{5+6}	4	-44.24	96.48	0	0.15	{5+6}	4	-48.13	104.26	0	0.12
{1+3+5+6}	6	-42.29	96.57	0.09	0.14	{1+2+5+6}	6	-46.34	104.69	0.43	0.1
{1+3+4+5+6}	7	-41.44	96.87	0.39	0.12	{2+5+6}	5	-47.39	104.79	0.53	0.1
{1+5+6}	5	-43.51	97.01	0.53	0.11	{1+5+6}	5	-47.65	105.3	1.04	0.07
{3+5+6}	5	-44.07	98.14	1.66	0.06	{4+5+6}	5	-47.93	105.85	1.6	0.06
{1+2+3+5+6}	7	-42.19	98.38	1.9	0.06	{3+5+6}	5	-47.95	105.9	1.64	0.05
{2+5+6}	5	-44.21	98.43	1.94	0.06	{1+3+5+6}	6	-47.27	106.54	2.29	0.04
{4+5+6}	5	-44.24	98.48	2	0.05	{1+2+3+5+6}	7	-46.29	106.58	2.32	0.04
Model at 50 m						Model at 70 m					
{1+2+3+4+5+6}	8	-44.32	104.64	0	0.07	{3+4+5+6}	6	-44.92	101.83	0	0.11
{1+2+3+4+6}	7	-45.36	104.72	0.08	0.07	{3+4+6}	5	-46.3	102.61	0.78	0.07
{1+3+4+6}	6	-46.4	104.8	0.16	0.06	{1+3+4+5+6}	7	-44.4	102.8	0.97	0.07
{1+3+4+5+6}	7	-45.46	104.92	0.27	0.06	{2+3+4+5+6}	7	-44.53	103.06	1.22	0.06
{3+4+5+6}	6	-46.47	104.95	0.3	0.06	{1+2+3+4+5+6}	8	-43.54	103.09	1.25	0.06
{3+4+6}	5	-47.73	105.45	0.81	0.05	{1+2+3+4+6}	7	-44.64	103.28	1.44	0.05
{1+2+4+6}	6	-46.73	105.46	0.82	0.05	{1+3+4+6}	6	-45.69	103.37	1.54	0.05
{1+2+4+5+6}	7	-45.82	105.64	1	0.04	{2+3+4+6}	6	-45.82	103.63	1.8	0.04

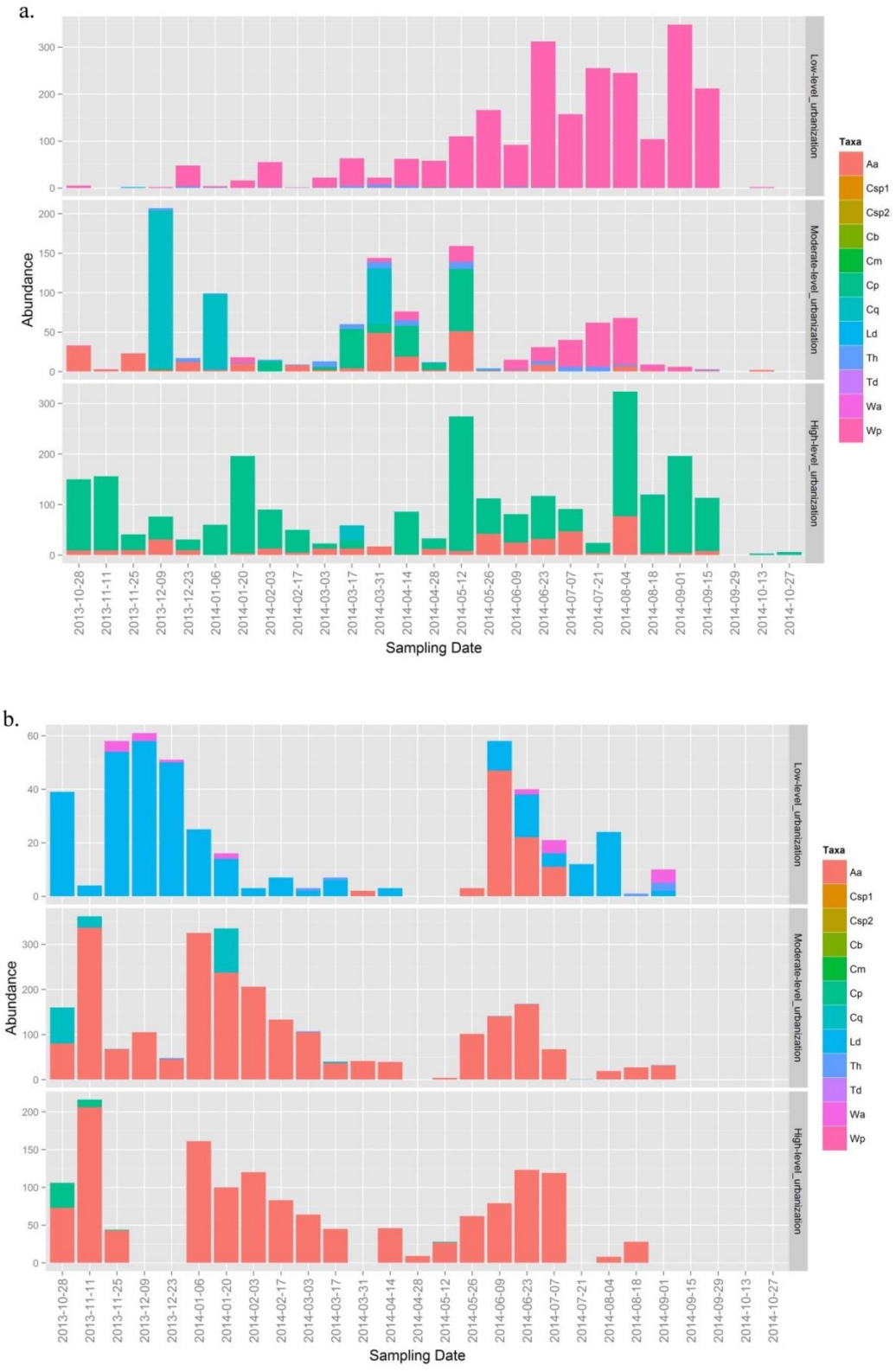
Wyeomyia (*Wyo.*) *pertinans*

Model at 10 m	*K*	log(L)	AIC	Δ_i	w_i	Model at 30 m	*K*	log(L)	AIC	Δ_i	w_i
{5}	3	-46.8	99.61	0	0.11	{2+4+5}	5	-46.03	102.07	0	0.09
{2+5}	4	-46.02	100.04	0.43	0.09	{4+5}	4	-47.33	102.65	0.59	0.07
{2+3+5}	5	-45.24	100.47	0.87	0.07	{2+5}	4	-47.62	103.23	1.17	0.05
{3+5}	4	-46.51	101.01	1.41	0.06	{4}	3	-48.85	103.7	1.64	0.04
{4+5}	4	-46.76	101.52	1.91	0.04	{2+4}	4	-47.95	103.9	1.84	0.04
{5+6}	4	-46.77	101.55	1.94	0.04	{1+2+4+5}	6	-46.01	104.03	1.96	0.03
{2+4+5}	5	-45.78	101.56	1.95	0.04	{2+3+4+5}	6	-46.03	104.06	1.99	0.03
{1+5}	4	-46.8	101.6	2	0.04	{2+4+5+6}	6	-46.03	104.06	2	0.03
Model at 50 m						Model at 70 m					
{2}	3	-49.11	104.22	0	0.06	{2}	3	-49.11	104.22	0	0.09
{2+5}	4	-48.17	104.34	0.12	0.06	{2+4}	4	-48.65	105.3	1.08	0.05
{2+4+5}	5	-47.31	104.62	0.4	0.05	{2+3}	4	-48.67	105.35	1.13	0.05
{2+3+5}	5	-47.5	105	0.78	0.04	{1+2}	4	-48.84	105.69	1.47	0.04
{2+4}	4	-48.58	105.17	0.95	0.04	{Null}	2	-50.85	105.71	1.48	0.04
{2+3}	4	-48.6	105.19	0.97	0.04	{2+5}	4	-49	106	1.78	0.04
{1+2}	4	-48.84	105.69	1.47	0.03	{2+6}	4	-49.07	106.15	1.92	0.03
{Null}	2	-50.85	105.71	1.48	0.03	{4}	3	-50.14	106.29	2.06	0.03

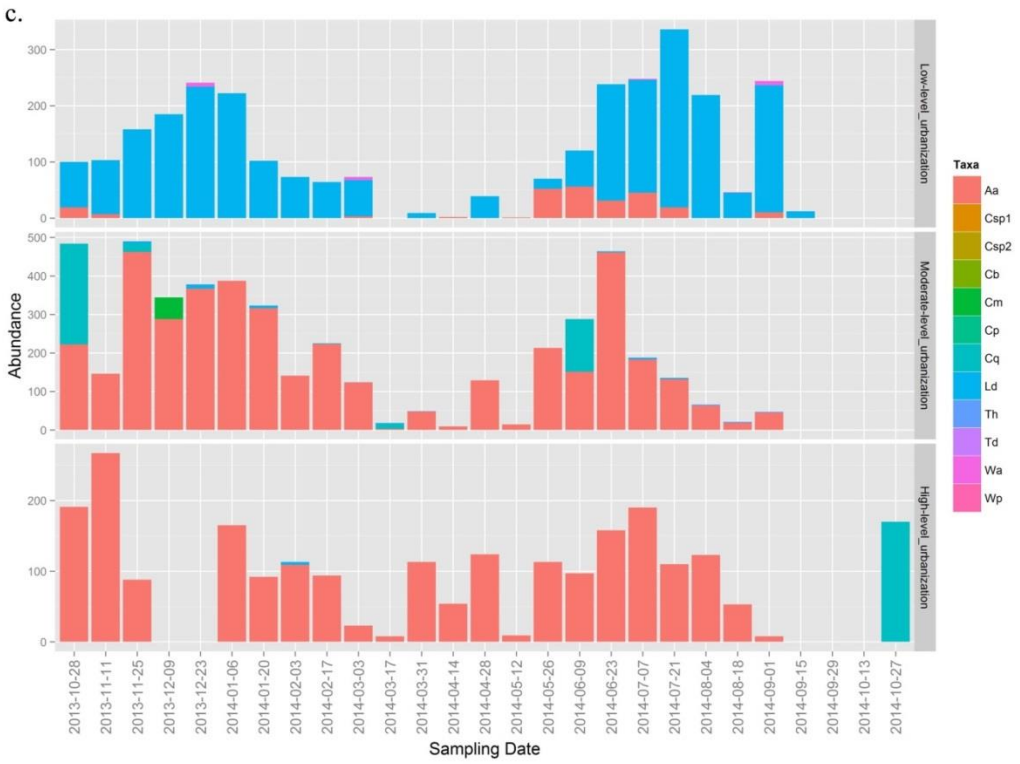
Toxorhynchites (*Lyn.*) *haemorrhoidalis*											
Model at 10 m	*K*	log(L)	AIC	Δ_i	w_i	Model at 30 m	*K*	log(L)	AIC	Δ_i	w_i
{Null}	1	-22.18	46.36	0	0.08	{1+3+4+5}	5	-18.15	46.3	0	0.05
{1}	2	-21.34	46.68	0.32	0.07	{Null}	1	-22.18	46.36	0.07	0.05
{3}	2	-21.48	46.96	0.59	0.06	{5}	2	-21.19	46.38	0.08	0.05
{4}	2	-21.65	47.29	0.93	0.05	{1+3+5}	4	-19.28	46.55	0.26	0.05
{5}	2	-21.88	47.77	1.41	0.04	{1}	2	-21.34	46.68	0.39	0.04
{1+4}	3	-21.04	48.08	1.72	0.03	{3+5}	3	-20.43	46.85	0.56	0.04
{1+5}	3	-21.07	48.14	1.78	0.03	{1+5}	3	-20.6	47.19	0.9	0.03
{1+2}	3	-21.15	48.3	1.94	0.03	{1+3}	3	-20.66	47.33	1.03	0.03
Model at 50 m						Model at 70 m					
{1+3+4}	4	-18.41	44.82	0	0.08	{1+3+4}	4	-17.84	43.68	0	0.09
{1+3}	3	-19.82	45.63	0.81	0.06	{3+4}	3	-18.85	43.7	0.02	0.08
{3}	2	-21	46	1.18	0.05	{3+4+5}	4	-18.44	44.87	1.19	0.05
{3+4}	3	-20.06	46.11	1.29	0.04	{1+3+4+5}	5	-17.46	44.93	1.25	0.05
{1+3+4+5}	5	-18.11	46.21	1.39	0.04	{1+2+3+4}	5	-17.5	45	1.32	0.04
{Null}	1	-22.18	46.36	1.54	0.04	{3+5}	3	-19.65	45.29	1.61	0.04
{1+2+3+4}	5	-18.31	46.62	1.79	0.03	{3}	2	-20.69	45.38	1.7	0.04
{3+5}	3	-20.32	46.63	1.81	0.03	{1+3}	3	-19.73	45.46	1.78	0.04

K indicates the number of estimable parameters in the model.

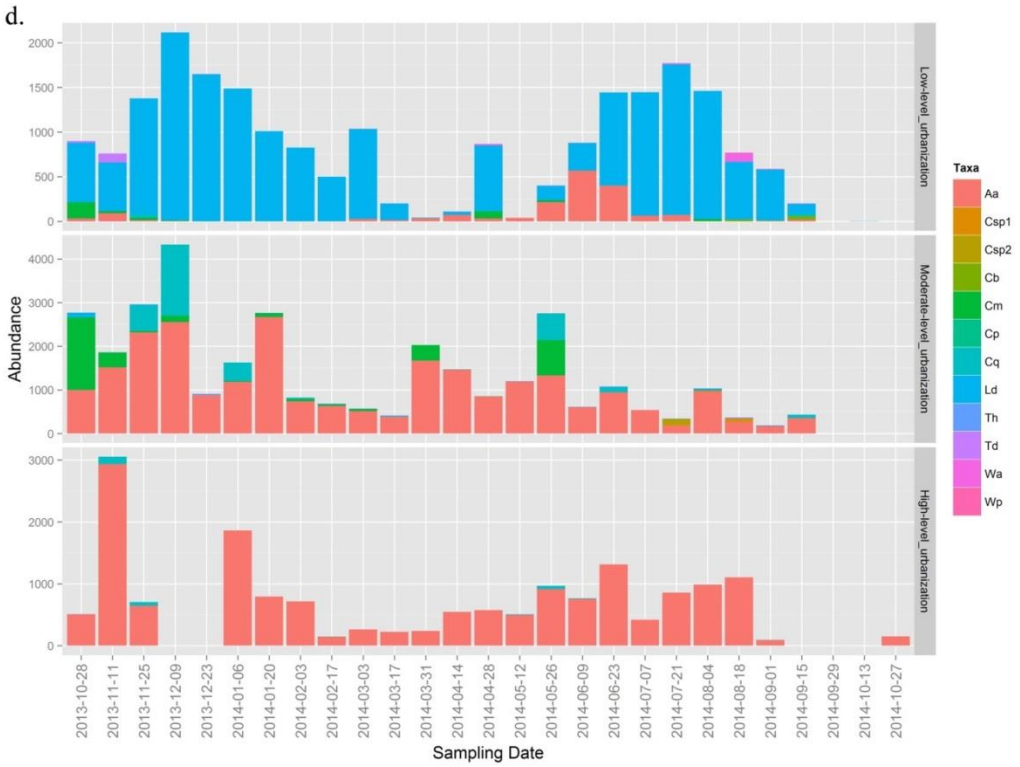
APPENDIX 6. Annual fluctuations in the abundance of immature mosquito taxa inside tank bromeliads (a.), bamboo stumps (b.), ovitraps (c.) and tires (d.) along an urbanization gradient in the city of Kourou, French Guiana. Mosquito taxa are abbreviated as follows. Aa: *Aedes* (*Stg.*) *aegypti*, Csp1: *Culex* sp.1, Csp2: *Culex* sp.2, Cb: *Culex* (*Car.*) *bonnei*, Cm: *Culex* (*Cx.*) *mollis*, Cp: *Culex* (*Mcx.*) *pleuristriatus*, Cq: *Culex* (*Cx.*) *quinquefasciatus*, Ld: *Limatus durhamii*, Th: *Toxorhynchites* (*Lyn.*) *haemorrhoidalis*, Td: *Trichoprosopon digitatum*, Wa: *Wyeomyia* (*Wyo.*) *aporonoma*, Wp: *Wyeomyia* (*Wyo.*) *pertinans*.



c.


Low-level_urbanization
Moderate-level_urbanization
High-level_urbanization
Abundance
Sampling Date
Taxa
Aa
Csp1
Csp2
Cb
Cm
Cp
Cq
Ld
Th
Td
Wa
Wp

d.


Low-level_urbanization
Moderate-level_urbanization
High-level_urbanization
Abundance
Sampling Date
Taxa
Aa
Csp1
Csp2
Cb
Cm
Cp
Cq
Ld
Th
Td
Wa
Wp