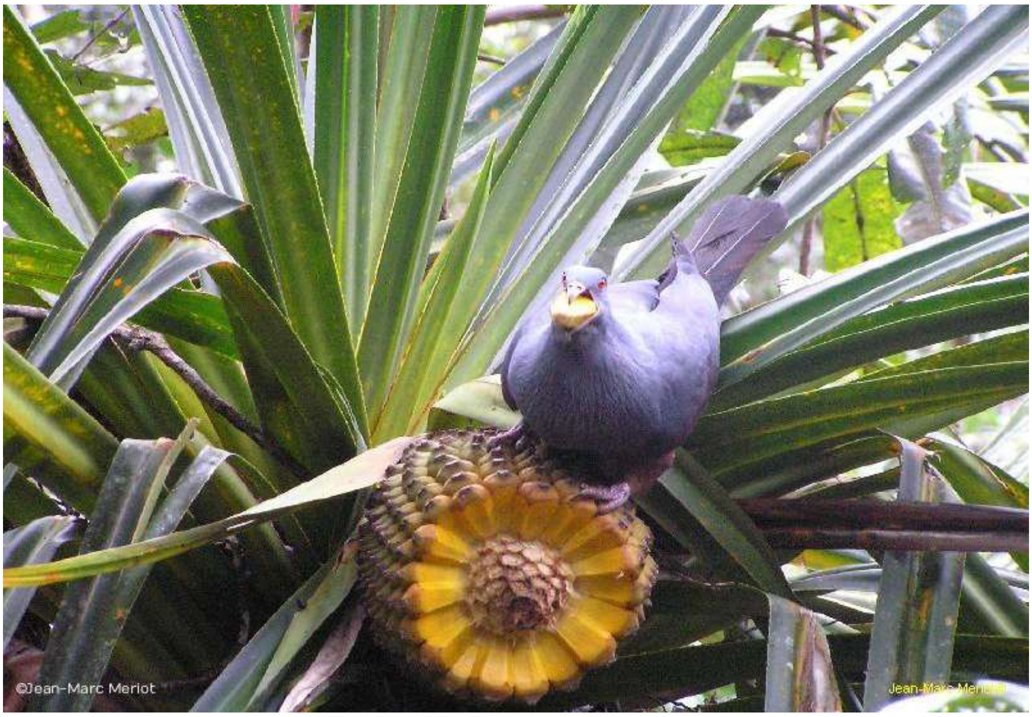
Distribution of dispersal syndromes in New Caledonian forests



Ducula goliath ©Jean-Marc Meriot

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ABSTRACT

Aim: To analyze the distribution of dispersal syndromes in humid forest communities. We test the hypothesis that (i) the proportion of plant dispersed by wind is lower in warm and wet environment, and (ii) whether species rich communities exhibit intermediate proportion of wind-dispersed plants (as proxy of disturbance regime).

Location: Main island of New Caledonia (Grande Terre), SW Pacific

Methods: We built a dispersal traits database covering 450 plant species inventoried in 16 1-ha plots. We then inferred dispersal syndromes (i.e. the more likely dispersal traits. We compile the proportion of different dispersal syndromes (i.e. wind-dispersed, animal-dispersed or other) in each 1-ha plots at both the species and individual levels. We first tested whether the proportion of wind-dispersed plants was correlated to mean annual temperature (MAT) and mean annual precipitation (MAP) using generalize linear models. We then tested whether species richness followed a humped pattern with the proportion of wind dispersed plants. To do that, we used a second order polynomial regression.

Results: Less than 10% of species and 6% of plants were likely to be dispersed by wind in studied forest. The proportion of wind dispersed plants ranged from about 0 to 15% and significantly increased with MAP and decrease with increasing MAT. We found that species richness was significantly correlated to the proportion of wind dispersed plants peaking at about 100 species per hectare for 10% of wind dispersed plants.

Conclusion: The proportion of wind dispersed plants was globally low compared to other forests in New Caledonia and elsewhere in tropics. The humped pattern between species richness and the proportion of wind dispersed plants verify the intermediate disturbance hypothesis according to which species richness is maximal for intermediate levels of disturbances. This suggests that the proportion of wind dispersed plants can be used as proxy of the level of disturbance.

Key words: Anemochory, Dispersal appendage, Fruit type, Richness, Zoochory

INTRODUCTION

Plants can be considered as immobile organisms and dispersal is therefore a key process in their life cycle. Plants produce a great variety of dispersal structures with fruit and seed of different type, size, color and the development of different dispersal appendages (e.g. arils, hair or wings) to enhance their dispersal abilities. These different dispersal features are observable or measurable functional traits that can be used to infer how plants are likely to be dispersed, i.e. their dispersal syndrome (Pérez-Harguindeguy et al., 2013). Fruits and the associated dispersal syndromes give information about the tree ecology and studying how the proportion of different dispersal syndrome (e.g. dispersed by wind or animals) varies between different plant communities may help to understand how plant communities are assembled.

Within a single plant family a staggering variety of fruit types can be found such as fleshy fruits including berries, pomes, and drupes and dry fruit structures like achenes, capsules, and follicles (Dardick & Callahan, 2014). Those characteristics of fleshy and dry structures have major impacts on energy investment in fruit dispersal strategy the plant are likely to employ (Howe & Smallwood, 1982). Species dispersed by wind are usually adapted to unstable environment (MacArthur, 1967). Unstable environment include unstable climate or frequently disturbed environment. For instance, Si-Chong Chen (2016) showed that in Australia, the proportion of plants with fleshy fruits (i.e. likely dispersed by animal) is higher in areas with wet, warm and stable climate. Several other studies have suggested that climate could play an important role in individual fruit type distribution (Bolmgre n & Eriksson, 2005).

Concerning disturbance regime, Ibanez et al. (2017) have shown that in the fragmented landscape of New Caledonia, the proportion of wind dispersed trees decrease from forest edge (i.e. exposed to disturbances) to forest core (i.e. relatively undisturbed). It is therefore possible to infer disturbance regime from the proportion of plants dispersed by wind (e.g. Molino & Sabatier, 2001). Communities with high proportion of plants dispersed by wind reflect habitats being theoretically recently or frequently disturbed.

In addition to the study from Ibanez et al. (2017), there is to our knowledge only two studies that explored the dispersal attributes of plants in the New Caledonian flora. Carpenter & al. (2007) have studied the reproductive traits of tropical humid forest trees on ultramafic substrate in

New Caledonia. These authors showed that the proportion of species dispersed by wind (about 21%) was relatively high in comparison with other tropical humid forests. They suggested that this relatively high proportion of wind-dispersed species may be related to the low nutrient availability in ultramafic substrates. Conversely, another study by Boquetal (2007) in dry forests has shown that the proportion of species dispersed by wind (about 19 %) was relatively low in comparison with other tropical dry forests. They suggested that this relatively low proportion of wind-dispersed species may be related to an insularity syndrome.

Here, we investigate the distribution of dispersal syndromes within New Caledonian humid forests mostly located on non-ultramafic substrate. According to the intermediate disturbance hypothesis, stating that the species richness is maximal in area with intermediate levels of disturbance (Connell, 1978), we expect that communities with an intermediate proportion of wind-dispersed trees would be the most species rich. Furthermore, we suggest that the mean annual temperature and the mean annual precipitations would impact the proportion of trees and species dispersed by wind. To test these hypotheses, I computed a database of functional traits related to the dispersal of 450 trees species. This database was used to infer dispersal syndromes and the distribution of dispersal syndrome in 16 forest communities.

I. MATERIALS AND METHODS

1. Geographical context of New Caledonia (study area)

New Caledonia is an archipelago located in the Pacific Ocean between 18°–23° S and 163°–169° E. It is approximately 1,500 km away from Australia, the nearest continent. It comprises a main island (Grande Terre), considered to be the oldest oceanic island (37Ma) and several smaller and much more recent islands, making a total land surface of about 18,760 km^2. Its landscape is characterized by a central mountain range running along the island, with five peaks over 1,500 m. New Caledonia is globally renowned for the diversity and originality of its flora and known as a hotspot for conservation priority given the high level of threats on its flora and habitats (Myers et al., 2000).

2. Study sites and species

In this study I analyzed the distribution of dispersal syndrome in 16 1-haplots (Fig. 1) from the New Caledonian plant inventories and Permanent Plots Network (NC-PIPPN, Ibanez et al., 2017). These plots are located in 13 geographically different sites mostly located in the Northern Province (only one plot, Grand Lac in the Southern Province) and on non-ultramafic substrates (only two plots Grand Lac and Wekori on ultramafic substrate). In these plots all plants with diameter at breast weight (DBH, i.e. at ~1.30 m above soil) ≥ 10 cm were inventoried. A total of 17 891 individuals categorized into 450 species from 180 genera and 81 families were inventoried.

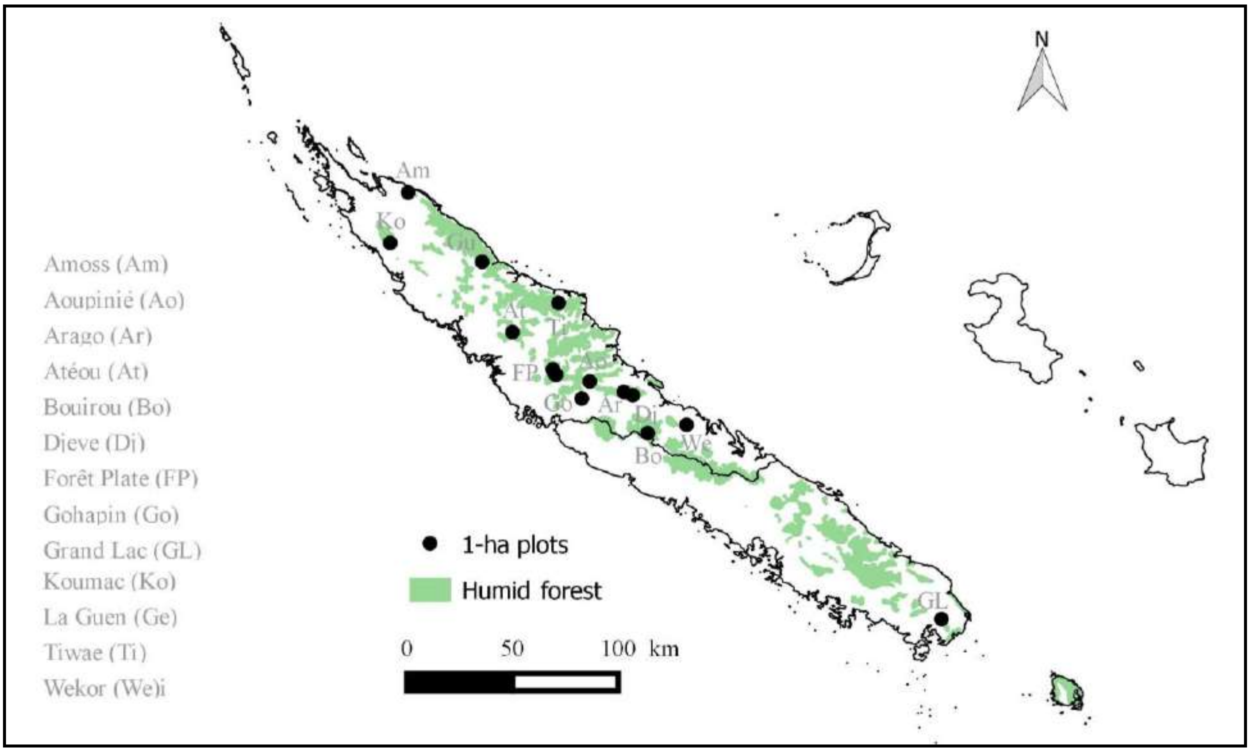

Figure 1: Location of the study plots (the humid forest layer is from the atlas of New-Caledonia)

Table 1. Descriptive table of the study plots (Latitudes, Longitude, Altitude, Mean annual precipitation, mean annual temperature)

Plot name	Lat (DD)	Long (DD)	Alt (m)	MAP (mm)	MAT (°C)
Amoss	-20,31	164,44	480	1547	20,88
Aoupinié	-21,18	165,28	882	1570	19,15
Arago	-21,24	165,48	484	1675	20,53
Ateou	-20,95	164,92	768	1785	19,28
Bouirou	-21,42	165,55	538	1477	20,30
Djeve	-21,23	165,44	376	1636	20,11
Forêt_plate_P09	-21,15	165,12	505	1569	20,47
Forêt_plate_p12	-21,15	165,12	510	1569	20,47
Forêt_plate_p17	-21,12	165,11	456	1631	20,78
Forêt_plate_p26	-21,13	165,11	482	1602	20,68
Gohapin	-21,26	165,24	269	1574	21,53
Grand_Lac	-22,27	166,90	288	2484	20,76
Koumac	-20,54	164,36	56	1104	23,25
Laguen	-20,63	164,78	581	1926	20,54
Tiwae	-20,81	165,13	238	2239	21,78
Wekori	-21,38	165,73	66	1714	22,71

3. Dispersal trait Database

We built a dispersal trait database using "Pl@ntNote software". Pl@ntNote is a free software developed for botanist and plant ecologist to manage plant occurrences and their attributes http://amap-collaboratif.cirad.fr/pages-logiciels/?page_id=410). We recorded all available information on the taxonomy (family, genus, species), and dispersal traits (fruit/seed type, color, shape and dimension, dispersal unit and dispersal appendage). For each species, I computed the fruit type (e.g. drupe, berry or capsule), the dispersal unit (fruit or seed), the presence of dispersal appendage (e.g. arils, hairs or wings), the fruit and seed colors, dimensions and shapes (see Annexes).

The database was first assembled by an exhaustive survey of the Flora of New Caledonia (Aubréville et al. 1967). We then add entries with additional information from the Endemia website (http://endemia.nc/) and published articles. When we did not find any information on dispersal traits we completed the database using botanist expertise. When information was not available for species we used the available information at the genus or the family level. We then created 482 entries in which we recorded all the available data of the 450 inventoried species. We finally observed nine different fruit types including drupes, berries, capsules, follicle, nuts, cloves, cone, sycone, sporangium and achene.

4. Data analysis

a) Determination of dispersal pattern

To infer the dispersal syndrome of each species from dispersal traits we followed the method described by Pérez-Harguindeguy et al, 2013 in the handbook for measurement of plant traits. These authors categorized species as dispersed by wind (anemochory) when they produce small dry seeds or dispersal unit with appendage allowing to “fly” in the wind including for instance seeds with hairs or wings.

Plant dispersed by animals (endo-and-exo-zoochory) included plant producing fleshy fruits (e.g.drupes and berries) or dispersal unit with fleshy appendages such as arils or and brightly colored. Moreover, it included fruits or seeds that become attached (e.g. to animal hair, feathers, legs, bills, aides by appendages such as hook, barbs, awns, burs or sctiky substances).

We succeeded to infer dispersal syndromes of 73 % of the studies species according to this classification and using dispersal traits we gathered in our database. The dispersal syndrome of 19 % was inferred using botanist expertise. However, it was tricky to determinate the dispersal syndrome for 8% of species so we choose to classified them as Non-identified to avoid confusion.

b) Statistical analysis

We first computed the proportion of species and individual dispersed by wind (anemochory), animals (zoochory) or indeterminate. We then assessed how the proportion of plants dispersed by wind or animals varies between plots and how the proportions changed when we considered the proportion of species or individual. We tested whether or not the proportion of species or individual dispersed by wind was correlated with mean annual temperature (MAT) and mean annual precipitation (MAP) using linear regressions. To do that, we used Generalized Linear Models with a logit link function. MAP and MAT were extracted for plot locations from the WorldClim climatology at a spatial resolution of 30 arc-seconds (≈ 1 km, http://www.worldclim.org/bioclim). We also tested whether the number of species (the species richness) inventoried in a plot was correlated to the proportion of wind dispersal plants. As we expected a hump pattern, we used a 2nd order polynomial regression. Statistical analyses were performed using R version and sub-version software for statistical computing.

II. RESULTS

Over the 450 studied species, 8.9% has been classified as wind dispersed (anemochory) and 82.7% as animal dispersed (zoochory, see Fig 2). The remaining 8.4% were classified as non-identified dispersal. Overall, we observed a dominance of zoochory followed by anemochory and non-identified species.

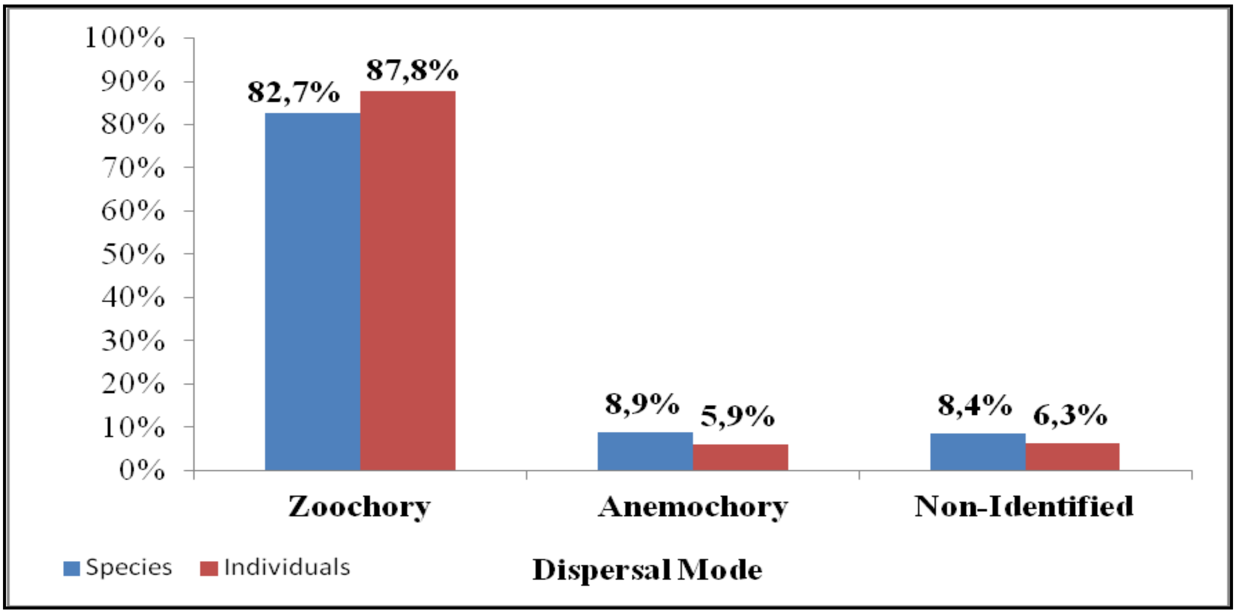

Figure 2: Distribution of dispersal syndromes in the whole dataset of 16 1-ha plots pooled together as the percentage of species or individuals dispersed by animals (zoochory), wind (anemochory) or non-identified.

At the plot scale the percentage of species dispersed by animals ranged from 80 % in Grand Lac to 94% in Forêt_plâte_P09 and was 87 % on average. The percentage of species dispersed by wind ranged from 3% in Wekori, Forêt_plâte_17 and Forêt_plâte_26 and 13% in Grand Lac and was 7% on average (Fig 3). Globally, the variation in the proportion of individuals dispersed by animals or wind was similar except in Gohapin, Koumac and Grand Lac where the percentage of individuals dispersed by animals was much lower than at the species level.

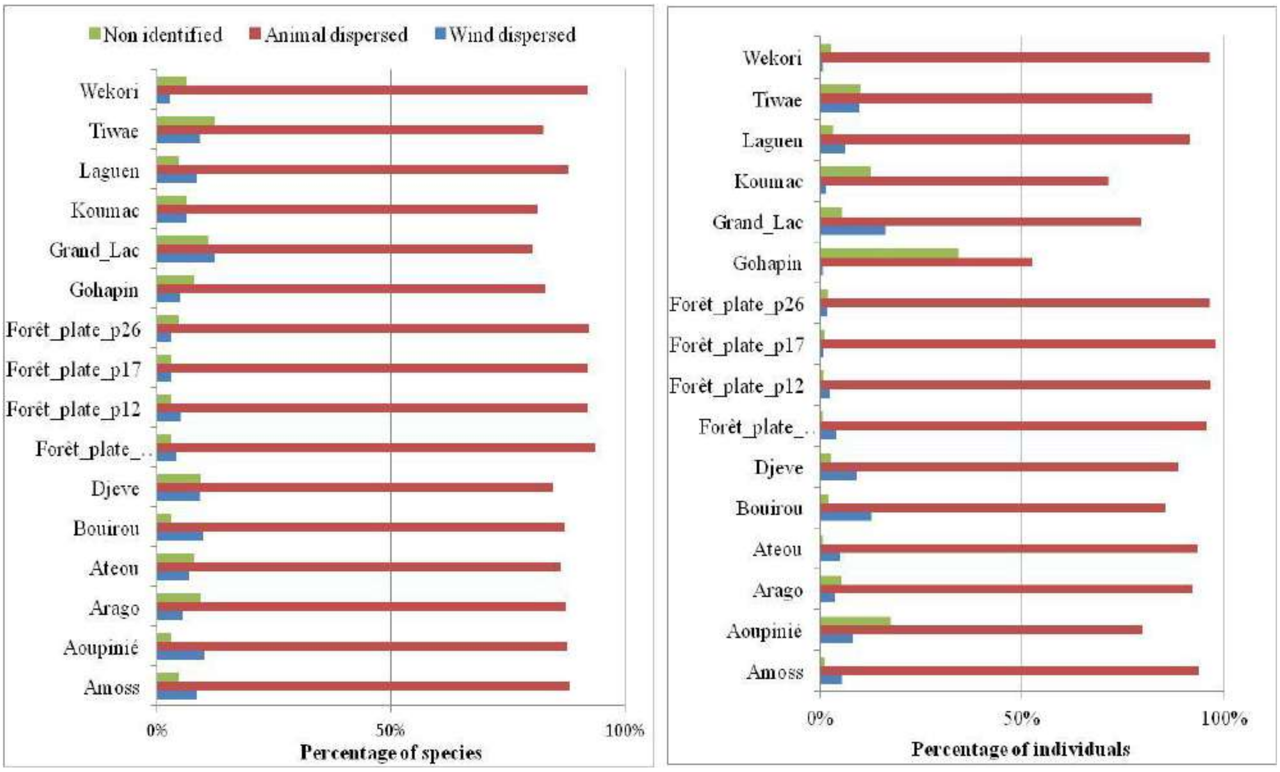

Figure 3: Distribution of dispersal syndromes in the 16 1-ha studied plots as the percentage of species (left-hand side) or as the percentage of individuals (right-hand side). Red bars represent dispersal by animals, blue bars represent dispersal by wind, and green bars represent non-identified dispersal syndrome.

The variation observed in the proportion of wind dispersed species or individuals were relatively independent of climate variation (Fig 5). However, the relations between climate and the proportion of dispersal syndrome were stronger at the individual level. The proportion of individuals dispersed by wind increased significantly with increasing mean annual precipitation (MAP) and decreased significantly with increasing mean annual temperature (MAT). In contrast, at the species level we only observed a non-significant tendency, with the proportion of wind dispersed species increasing with increasing MAP.

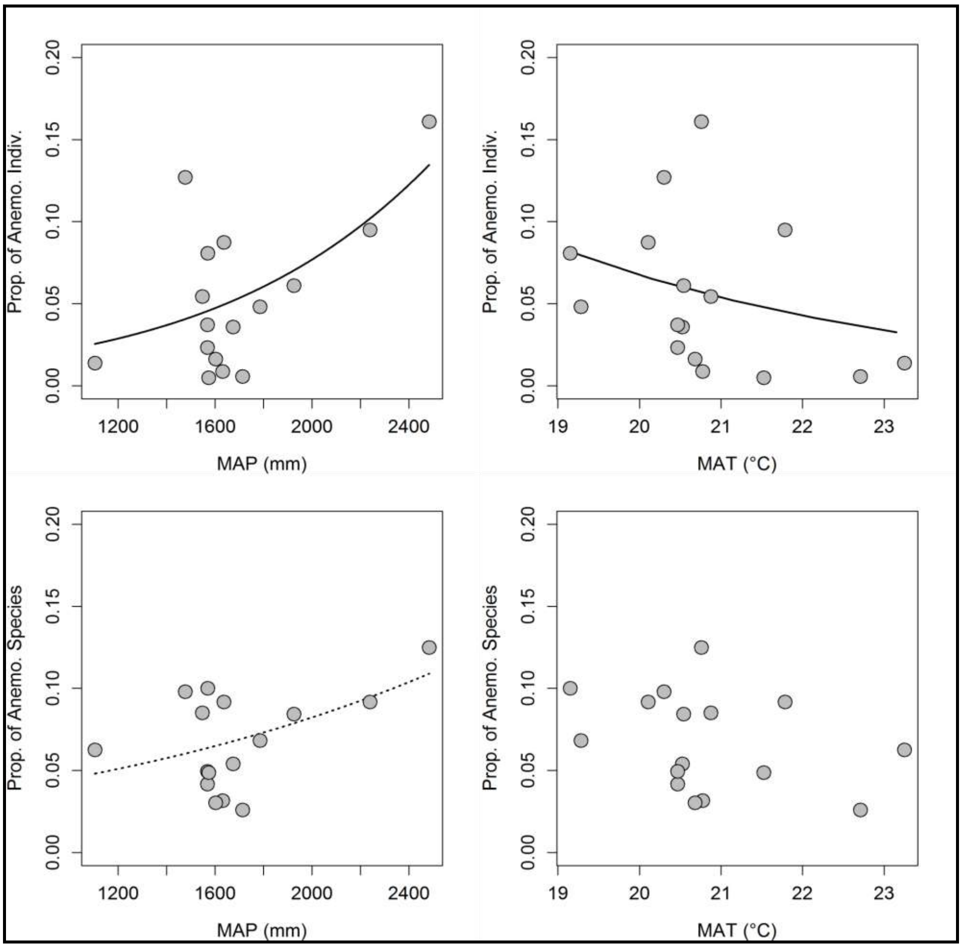

Figure 4: Correlation between winds dispersed species and individuals proportion and climate variables (MAP & MAT). Full lines indicate significant correlations (P value <0.05); and dotted lines indicate non-significant trends (0.05< P value < 0.1). The absence of lines showed no trends.

Species richness was significantly and positively correlated with the proportion of individuals dispersed by wind (R^2 = 0.48, P value ≤ 0.05), while we did not observed any significant trend with the proportion of wind dispersed species. Species richness increased with the proportion of wind dispersed individuals and peaked around 100 species for 10% of individuals dispersed by wind. Beyond this peak species richness tended to decrease slowly.

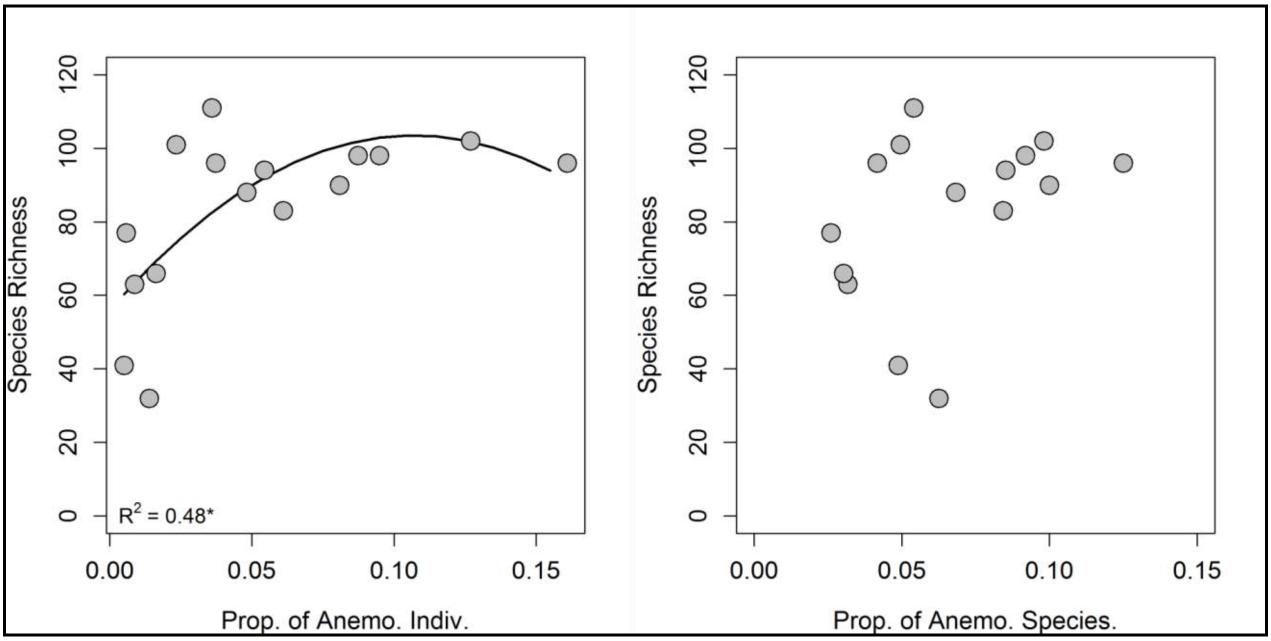

Figure 5: Correlations between the species richness and the proportion of anemochory species and individuals ("*" P value < 0.05).

III. DISCUSSION

We showed that more than 80 % of species and individuals were dispersed by animals (zoochory) in the studied forests. This is consistent with Howe and Smallwood's (1982) that showed that a large proportion of plants in most communities are dispersed by animals. Moreover, our results confirm that in tropical forest, often 75% or more of the tree species produce fleshy fruits adapted for birds or mammal consumption. Dispersal by animals could help seeds escape high mortality conditions near their parent, where predation, abundance of pathogens and intraspecific competition are at their highest (Du et al., 2009).

Conversely, the proportion of species dispersed by wind (about 9%) was very low in comparison with the results founded on ultramafic substrate (21%) by Carpenter et al. (2003) and in dry forest (19%) by Bocquetal et al. (2007) in New Caledonia. Moreover, the proportion of wind dispersed species we found is even lower in comparison with similar studies conducted in Brazil (Griz & machado, 2001), China (Du et al.,2009), Mexico (Cortés-Flores et al., 2013) and Ecuador (Jara-Guerrero et al., 2011). These authors founded respectively 33%, 18.5%, 30% and 28% of anemochorous species. This observation could be explained by the fact that there were relatively high percentages of non-identified dispersal syndromes in the studied plots.

At the plot scale, we have founded that wind dispersed species were relatively high in three sites, Aoupinié, Bouirou and Grand Lac with respectively 10 %, 10 % and 13 % of species. According to Ibanez et al. (2017) a high number of winds dispersed species are usually observable near forest edges (about 60-80 %) due to the disturbances. Species that grows near the forest edge were mostly dispersed by wind while those in the interior of the forest were more likely to be dispersed by fruit eaters (animals). Indeed, in the forest interior (150 m from the nearest forest edge), these author found about 0-20 % of species dispersed by wind. The relatively high proportion of wind dispersed individuals observed in Grand Lac (13 %), which is located near forest edges in the fragmented landscape of Grand Sud may therefore be explained by edge effects. Carpenter et al. (2003) also suggested that the high proportion of wind dispersed species on ultramafic substrate may be related to nutrient deficient soils and low diversity of vertebrates. It may also explain the relatively high proportion of wind dispersed individuals observed in Grand Lac as this plot is located on ultramafic substrate.

The global lack of animals could be another explanation to the significant proportion of wind dispersed recorded in the three study sites. This lack in animals effectives is nonetheless related to mining and logging activities together with bush fires that threat their abundance thus the effectives of fruit eater and disperser. Carpenter et al. (2003) have mentioned the example of “notou” (*Ducula goliath*) a fruit disperser that its situation in New Caledonia is in decline due to over poaching and hunting. He also highlighted that its population in fragmented patches is highly deleterious.

Contrary to our expectation the proportion of wind dispersed individuals increased with mean annual precipitation (MAP) and decrease with mean annual temperature (MAT). At the species level, we only found a peak relationship between the proportions of wind dispersed species and MAP. These results are not consistent with the finding of Si-Chong Chen et al. (2016) and Butler et al. (2007) in Australia. Indeed, these authors found that the proportion of fleshy fruits (i.e. likely dispersed by animals) increase with increasing MAP and MAT. This difference may arise because the MAP and MAT ranges were limited to only 16 study plots located between 1104 – 2484 mm and 19.15 – 23.25 °C. These observations allow us to consider that the proportion of individuals dispersed is more impacted by the precipitation variation but this need further work to test this hypothesis. Notably, future studies should consider different climatic factors such as water availability to improve our knowledge of how climate drive the variations in dispersal syndromes in New Caledonian forests.

We found a significant humped relationship between species richness and the proportion of individuals dispersed by wind. Species richness increased with the proportion of individuals dispersed by wind towards a peak of about 100 species for 10 % of wind dispersed individuals and tend to decrease for higher proportion of wind dispersed individuals. The intermediate disturbance hypothesis (IDH) suggested that species diversity is maximized when ecological disturbance is neither too rare nor too frequent. It was also based on premises that included the interspecific competition results from one species driving a competitor to extinction and becoming dominant within the area of disturbance. Our results could be justified by the dominance of few species in these three plots. Those study plots were associated to less species but with many representative individuals and this is consistent with the theory of intermediate disturbance (Connell 1978). Therefore, our results suggest that the proportion of wind dispersal species can be used as an indicator of disturbance level (Molino & Sabatier, 2001). Indeed, wind dispersed species are often adapted to recently or frequently disturbed environment.

CONCLUSION

Our results contribute to the knowledge of the distribution of the dispersal syndromes in New Caledonian forests. We found that the proportion of wind dispersed species and individual is very low compare to other studies conducted in New Caledonia or in other countries in the tropics. Surprisingly, we have shown that the proportion of species or individual dispersed by wind increased with increasing mean annual precipitation. We found that species richness is maximal for intermediate proportion of individuals dispersed by wind which is consistent with intermediate disturbance theory. This suggests that the proportion of wind dispersed individuals may be use as proxy of the level of disturbances.

In order to improve our understanding on how climate drive the variations in dispersal syndromes in New Caledonia forests; future studies should consider different environmental factors such as water availability. Moreover, they should extend the studied range of precipitation as well as the studied soil type. It is also critical to complete the research work on the non-identified dispersal syndrome recorded in this study.

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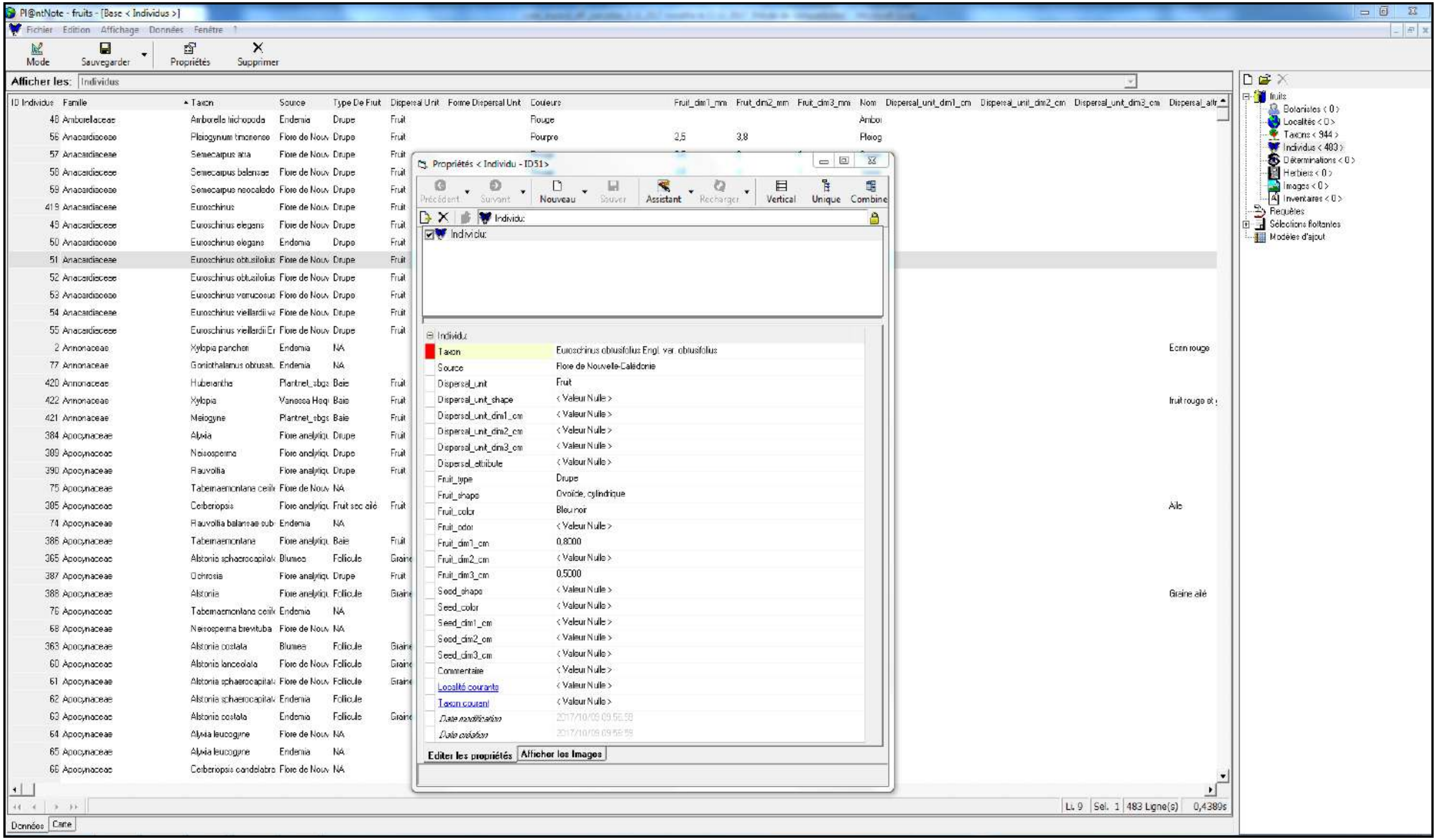
ANNEXES

Annex 1: List of sources used to collect data on fruit type

Source number	Source details
1	A revision of Malesian species of Zanthoxylum (Rutaceae)-journal
2	Adansonia, ser3-2009
3	Adansonia, ser3-2012-34(2)
4	Austr-syst bot-2015, 28,91-110
5	Autralian systematic botany 17 (4)-2004
6	Blumea
7	Boll-Mus-Natn-hist-nat-Paris 4e ser-8,1996 section B
8	Brittonia 65 (1), 2013, pp 42-61, 2012
9	Delta-intkey-com
10	Endemia
11	Flora of China
12	Flore analytique et synoptique de la Nouvelle Caledonie-Guillaumin
13	Flore de Fidji
14	Flore de la Nouvelle Calédonie
15	Floweringplants-eudicots:sapindales, cucurbitales, myrtaceae-kla
16	Jaffré 2002, Adansonia ser3, 24 (2): 159-168
17	Kewboll,dec 2015,70:42
18	Laure Barrabe
19	Leiden botanical series, volume 12
20	Leiden Hortus botanicus, 1991
21	Major Clades of Australian Rutoïdaea-plots one vol 8(8)-2013
22	Mobot-org
23	Munzinger & al 2016-syst-Bot 41 (2): pp 387-400
24	Plantnet-sbgsyd-nsw-au
25	Syst-bot Bot 41 (2): 387-400
26	The family and genera of vascular plants klaus kubitaki vol II
27	The family of flowering plants (www)-biologie-Uni hamburg-de
28	Two new species of agata, Muzinger 2001,Bot journal-of the lin-S
29	Vanessa Hequet

Annex 2: Screen shot of a Pl@ntNote window



Annex 3: Table summarizing the raw data of dispersal syndrome within the 16 studied plots in New Caledonia and their climate data

Plot_name	N_indiv	N_species	N_indiv_Anemo	N_species_Anemo	N_indiv_Zoo	N_species_Zoo	N_Ind_ND	N_species_ND
Amoss	1396	94	76	8	1308	83	12	3
Aoupinié	1583	90	128	9	1265	79	190	2
Arago	1366	111	49	6	1258	97	56	6
Ateou	1182	88	57	6	1104	76	7	5
Bouirou	1181	102	150	10	1008	89	22	2
Djeve	1019	98	89	9	903	83	27	6
Forêt_plate_P09	995	96	37	4	951	90	7	2
Forêt_plate_p12	901	101	21	5	872	93	8	2
Forêt_plate_p17	1149	63	10	2	1125	58	12	2
Forêt_plate_p26	983	66	16	2	948	61	19	3
Gohapin	802	41	4	2	421	34	377	5
Grand_Lac	1261	96	203	12	1000	77	58	7
Koumac	502	32	7	2	358	26	137	4
Laguen	1393	83	85	7	1275	73	33	3
Tiwae	1306	98	124	9	1074	81	108	8
Wekori	872	77	5	2	840	71	27	4

Annex 4: Percentages of dispersal syndromes within the 16 1-ha plots of study

Plot-name	N_indiv_Anemo	N_species_Anemo	N_indiv_Zoo	N_species_Zoo	Non identified species	Non identified individual
Amoss	5%	9%	94%	88%	5%	1%
Aoupinié	8%	10%	80%	88%	3%	17%
Arago	4%	5%	92%	87%	9%	5%
Ateou	5%	7%	93%	86%	8%	1%
Bouirou	13%	10%	85%	87%	3%	2%
Djeve	9%	9%	89%	85%	9%	2%
Forêt_plate_P09	4%	4%	96%	94%	3%	1%
Forêt_plate_p12	2%	5%	97%	92%	3%	1%
Forêt_plate_p17	1%	3%	98%	92%	3%	1%
Forêt_plate_p26	2%	3%	96%	92%	5%	2%
Gohapin	0%	5%	52%	83%	8%	34%
Grand_Lac	16%	13%	79%	80%	11%	5%
Koumac	1%	6%	71%	81%	6%	12%
Laguen	6%	8%	92%	88%	5%	3%
Tiwae	9%	9%	82%	83%	13%	10%
Wekori	1%	3%	96%	92%	6%	2%
Average	**5%**	**7%**	**87%**	**87%**	**6%**	**6%**