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Dynamics of a Mixed Ombrophilous Forest Fragment Located in the Irati National Forest, Paraná

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Abstract
The present study aimed to evaluate the processes governing forest dynamics in a fragment of Mixed Ombrophilous Forest located in the Irati National Forest, Paraná. For this purpose, growth, recruitment, and mortality were described at the botanical family, species, and ecological group levels, based on data from a Continuous Forest Inventory conducted over nine years. Data from 25 permanent one-hectare plots (100 m × 100 m) were used. All individuals with a diameter at breast height greater than or equal to 10 cm (DBH 10 cm) were properly identified and measured in the years 2002, 2005, 2008, and 2011. Growth was assessed based on the increase in diameter and basal area of trees measured on the four occasions. Recruitment was defined as all trees that reached a DBH of 10 cm or more in a given remeasurement. Mortality was obtained by counting trees that died during the evaluated periods. The forest exhibited an average diameter increment of 0.23 cm.year^{-1}, with the highest increments observed for the species *Araucaria angustifolia* (0.42 cm.year^{-1}), *Ocotea porosa* (0.38 cm.year^{-1}), and *Cedrela fissilis* (0.35 cm.year^{-1}). The forest's basal area increment was 0.21 m².ha.year^{-1}. In percentage terms, the basal area increase over the study period was 6.62%, corresponding to an annual growth rate of 0.74%. In this regard, *A. angustifolia* stood out, with an increment of 0.12 m².ha.year^{-1}. The average mortality rate of the forest was higher than the recruitment rate (1.69% and 1.31%, respectively), with the species *Coussarea contracta* and *Ilex paraguariensis* accounting for the highest number of recruited and dead individuals, respectively. The family Myrtaceae was the most representative in terms of recruited individuals (22.3% of the total), while Aquifoliaceae was the most representative in terms of mortality (18.9% of the total). Individuals belonging to the early secondary group showed the highest recruitment and mortality rates during the period, with annual rates of 1.04% and 1.98%, respectively. The higher mortality compared to recruitment did not affect the net growth of the average basal area per hectare, characterizing the successional advancement of the forest, which increasingly assumes the characteristics of its primary configuration and evolves toward reaching its full stock.

Keywords
Araucaria Forest — Growth — Recruitment — Mortality

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1. Introduction

The processes that govern the dynamics of a forest are known as growth, recruitment, and mortality, and they are of great importance, as studying these parameters indicates the growth and changes in its composition and structure. Therefore, reliable prediction of these processes becomes essential for the adoption of more appropriate silvicultural treatments and measures for the management of the forest under sustained yield regime (Mendonça, 2003).

The dynamics of natural forests depend primarily on the ecological factors that contribute during their development, such as succession, competition, exposure, site conditions, and light availability. These factors directly

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influence the growth and development of all the trees that make up the stand. Understanding the interactions of these factors in forest dynamics facilitates the interpretation of how vegetation has developed over time (Moscovich, 2006).

The study of forest dynamics is the main parameter that can be used to predict the development of a natural forest. This estimation is mainly carried out through continuous forest inventory with permanent plots monitored over the medium and long term. Thus, the study of dynamics can enable the understanding of growth and the processes through which changes occur in composition and structure, both at the species level and for the forest as a whole.

Among the necessary knowledge for determining the growth dynamics of species, one can highlight the need to understand their quantities, dimensions, and distribution, their behavior over time, and their requirements regarding soil conditions and light availability. The study of the behavior of species as a whole provides the scientific foundation necessary for rational and sustainable forestry practices.

Therefore, it is necessary to understand the structural characteristics of a forest to ensure its orderly use. Lack of knowledge about the forest's dynamics can lead to its improper use, putting its sustainability at risk.

In light of this, the present study aims to evaluate the increment, mortality, and recruitment using data from permanent plots monitored over nine years in a fragment of Mixed Ombrophilous Forest located in the Irati National Forest, state of Paraná.

2. Material and Methods

2.1 Data Origin and Study Area Location

The study was conducted in the Irati National Forest (FLONA) in Paraná, where the characteristic vegetation is Mixed Ombrophilous Forest (Figure 1). The data used in the study come from a Continuous Forest Inventory carried out between 2002 and 2011, every three years, in 25 permanent plots, each with an area of 1 ha (100 m × 100 m). All individuals with a diameter at breast height equal to or greater than 10 cm (DBH 10 cm) were measured.

The analysis of forest dynamics was based on the characterization of growth, recruitment, and mortality at the botanical family, species, and ecological group levels, as described below.

2.2 Diameter Growth

The diameter growth was determined based on the diameter increase of trees measured on four occasions, specifically those that remained alive throughout the study period. Thus, the diameter increments recorded between 2002 to 2005, 2005 to 2008, and 2008 to 2011 were described, along with the average increment over the entire period from 2002 to 2011. The Periodic Increment (PI) and diameter Periodic Annual Increment (PAI) increments were calculated using:

$PI = d_f - d_i$ (1)

$PAI_d = \frac{PI_d}{P}$ (2)

Where:
PId = Periodic Diameter Increment (cm); *PAId* = Diameter Periodic Annual Increment (cm.year^{-1}); *df* = DBH at the end of the evaluated growth period (cm); *di* = DBH at the beginning of the evaluated growth period (cm); *P* = Measurement interval (years).

2.3 Basal Area Increment

The same procedure was used to evaluate the basal area increment, that is, the basal area increments were described for the periods from 2002 to 2005, 2005 to 2008, 2008 to 2011, and also the average basal area increment for the entire evaluation period, from 2002 to 2011. The periodic increment (PI) and the periodic annual increment (PAI) in basal area per hectare were obtained using the following formulas:

$PI_G = G_f - G_i$ (3)

$PAI_G = \frac{PI_G}{P}$ (4)

Where:
PI_G = Periodic Increment in Basal Area (m².ha^{-1});PAI_G = Periodic Annual Increment in Basal Area (m².ha^{-1});G_f = Basal Area at the end of the evaluated period (m².ha^{-1});*G*i = Basal Area at the beginning of the evaluated period (m².ha^{-1}); *P* = Measurement interval (years).

2.4 Ingrowth

Ingrowth or recruitment was considered as all trees that reached a DBH greater than or equal to 10 cm in a given remeasurement. The ingrowth rate was defined based on the following formula:

$In\% = \frac{N_{In}}{N_i}$ (5)

Where:
In% = ingrowth rate (%);N_{In} = number of ingrown trees in the evaluated period;N_i = number of trees at the beginning of the considered period.

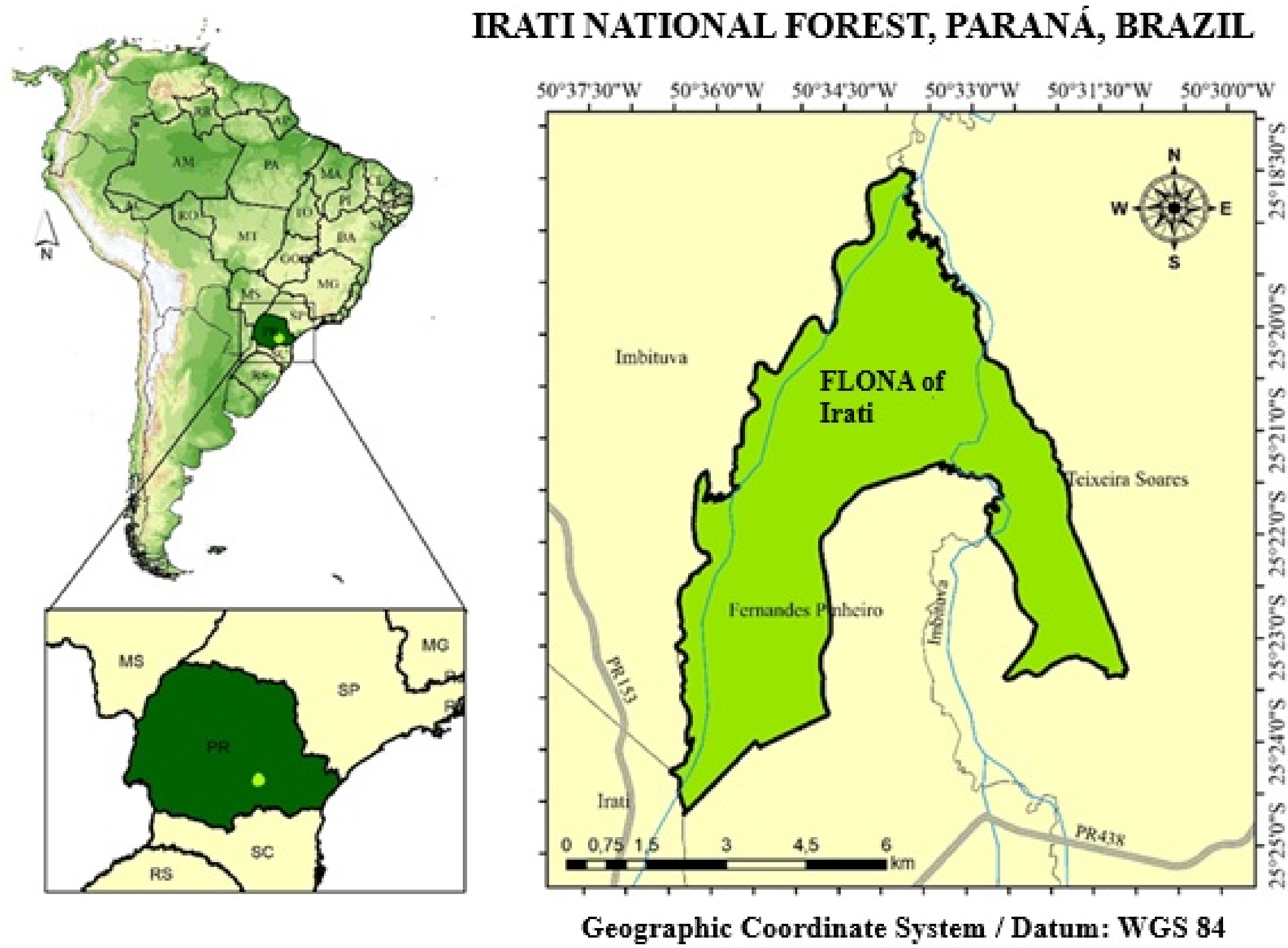

Figure 1. Location of the Irati National Forest (FLONA), State of Paraná.

2.5 Mortality

Mortality was obtained by counting the trees that died during the assessed period. The mortality rate was calculated both absolutely and as a percentage using the formula:

$$M\% = \frac{N_m}{N_i} \times 100 \quad (6)$$

Where:
$M\%$ = mortality rate (%); N_m = number of trees dead in the evaluated period; N_i = number of trees at the beginning of the considered period.

3. Results and Discussion

3.1 Increment in diameter

The analysis of diameter growth in the forest indicated significant variability in growth patterns between species and even between individuals of the same species. During the nine years of monitoring the fragment, the forest exhibited an average increment of 0.23 cm.year^{-1}, ranging from -0.28 to 1.56 cm.year^{-1}.

Some individuals showed negative increments, which could be caused by bark shedding in some species between measurements; by environmental factors such as periods of higher or lower precipitation, which could cause changes in the stems of some individuals due to swelling; or even by the very slow growth of some species or small variations during the measurement.

The highest average growth rates were generally observed in species with low individual density, such as *Cedrela lilloi*, *Cinnamomum glaziovii*, *Anadenanthera col-*

ubrina, and *Lonchocarpus muehlbergianus*, whose increment rates ranged from 0.6 to 1.0 cm.year^{-1}. Table 1 shows the average Periodic Diameter Increment for the ten species with the highest Importance Value in the fragment, along with their respective increment rates.

Table 1. Diameter Periodic Annual Increment for the ten species with the highest Importance Value in a fragment of Seasonal Semideciduous Forest in the Irati National Forest, Paraná.

Species	IV	Diameter Increment (cm.year^{-1})				CV. (%)
	2011	Mean	Min.	Max.	SD.	
Araucaria angustifolia	**13.12**	**0.417**	**-0.283**	**1.220**	**0.229**	**54.92**
Ocotea porosa	6.68	0.376	-0.025	1.379	0.243	64.66
Cedrela fissilis	6.31	0.348	0.000	1.139	0.201	57.80
Ocotea puberula	5.49	0.300	0.000	1.082	0.193	64.46
Nectandra megapotamica	5.20	0.232	-0.071	1.556	0.172	73.94
Coussarea contracta	4.22	0.215	0.018	0.637	0.104	48.23
Nectandra grandiflora	3.71	0.213	-0.124	1.273	0.169	79.42
Ilex paraguariensis	3.36	0.199	-0.110	0.955	0.159	79.65
Casearia decandra	3.27	0.181	-0.265	0.644	0.121	67.15
Ocotea odorifera	3.16	0.141	-0.071	0.760	0.103	73.04

*IV= Importance Value (%), MINIMUM (Min.)= lowest observed value for the species, MAXIMUM (Max.)= highest observed value for the species, STANDARD DEVIATION (SD.)= standard deviation (cm.year^{-1}), CV= coefficient of variation (%).

Araucaria angustifolia was the species with the highest growth rate, at 0.42 cm.year^{-1}, followed by *Ocotea porosa* (0.38 cm.year^{-1}), *Cedrela fissilis* (0.35 cm.year^{-1}), and *Ocotea puberulla* (0.30 cm.year^{-1}). Species with intermediate growth rates include *Nectandra megapotamica*, *Coussarea contracta*, *Nectandra grandiflora*, *Ilex paraguariensis*, and *Casearia decandra*, with increment rates ranging from 0.18 to 0.23 cm.year^{-1}. Among the species with the highest importance value, *Ocotea odorifera* showed the lowest growth rate (0.14 cm.year^{-1}). A high variation in growth was observed among species and even between individuals of the same species, as evidenced by the high coefficients of variation. Considering the botanical families present in the fragment between 2002 and 2011, the Annual Periodic Diameter Increment varied from 0.10 to 0.42 cm.year^{-1}.

Araucariaceae was the family with the most significant growth rate, 0.42 cm.year^{-1}, followed by the *Araliaceae* family (0.39 cm.year^{-1}), *Symplocaceae* (0.38 cm.year^{-1}), and *Asteraceae* (0.37 cm.year^{-1}). Regarding the families with the highest importance value (Table 2), *Meliaceae* and *Rubiaceae* stood out, showing more significant growth, with increment rates of 0.35 and 0.27 cm.year^{-1}, respectively. The families *Lauraceae*, *Salicaceae*, *Myrtaceae*, *Fabaceae*, *Sapindaceae*, and *Aquifoliaceae* showed intermediate growth rates, ranging from 0.18 to 0.23 cm.year^{-1}. The *Myrsinaceae* family showed the lowest growth rate, at 0.13 cm.year^{-1}.

Regarding the growth rates observed for each ecological group (Figure 2), the pioneer species group stands out with an average increment of 0.32 cm.year^{-1}, followed by the climax species group with 0.30 cm.year^{-1}, late secondary species with 0.20 cm.year^{-1}, and early secondary species with an annual increment rate of 0.19 cm.

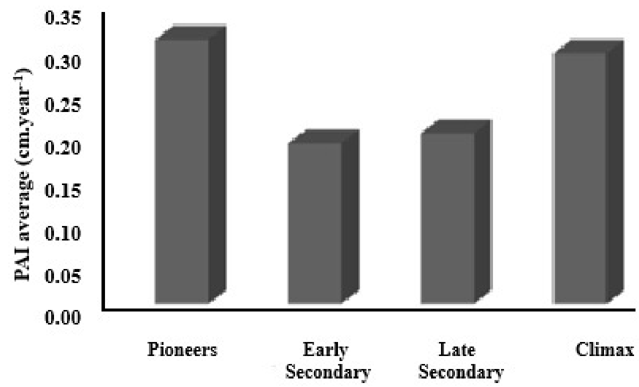

Figure 2. Diameter Periodic Annual Increment in diameter by ecological group in a fragment of Mixed Ombrophilous Forest in FLONA de Irati, Paraná.

Table 2. Diameter Periodic Annual Increment for the ten families with the highest Importance Value in a MOF fragment located in the Irati National Forest, Paraná.

Family	IV	Diameter Increment (cm.year^{-1})				CV (%)
	2011	Mean	Min.	Max.	SD.	
Araucariaceae	**13.99**	**0.417**	**-0.283**	**1.220**	**0.229**	**54.92**
Meliaceae	4.42	0.350	0.000	1.139	0.203	58.05
Rubiaceae	4.78	0.271	0.018	1.305	0.195	71.76
Lauraceae	23.10	0.225	-0.124	1.556	0.185	82.31
Salicaceae	7.56	0.205	-0.265	0.697	0.129	63.01
Myrtaceae	7.34	0.200	-0.053	0.867	0.133	66.31
Fabaceae	3.49	0.195	-0.035	1.093	0.179	91.86
Sapindaceae	5.01	0.185	-0.035	0.785	0.127	68.53
Aquifoliaceae	8.76	0.184	-0.110	0.955	0.153	83.07
Myrsinaceae	3.05	0.131	-0.039	0.637	0.111	84.40

*IV= Importance Value (%), MINIMUM (Min.)= lowest value observed for the family, MAXIMUM (Max.)= highest value observed for the family, SD= STANDARD DEVIATION (cm.year^{-1}), CV= coefficient of variation (%).

Figure 3 shows the evolution of the growth rates as well as the average diameter of the fragment throughout the monitoring period.

It is observed that the average diameter increment rate of the fragment decreased over the evaluation period, from 0.31 cm.year^{-1} to 0.23 cm.year^{-1} . In contrast, the

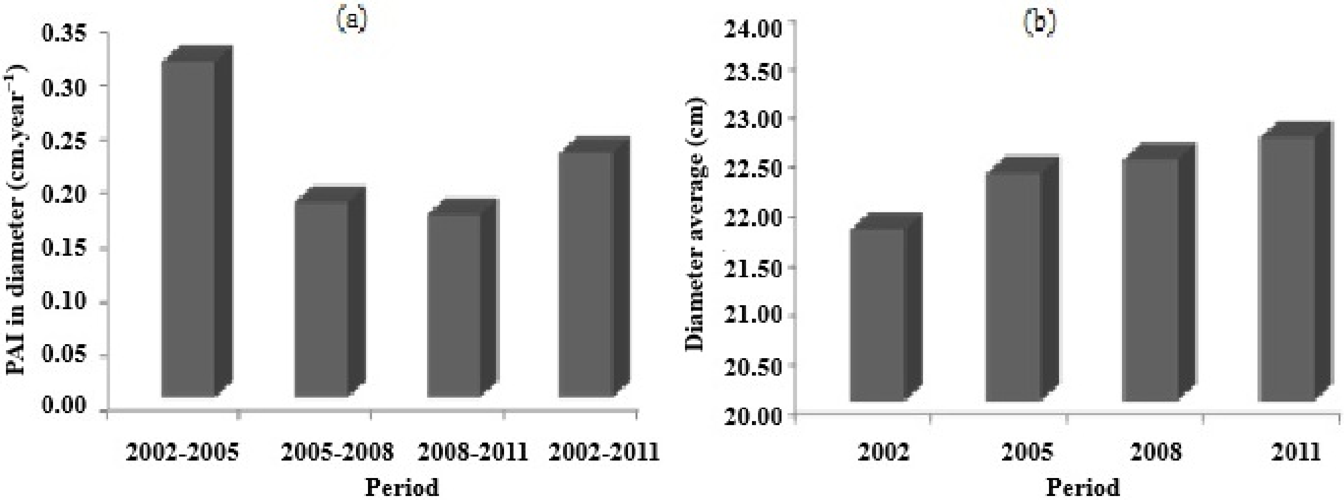

Figure 3. Evolution of diameter increment rate (a) and average diameter (b) from 2002 to 2011 in a MOF fragment located in the FLONA of Irati, Paraná.

average diameter increased over the years, from 21.7 cm in 2002 to 22.7 cm in 2011. The highest increment rate, observed in the 2002-2005 period, may be related to a cyclical growth phase of the forest, influenced by large gaps caused by the bamboo dieback that occurred during that period, where canopy opening favored light entry into the forest interior and may have promoted tree growth.

The average diameter and growth rate observed for the fragment under analysis are similar to other values found in various studies conducted in fragments of Mixed Ombrophilous Forests located in the southern states of Brazil. Pizatto (1999), studying the structure and dynamics of a Mixed Ombrophilous Forest in the region of São João do Triunfo, state of Paraná, observed an average diameter of 21.8 cm and an annual periodic increment of 0.18 cm.year^{-1} . Barth Filho (2002), studying a Mixed Ombrophilous Forest under sustainable management in the region of General Carneiro, Paraná, reported that the average diameter and growth rate were 24.6 cm and 0.13 cm.year^{-1} , respectively. Moscovich (2006), evaluating the growth dynamics of a Mixed Ombrophilous Forest in Nova Prata, Rio Grande do Sul, observed an average diameter of 22.1 cm and an average diameter increment of 0.17 cm.year^{-1} , for a 9.5 cm DBH inclusion limit.

3.2 Basal area increment

The forest showed a total basal area increment of 1.90 m².ha^{-1} during the evaluated period, which represents an annual periodic increment of 0.21 m².ha.year^{-1} , considering only the total basal area of individuals assessed in 2002 and that remained alive until 2011. In percentage terms, the basal area increment during the considered period was 6.62%, which corresponds to an annual increase of 0.74%. Table 3 presents the species with the highest basal area increments observed throughout the entire evaluation period.

Comparing the results obtained in this study with those from other studies conducted in fragments of Mixed Ombrophilous Forest in southern Brazil, it is observed that the average basal area values are generally quite similar. However, the average periodic annual increment of the studied forest is lower than those found by other authors. For example, Durigan (1999) found that the forest in São João do Triunfo grew at a rate of 0.71 m².ha.year^{-1} and had an average basal area of 36.97 m².ha^{-1} . However, Pizatto (1999), using data also from São João do Triunfo, obtained an increment of 0.35 m².ha.year^{-1} and a basal area of 33.07 m².ha^{-1} . For the same forest, Rossi (2007) observed a growth of 0.48 m².ha.year^{-1} and a basal area of 34.90 m².ha^{-1} . Moscovich (2006), in Nova Prata, Rio Grande do Sul, observed that the forest grew at a rate of 0.37 m².ha.year^{-1} and had an average basal area of 33.76 m².ha^{-1} .

Araucaria angustifolia was the species that showed the highest increment during the period, with 1.05 m².ha^{-1} , which corresponds to a periodic annual increment of 0.12 m².ha.year^{-1} and an annual increase of 1.65%. *Ocotea porosa* had the second-highest increment during the period, with a gain of 0.35 m².ha^{-1} over nine years, corresponding to a periodic annual increment of 0.04 m².ha.year^{-1} . *Cedrela fissilis* and *Ocotea odorifera* also showed considerable increments, 0.023 and

Table 3. Basal Area Annual Increment for the period 2002-2011, of the species with the highest growth, in a fragment of Mixed Ombrophilous Forest (MOF) in FLONA of Irati, Paraná.

Specie	Basal Area		Increment in Basal Area			
	$m^2.ha^{-1}$ 2002	$m^2.ha^{-1}$ 2011	$m^2.ha^{-1}$ 2002-2011	$m^2.ha.year^{-1}$ 2002-2011	% In the period	% Annual
Araucaria angustifolia	7.068	8.118	1.050	0.117	14.86	1.65
Ocotea porosa	2.497	2.843	0.346	0.038	13.88	1.54
Cedrela fissilis	1.320	1.526	0.206	0.023	15.57	1.73
Ocotea odorifera	1.494	1.671	0.177	0.020	11.83	1.31
Coussarea contracta	0.263	0.383	0.120	0.013	45.73	5.08
Ocotea diospyrifolia	0.708	0.803	0.096	0.011	13.51	1.50
Casearia sylvestris	0.257	0.339	0.082	0.009	31.93	3.55
Psychotria vellosiana	0.173	0.240	0.067	0.007	38.59	4.29
Nectandra megapotamica	0.935	1.001	0.066	0.007	7.09	0.79
Campomanesia xanthocarpa	0.300	0.361	0.061	0.007	20.40	2.27
Eugenia involucrata	0.119	0.172	0.052	0.006	43.94	4.88
Myrcia hebepetala	0.135	0.187	0.052	0.006	38.53	4.28
Myrciaria floribunda	0.096	0.142	0.046	0.005	47.38	5.26
Casearia obliqua	0.173	0.210	0.037	0.004	21.27	2.36
Syagrus romanzoffiana	0.733	0.769	0.036	0.004	4.91	0.55
Diatenopteryx sorbifolia	0.085	0.114	0.029	0.003	33.98	3.78
Ocotea puberula	1.420	1.448	0.028	0.003	1.98	0.22
Total for the sampled area	**28.66**	**30.56**	**1.90**	**0.21**	**6.62**	**0.74**

0.020 $m^2.ha.year^{-1}$, respectively, which corresponds to an annual increase of 1.7% and 1.3%.

Regarding the species with the highest importance value, *Coussarea contracta* stood out with an increment of 0.013 $m^2.ha.year^{-1}$, corresponding to an annual basal area gain of 5.08%. On the other hand, *Nectandra grandiflora* and *Ilex paraguariensis* showed a slight reduction in basal area, corresponding to 0.02% and 0.5%, respectively.

When studying the basal area increment of species in the Mixed Ombrophilous Forest in São João do Triunfo, Paraná, Schaaf (2001) observed that *Nectandra megapotamica*, *Cedrela fissilis*, *Ocotea porosa*, *Cinnamomum sellowianum*, and *Ocotea puberula* were the species with the highest basal area increment over a 21-year period. Similarly, Durigan (1999), also in São João do Triunfo, Paraná, found that *Piptocarpha angustifolia*, *Ocotea porosa*, *Luehea divaricata*, *Clethra scabra*, and *Araucaria angustifolia* had the highest basal area increment.

It is observed, based on the present study and the cited works, that the basal area increment is highly variable, depending on the forest typology and successional stage. The species with the highest increments also vary considerably, indicating different behavior of the same species when subjected to different environments.

In Figure 4, the botanical families with the most significant increments over the period are presented, along with their annual growth rates. The Araucariaceae family showed the highest increment in the period, with 0.12 $m^2.ha.year^{-1}$, representing an annual basal area increase of 1.65%. The basal area of the Lauraceae family increased from 9.20 $m^2.^{-1}$ in 2002 to 9.95 $m^2.ha^{-1}$ in 2011, corresponding to a periodic increment of 0.08 $m^2.ha.year^{-1}$. However, considering relative values that is, the ratio between the basal area increment and the basal area observed at the beginning of the evaluation period—the Rubiaceae and Myrtaceae families stand out, with an annual basal area increase of 4.85% and 2.91%, respectively.

Regarding basal area growth by ecological group (Figure 5), the highest increment was observed for the pioneer species group, with 0.12 $m^2.ha.year^{-1}$, followed by

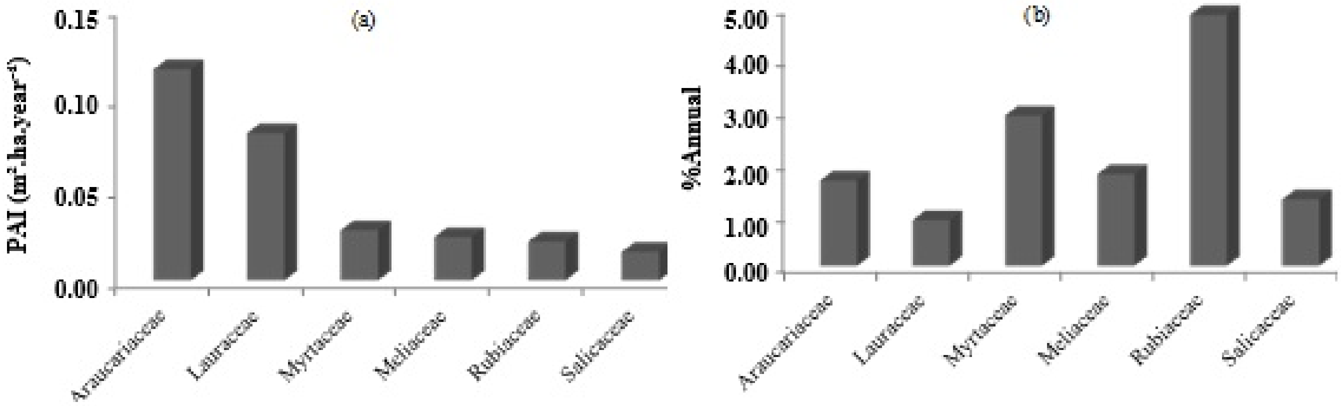

Figure 4. Periodic Annual Increment (a) and Relative Increment (b) for the families with the highest basal area growth in the period 2002-2011 in a Mixed Ombrophilous Forest fragment in the FLONA of Irati, Paraná.

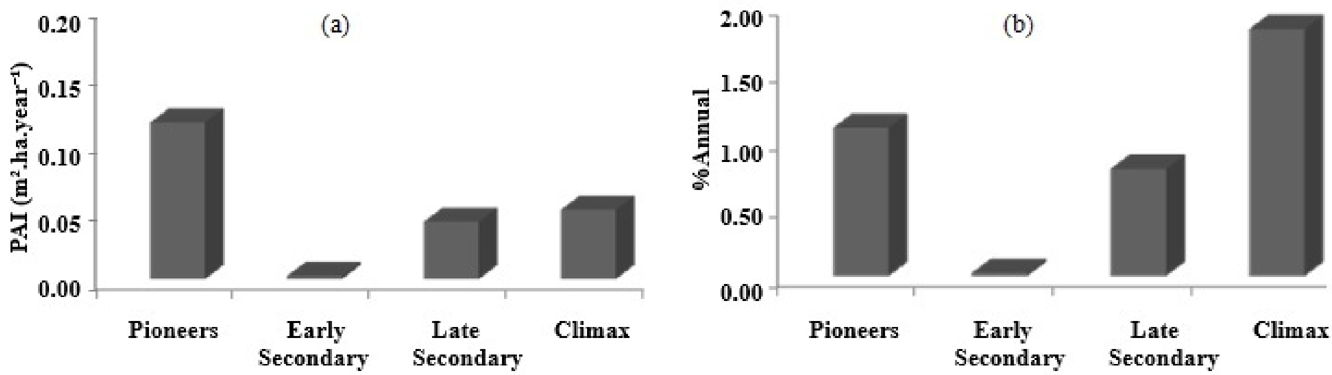

Figure 5. Periodic Annual Increment in Basal Area (a) and Relative Increment (b) by Ecological Group in the Period 2002-2011 in a Mixed Ombrophilous Forest (MOF) Fragment in FLONA of Irati, Paraná.

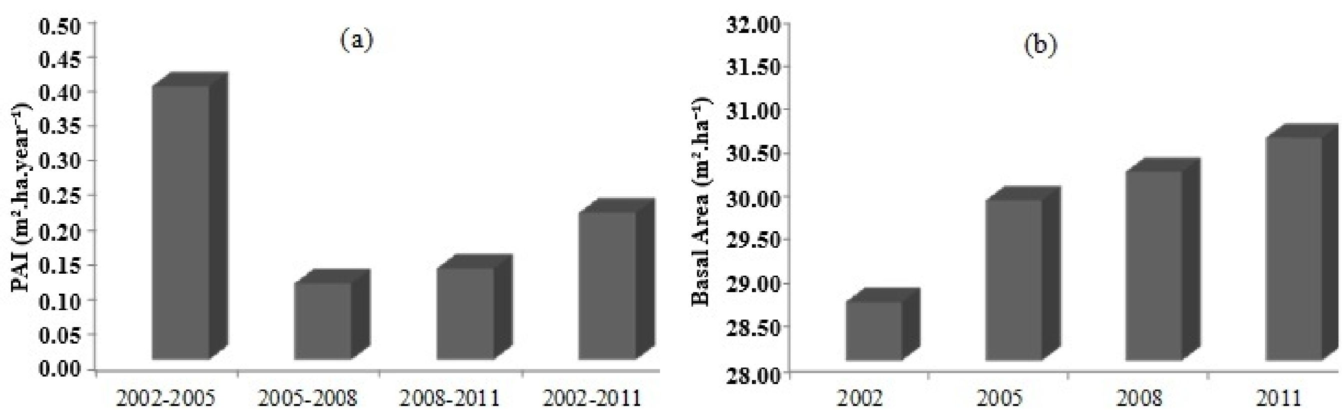

Figure 6. Evolution of the Periodic Annual Increment in basal area (a) and the average basal area (b) in a Mixed Ombrophilous Forest fragment (MOF) in the FLONA of Irati, Paraná.

the climax species group with 0.05 m².ha.year^{-1} , late secondary species with 0.04 m².ha.year^{-1} , and finally, the early secondary species group, which showed an increment of 0.01 m².ha.year^{-1} . The low basal area increment of early secondary species is related to the difference between recruitment and mortality rates within this group. Thus, the higher mortality rate (2.0%) compared to the recruitment rate (1.0%) is responsible for the low basal area increment in this group, making it the only one with a mortality rate exceeding the recruitment rate.

Based on the proportion between the basal area increment and the basal area of each group at the beginning of the evaluation period, the climax species stand out with an annual gain of 1.83%, followed by the group of pioneer species (1.10%), late secondary species (0.79%), and early secondary species (0.02%).

In Figure 6, it can be observed that the forest's average basal area continues to increase over time, while the average basal area increment experienced a significant reduction from the first to the second evaluation period, followed by a slight increase, indicating that the forest has not yet reached its climax stage.

The highest basal area increment rate, observed for the period 2002-2005, may also be related to a cyclical growth phase of the forest, influenced by the opening of large clearings caused by the bamboo dieback that occurred during this period, as previously mentioned. The increased light penetration into the forest interior favored the growth of already established trees and the recruitment of new individuals. This period also recorded the highest recruitment rate among all evaluated periods.

3.3 Recruitment and Mortality

In Table S1 presents the list of species present in the fragment in 2002 that remained alive until 2011, along with their respective annual recruitment and mortality rates.

Considering the entire evaluated fragment, the number of trees that died was higher than the number of trees that entered. In this regard, it was observed that, between 2002 and 2011, there was the loss of 88.12 individuals.ha^{-1} , corresponding to an annual mortality rate of 1.69%. During the same period, 68.24 individuals. ha^{-1} entered, corresponding to an annual ingress rate of 1.31%.

Considering all the evaluation periods, it can be observed that the mortality rate was always higher than the ingress rate (Figure 7). This higher number of dead trees compared to the number of ingressed trees may be attributed to a cyclical phase of the forest or due to increased competition among trees, particularly in the smaller diameter classes, which represent the highest mortality rates.

It can also be observed that over time, both the mortality rate and the ingress rate have experienced a slight reduction, indicating that fewer individuals are entering the fragment due to the reduced available space for the establishment of new individuals, caused by the decrease in the mortality rate, which directly influences the opening of gaps from the fall of dead trees.

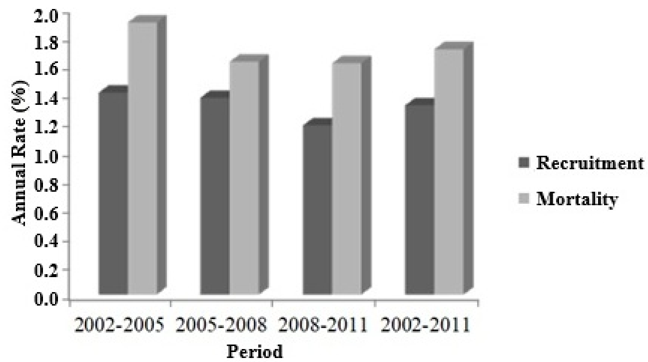

Figure 7. Annual rates of ingress and mortality in each evaluation period in a Mixed Ombrophilous Forest (MOF) fragment in the FLONA of Irati, Paraná.

Several studies conducted in fragments of Mixed Ombrophilous Forests (MOF) in southern Brazil can be used to compare the annual rates of ingress and mortality across different regions. Pizatto (1999) reported an annual ingress rate of 3.50% and a mortality rate of 1.49% for a MOF in the São João do Triunfo region, state of Paraná. Durigan (1999), in a study conducted in a MOF fragment also located in São João do Triunfo, described annual ingress and mortality rates of 1.62% and 0.21%, respectively. Barth Filho (2002), studying a MOF under sustainable management in the General Carneiro region, Paraná, reported annual ingress and mortality rates of 5.03% and 1.84%, respectively.

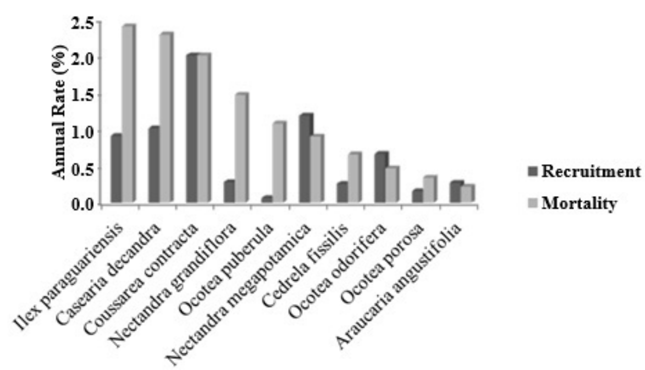

Figure 8. Annual rates of recruitment and mortality for the ten most important species in a fragment of Mixed Ombrophilous Forest (MOF) in the FLONA of Irati, Paraná.

Moscovich (2006), evaluating a remnant of MOF in Nova Prata, Rio Grande do Sul, observed that the annual ingress and mortality rates were 3.05% and 7.40%, respectively, for an inclusion limit of 9.5 cm in DBH. Sanquetta et al. (2003), assessing the dynamics in two Araucaria forests, reported that for the General Carneiro region, Paraná, the annual ingress and mortality rates were 5.58% and 1.01%, respectively, while for the São João do Triunfo region, Paraná, these same rates were 2.87% and 1.90%, respectively. Rossi (2007), studying a remnant also in the São João do Triunfo region, observed an ingress rate of 3.00%, while the mortality rate was 1.10%.

It can be observed that, among all the cited studies, only Moscovich (2006) found mortality rates higher than the ingress rates. The values closest to those found in the present study were, for ingress rates, those observed by Durigan (1999), and for mortality rates, those found in the works of Barth Filho (2002), Pizatto (1999), and Sanquetta et al. (2003), all for the São João do Triunfo region. These results indicate instability in the forest's dynamic processes, as the pattern for conserved forests is one of equilibrium between mortality and recruitment rates (Lieberman et al., 1985).

Among all the species, *Symplocos tenuifolia* exhibited the highest annual ingress and mortality rates, 55.6% and 33.3%, respectively, with the species' density increasing from 0.04 individuals.ha^{-1} in 2002 to 0.12 individuals.ha^{-1} in 2011. Significant ingress rates were also observed for the species *Maytenus grandiflora*, *Myrcia lajeana*, and *Rudgea jasminoides*, all with an annual rate of 44.4%.

Regarding mortality, the species that stand out are: *Actinostemon concolor*, *Randia ferox*, and *Annona rugulosa*, with an annual rate of 11.1%, *Mimosa scabrella* with 9.1%, and *Vernonanthura petiolaris* with 6.75%.

The same trend in the behavior between the rates of ingress and mortality observed for the forest as a whole was verified in the species with the highest importance values, except for *Coussarea contracta*, which presented the same annual rates of ingress and mortality (2%); *Nectandra megapotamica*, *Ocotea odorifera*, and *Araucaria angustifolia*, which had higher annual ingress rates than mortality rates (Figure 8).

Considering the representativeness of each species in relation to the total number of ingressed individuals, the following stand out: *Coussarea contracta* (responsible for 14.5% of the total ingressed individuals), *Ilex paraguariensis* (7.3%), *Myrciaria floribunda* (6.4%), *Myrcia hebepetala* and *Casearia sylvestris* (4.9%), *Casearia decandra* (4.7%) and *Ocotea odorifera* (4.6%). The remaining species together account for 52.8% of the total ingressed individuals.

Regarding the total number of egressed individuals, the following stand out: *Ilex paraguariensis* (responsible for 14.8% of the total dead individuals), *Myrsine umbellata* (9.0%), *Casearia decandra* (8.3%), *Nectandra grandiflora* (5.7%), *Prunus myrtifolia* (4.9%), *Coussarea contracta* (4.1%) and *Matayba elaeagnoides* (3.9%). The remaining species together account for 49.3% of the total egressed individuals (Figure 9).

In relation to the ingress among botanical families, the highest annual rate was observed for the family *Symplocaceae* (22.2%), followed by *Celastraceae* (14.8%), *Loganiaceae* (11.1%), and *Annonaceae* (7.4%). Regarding mortality, the family *Symplocaceae* also showed the highest annual rate (14.8%), followed by *Asteraceae* (5.3%) and the families *Theaceae*, *Styracaceae*, and *Malvaceae*, whose annual mortality rates were 4.4%, 4.3%, and 4.1%, respectively.

In Figure 10, the botanical families are presented with their respective representativeness in relation to the total number of incoming and outgoing individuals. In this regard, the family Myrtaceae stands out, being responsible for 22.3% of the total incoming individuals, showing an ingress rate higher than the mortality rate, with values of 3.8% and 1.5%, respectively. The same was observed for the family Rubiaceae, with an annual ingress rate of 5.3%, while the mortality rate was 2.0%.

A higher mortality was observed for individuals belonging to the following families: Aquifoliaceae (responsible for 18.9% of the total individuals that died), Lauraceae (13.5%), Salicaceae (10.1%), Myrsinaceae (9.1%), Myrtaceae (7.0%), Rubiaceae (5.1%), Asteraceae and Rosaceae (4.9%), and Sapindaceae (4.5%). The remaining families together correspond to 41.3% of the total outgoing individuals (Figure 10).

The analysis of incoming individuals by ecological group indicated the highest annual rates for climax species (2.6%), followed by the pioneer group (1.6%), late secondary species (1.2%), and early secondary species (1.0%). Regarding mortality, the highest rates were observed for the early secondary group (2.0%), followed by the pioneer group (1.8%), late secondary species (1.2%), and climax species (0.7%).

Regarding the representativeness of each group (Figure 11), early secondary species accounted for 40% of the recruitments during the period, pioneers for 26%, late secondary species for 21%, and climax species for 12%. Regarding mortality, early secondary species were responsible for 59% of the total egress during the period, pioneers for 22%, late secondary species for 16%, and climax species for 3%.

The higher mortality of the early secondary species is mainly related to competition for space, nutrients, light, and water with individuals of other species. In general, early secondary species are small or medium-sized, and in the competition, especially for light, with larger

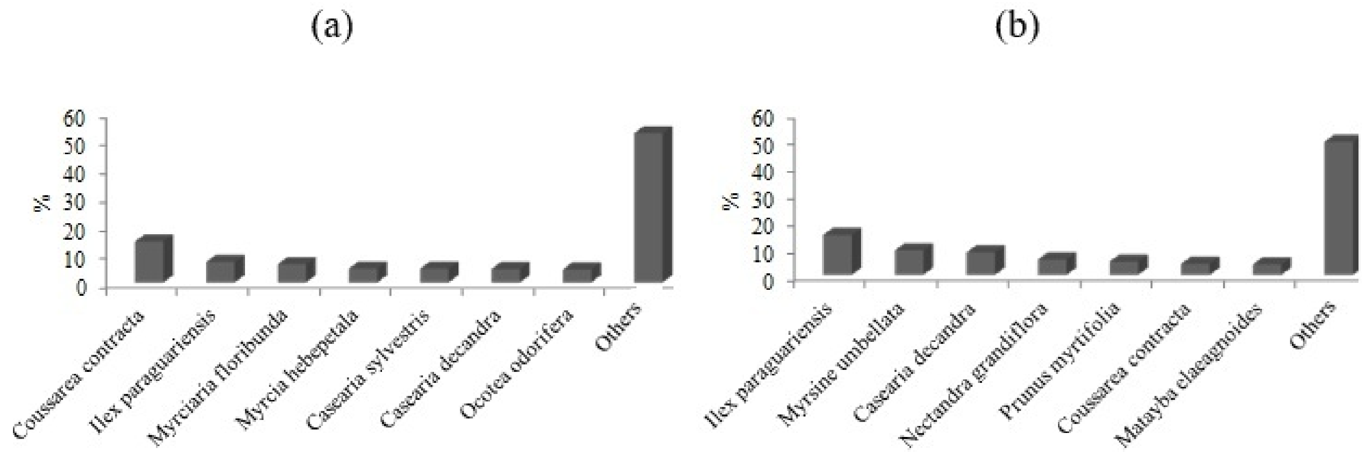

Figure 9. Percentage of incoming (a) and outgoing (b) individuals by species, in the period 2002-2011, in a Mixed Ombrophilous Forest (MOF) fragment in the FLONA of Irati, Paraná.

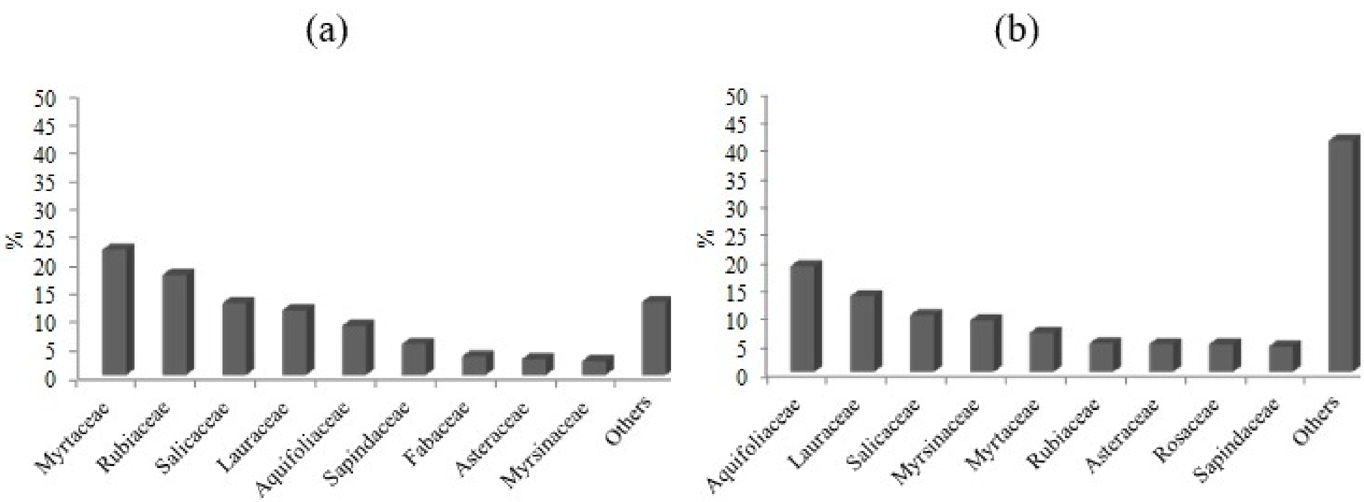

Figure 10. Percentage of incoming individuals by botanical family, in the period 2002-2011, in a fragment of Mixed Ombrophilous Forest (MOF) in FLONA de Irati, Paraná.

species such as *Araucaria angustifolia*, *Ocotea porosa*, and *Ocotea odorifera*, they do not find ideal conditions for their development.

On the other hand, the higher recruitment of early secondary species, as well as pioneer species, is related to the opening of large gaps in the sampled area, also caused by the bamboo drought that occurred during the period, as mentioned earlier. The increased light availability inside the forest favored the recruitment of these species, which require full light for their development.

4. Conclusion

• The species *Araucaria angustifolia*, *Ocotea porosa*, and *Cedrela fissilis* exhibited the highest increment rates, both for diameter and basal area;

• Higher mortality was observed compared to ingrowth, along with a reduction in forest density; however, this did not affect the net growth of the average basal area per hectare, characterizing the forest's successional advancement;

• The species *Coussarea contracta* and *Ilex paraguariensis* were responsible for the highest number of ingrown and outgoing individuals, respectively;

• The families Myrtaceae and Aquifoliaceae were the most representative in terms of ingrowth and mortality,

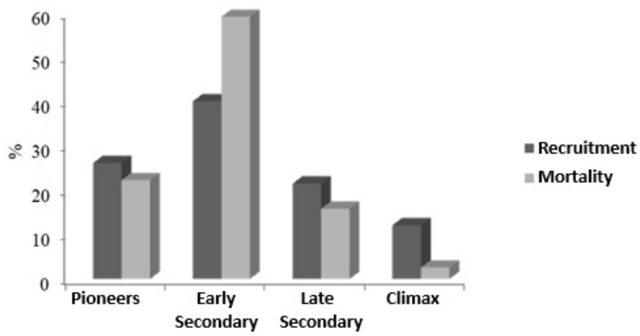

Figure 11. Percentage of dead and recruited individuals by ecological group, in the period 2002-2011, in a fragment of Mixed Ombrophilous Forest (MOF) in the FLONA of Irati, Paraná.

respectively; e

• Individuals from the early secondary group were the ones that had the highest ingrowth and also the highest mortality during the period.

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Author Statements

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✓ All existing funding sources were acknowledged.

✓

✓ There is no evidence of plagiarism in this article.

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TREED0045 - Supplementary Material

Dynamics of a Mixed Ombrophilous Forest Fragment Located in the Irati National Forest, Paraná

Mailson Roi **et al., 2025.**

Table S1. List of species and their respective annual recruitment and mortality rates for the period 2002-2011 in a Mixed Ombrophilous Forest (MOF) fragment in the FLONA of Irati, Paraná.

Specie			RECRUITMENT		MORTALITY	
	$N.ha^{-1}$	$N.ha^{-1}$	$N.ha^{-1}$	Annual Rate	$N.ha^{-1}$	Annual Rate
	2002	2011	2002-2011	(%)	2002-2011	(%)
Actinostemon concolor	0.08	0.04	0.04	5.56	0.08	11.11
Aegiphila integrifolia	0.24	0.20	0.04	1.85	0.08	3.70
Albizia edwallii	0.28	0.28	0	0	0	0
Allophylus edulis	4.88	6.36	1.92	4.37	0.44	1.00
Allophylus petiolulatus	1.04	1.68	0.72	7.69	0.08	0.85
Anadenanthera colubrina	0.20	0.20	0	0	0	0
Annona rugulosa	0.04	0	0	0	0.04	11.11
Annona sylvatica	0.08	0.16	0.08	11.11	0	0

Araucaria angustifolia	42.12	42.32	1.04	0.27	0.84	0.22
Cabralea canjerana	0.56	0.64	0.12	2.38	0.04	0.79
Campomanesia guazumifolia	0.08	0.08	0	0	0	0
Campomanesia xanthocarpa	6.08	6.44	0.64	1.17	0.28	0.51
Casearia decandra	35.40	31.32	3.24	1.02	7.32	2.30
Casearia gossypiosperma	0.04	0.04	0	0	0	0
Casearia lasiophylla	1.52	2.32	1.16	8.48	0.36	2.63
Casearia obliqua	5.20	5.80	0.68	1.45	0.08	0.17
Casearia sylvestris	12.28	14.44	3.32	3.00	1.16	1.05
Cassia leptophylla	0.76	0.72	0	0	0.04	0.58
Cedrela fissilis	15.44	14.88	0.36	0.26	0.92	0.66
Cedrela lilloi	0.04	0.04	0	0	0	0
Chrysophyllum gonocarpum	3.68	4.04	0.52	1.57	0.16	0.48
Chrysophyllum marginatum	1.16	1.32	0.24	2.30	0.08	0.77
Cinnamodendron dinisii	14.36	11.96	0.40	0.31	2.80	2.17
Cinnamomum amoenum	0.40	0.32	0.04	1.11	0.12	3.33
Cinnamomum glaziovii	0.08	0.04	0	0	0.04	5.56
Cinnamomum sellowianum	2.56	2.32	0.20	0.87	0.44	1.91

Citrus sinensis	0.08	0.12	0.04	5.56	0	0
Clethra scabra	5.60	4.24	0.20	0.40	1.56	3.10
Coussarea contracta	19.88	26.16	9.88	5.52	3.60	2.01
Cryptocarya aschersoniana	0.32	0.36	0.04	1.39	0	0
Cupania vernalis	1.84	1.92	0.12	0.72	0.04	0.24
Curitiba prismatica	4.40	5.24	1.36	3.43	0.52	1.31
Dalbergia brasiliensis	9.84	8.92	0.48	0.54	1.40	1.58
Diatenopteryx sorbifolia	1.60	2.28	0.72	5.00	0.04	0.28
Drimys brasiliensis	2.60	2.32	0.24	1.03	0.52	2.22
Erythroxylum deciduum	0.04	0.04	0	0	0	0
Eugenia involucrata	5.76	8.12	2.48	4.78	0.12	0.23
Eugenia pluriflora	0.20	0.12	0	0	0.08	4.44
Eugenia pyriformis	0.16	0.20	0.08	5.56	0.04	2.78
Eugenia uniflora	0.36	0.20	0.04	1.23	0.20	6.17
Ficus enormis	0.24	0.20	0	0	0.04	1.85
Handroanthus albus	0.04	0.04	0	0	0	0
Ilex brevicuspis	0.36	0.40	0.04	1.23	0	0
Ilex dumosa	1.60	1.12	0	0	0.48	3.33

Ilex paraguariensis	60.20	52.12	4.96	0.92	13.04	2.41
Ilex theezans	12.68	10.52	0.96	0.84	3.12	2.73
Inga virescens	1.56	1.64	0.16	1.14	0.08	0.57
Jacaranda micrantha	3.16	3.40	0.28	0.98	0.04	0.14
Lafoensia pacari	1.00	0.88	0.04	0.44	0.16	1.78
Lamanonia ternata	0.20	0.20	0	0	0	0
Laplacea fruticosa	1.80	1.12	0.04	0.25	0.72	4.44
Lithraea molleoides	1.24	0.84	0	0	0.40	3.58
Lonchocarpus muehlbergianus	0.04	0.08	0.04	11.11	0	0
Luehea divaricata	0.76	0.48	0	0	0.28	4.09
Machaerium stipitatum	3.52	2.68	0.04	0.13	0.88	2.78
Matayba elaeagnoides	18.08	14.96	0.28	0.17	3.40	2.09
Maytenus grandiflora	0.04	0.20	0.16	44.44	0	0
Maytenus officinalis	0.20	0.36	0.16	8.89	0	0
Mimosa scabrella	1.08	1.44	1.24	12.76	0.88	9.05
Myrceugenia miersiana	0.04	0.04	0	0	0	0
Myrcia guianensis	0.08	0.20	0.12	16.67	0	0
Myrcia hebepetala	9.52	11.80	3.32	3.87	1.04	1.21

Myrcia lajeana	0.08	0.40	0.32	44.44	0	0
Myrcia splendens	8.88	7.96	1.84	2.30	2.76	3.45
Myrciaria delicatula	1.24	1.48	0.28	2.51	0.04	0.36
Myrciaria floribunda	6.28	9.56	4.36	7.71	1.08	1.91
Myrsine coriacea	0.28	0.40	0.24	9.52	0.12	4.76
Myrsine umbellata	23.28	16.72	1.40	0.67	7.96	3.80
Nectandra grandiflora	37.72	33.68	0.96	0.28	5.00	1.47
Nectandra megapotamica	17.16	17.60	1.84	1.19	1.40	0.91
Ocotea corymbosa	1.40	2.04	0.92	7.30	0.28	2.22
Ocotea diospyrifolia	9.24	9.08	0.20	0.24	0.36	0.43
Ocotea indecora	0.60	0.68	0.08	1.48	0	0
Ocotea odorifera	51.96	52.88	3.12	0.67	2.20	0.47
Ocotea porosa	19.32	19.00	0.28	0.16	0.60	0.35
Ocotea puberula	13.96	12.68	0.08	0.06	1.36	1.08
Ormosia arborea	0.08	0.08	0.04	5.56	0.04	5.56
Parapiptadenia rigida	0.80	1.04	0.24	3.33	0	0
Persea major	0.76	0.64	0	0	0.12	1.75
Picramnia parvifolia	0.20	0.20	0.04	2.22	0.04	2.22

Picrasma crenata	2.24	2.48	0.40	1.98	0.16	0.79
Piptocarpha angustifolia	2.24	1.84	0.52	2.58	0.92	4.56
Piptocarpha axillaris	0.60	1.00	0.52	9.63	0.12	2.22
Plinia cauliflora	1.56	1.56	0	0	0	0
Prockia crucis	0.24	0.40	0.16	7.41	0	0
Prunus myrtifolia	13.20	10.28	1.40	1.18	4.32	3.64
Psychotria vellosiana	5.16	5.96	1.56	3.36	0.76	1.64
Quillaja brasiliensis	0.24	0.24	0.04	1.85	0.04	1.85
Randia ferox	0.08	0.04	0.04	5.56	0.08	11.11
Roupala montana	1.00	0.84	0.04	0.44	0.20	2.22
Rudgea jasminoides	0.16	0.76	0.64	44.44	0.04	2.78
Sapium glandulosum	1.08	1.08	0.12	1.23	0.12	1.23
Schefflera morototoni	1.32	1.08	0.20	1.68	0.44	3.70
Sebastiania commersoniana	0.20	0.28	0.08	4.44	0	0
Sloanea hirsuta	4.92	4.08	0.04	0.09	0.88	1.99
Solanum bullatum	0.08	0.08	0	0	0	0
Solanum pseudoquina	0.04	0.16	0.12	33.33	0	0
Solanum sanctaecatharinae	0.36	0.32	0.12	3.70	0.16	4.94

Sorocea bonplandii	0.04	0.04	0	0	0	0
Strychnos brasiliensis	0.04	0.08	0.04	11.11	0	0
Styrax leprosus	6.24	4.00	0.20	0.36	2.44	4.34
Syagrus romanzoffiana	18.00	18.08	1.20	0.74	1.12	0.69
Symplocos tenuifolia	0.04	0.12	0.20	55.56	0.12	33.33
Symplocos tetrandra	0.08	0.04	0	0	0.04	5.56
Vernonanthura discolor	2.00	1.88	0.56	3.11	0.68	3.78
Vernonanthura petiolaris	4.28	1.92	0.24	0.62	2.60	6.75
Vitex megapotamica	0.08	0.08	0	0	0	0
Xylosma pseudosalzmanii	0.72	0.84	0.12	1.85	0	0
Zanthoxylum kleinii	0.48	0.48	0.04	0.93	0.04	0.93
Zanthoxylum rhoifolium	1.28	1.04	0.04	0.35	0.28	2.43
Total	**580.8**	**560.9**	**68.24**	**1.31**	**88.12**	**1.69**

$N.ha^{-1}$ = Number of individuals per hectare.