



Inferring population dynamic trends of *Nothofagus pumilio* and *N. betuloides* in coastal and mountain forests of Tierra del Fuego: contrasting from flowering to seedling survival through several reproductive cycles

Mónica D. R. Toro-Manríquez^{1,2} · Rosina Soler³ · Alejandro Huertas Herrera^{1,2} · María Vanessa Lencinas³ · Álvaro Promis⁴ · Ana Paula Blazina³ · Guillermo Martínez Pastur³

Received: 2 November 2020 / Accepted: 6 August 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Key message Flower to fruits \times and seed-to-seedling were the most critical transition in the early regeneration cycle of pure and mixed *Nothofagus* forests, both in coastal and mountain geographic locations. Within mixed forest, the deciduous *N. pumilio* shows better recruitment performance (e.g., highest transition probabilities) than the evergreen *N. betuloides*. The evergreen species fails to recruit in the mixed coastal forests for two of the three analysed cohorts, which implies an advantage of *N. pumilio* over *N. betuloides* that must be further examined. However, *N. betuloides* in average value had a higher probability of reaching 2-year survivor in mixed forest.

Abstract Transition from flower to seedling encompasses major processes that define the success of the tree regeneration, and consequently, its study is crucial in the context of forest management. Here, we analysed the transition probability of the reproductive cycle of two *Nothofagus* species, which formed pure and mixed forests in coastal and mountain geographic locations of Tierra del Fuego (Argentina). Pure deciduous *N. pumilio* (Np), pure evergreen *N. betuloides* (Nb), and mixed *N. pumilio*–*N. betuloides* (M) forests in coasts and mountains (3 forest types \times 2 geographic locations \times 20 replicas = 120 replicas) were evaluated. Reproductive structures (female flowers, fruits, seeds, sound seeds, emerged seedlings and surviving seedlings up to 2 years) were studied since 2012–2018. Our results suggested that transition probabilities from flower to surviving seedlings varied inter-annually between *N. pumilio* and *N. betuloides*. The hazard ratio in the transition showed an influence of the cohorts and the geographic location on *N. pumilio*, while forest type and geographic location influenced on *N. betuloides*. Flower to fruits and seed to seedling were the most critical process in all forest types and locations. Cumulative transition probabilities (female flowers to 2-year-old seedlings) for *N. pumilio* were 0.3–46.2% in Np and 1.4–30.2% in M, and pure and mixed forests reached similar probabilities only in cohort 3. For *N. betuloides*, these were 2.8–24.4% in Nb and 0.0–6.5% in M. Both *Nothofagus* species showed a better performance of pure forests in mountains (15.9–46.2% Np; 3.8–24.8% Nb) than in coasts (0.3–16.1% Np; 2.8–5.3% Nb). Through this integrated approach, considering the full reproductive cycle, it is possible to quantify the influence of canopy composition and inter-annual variability in natural forest dynamic, and allows to identify the critical stages of tree recruitment in pure and mixed *Nothofagus* forests.

Keywords Transition probability · Reproductive phenology · Seed production · Pure forests · Mixed forests · Southern Patagonia

Introduction

Knowledge of the reproductive biology is crucial to understand the population dynamic of plants (Menges 2000; Chen et al. 2016; Traveset et al. 2016). Understanding recruitment and mortality is critical to assessing tree species population status and implementing management strategies (Menges

Communicated by José I. Hormaza.

✉ Mónica D. R. Toro-Manríquez
monica.toro.manriquez@ulterarius.com;
monica.toro@umag.cl

Extended author information available on the last page of the article

2000; Crone et al. 2013). In species relying in sexual reproduction, pollen availability, flower fecundity and seed production shape population structure and dynamic, as well as seed quality, seed predation and seedling establishment (Moles and Leishman 2008; Espelta et al. 2009; Soler et al. 2017).

The ability of trees to pass reproductive transitions determines the composition of forest regeneration (Moles and Leishman 2008; Löf et al. 2018; Pillay et al. 2018). In mixed forests, the co-occurrence of two or more tree species is usually explained by niche partitioning (a differential performance of the dominant species) (Zhang et al. 2012; Ali et al. 2019) or the complementarity of functional traits of different species conforming the mixed forests (e.g., seed size, predation rate, light demand). Reproductive traits and ability of the species to overcome different natural limitations affect early stages of the tree life cycle, determining the degree of the mixture at maturity (Löf et al. 2018). Mixed forests can have ecological advantages compared to pure ones, associated to tree health, nutrient cycling, timber productivity, resilience to climatic events (e.g., drought) and other potential environmental risks (Fisichelli et al. 2014; Löf et al. 2018). However, it is not clear if two coexisting species have similar reproductive success, or if one of them is able to outperform the other in the long time, making that mixed forests start to be dominated by the more successful species (e.g., conversion to pure forests), as we hypothesize for *Nothofagus* forests. Few studies (Espelta et al. 2009; Löf et al. 2018) have addressed the specific seed production conditions in natural mixed forests, or the species interactions to surpass loss factors during preceding development processes (e.g., biotic and abiotic stressors during flowering and seeding). Therefore, it is difficult to predict the natural regeneration success of different species in mixed forests. The specific seed production conditions in mixed forests have gained more interest during the last decades and most of the knowledge is focused on European tree species, and mainly for broadleaved–coniferous mixed forests (Espelta et al. 2009; Wesolowski et al. 2015; Bogdziewicz et al. 2017).

At the southern end of South America, mixed *Nothofagus* forests (Nothofagaceae) are composed of the deciduous *N. pumilio* (Poepp. et Endl.) Krasser and the evergreen *N. betuloides* (Mirb.) Oerst. This forest occupies a small area compared to monospecific pure forests: < 15% of the total forests in the Argentinean part of Tierra del Fuego Island, and < 20% in the Chilean part (Frangi et al. 2005; CONAF Corporación Nacional Forestal 2011). The mixed forests are usually considered transitional conditions between *N. pumilio* and *N. betuloides* pure forests (Frangi et al. 2005). In pure *Nothofagus* forests, most of the literature describes abiotic (e.g., air temperature during flowering) and biotic factors (e.g., seed predation during dispersion) influencing flowering and fruiting patterns (Martínez Pastur et al. 2013),

as well as seedling emergence and establishment (Burgos et al. 2008; Bahamonde et al. 2011; Torres et al. 2015). Therefore, biotic and abiotic factors affecting each tree species could differentially influence their reproductive success, mainly those associated with the characteristics of the overstory canopy. For example, spontaneous abscission of female flowers and immature fruits caused by frost or heavy rains in pure deciduous forests during spring or early summer (Riveros et al. 1995; Martínez Pastur et al. 2013) could be damped out in mixed forests due to partial protection of the canopy of evergreen tree species. Moreover, a greater variety of food resources (e.g., different sizes and shapes of seeds) in mixed forests can attract more and diverse seed predators (Leishman et al. 2000), resulting in a higher predation rate than in pure homogeneous forests (Villacide and Corely 2008).

The intrinsic variability of tree species to produce propagules and the factors that trigger reproductive losses can cause a large variation in regeneration success in southern temperate forests (Toro Manríquez 2019). Yet, it is not clear if the mixed condition in these forests is stable or dynamic over time (e.g., throughout the new seedlings cohorts). If one of the tree species in the mixed forests overpass the other species in terms of reproductive success (e.g., proportion of seed production and seed viability), and attains higher transition values between flowering–fruiting–seed production–seedling, then that species will have a better chance of remain, and maybe dominate the canopy in the future. The aim of this study was to analyse the transition probabilities throughout the reproductive cycle of two coexisting *Nothofagus* species, considering pure and mixed forests in two contrasting geographic locations of Tierra del Fuego. Related to this objective, the following questions were addressed: (i) how does canopy composition influence the transition of flowers to fruits, seeds, and emerged seedlings? (ii) Are this influence and the magnitude of the reproductive losses similar among different cohorts? (iii) How does the reproductive performance of the two species vary within the mixed and pure forests? We expect that this study can contribute to the understanding of early stages of the tree life cycle of two southern native tree species growing in pure and mixed forests, and to detect the bottleneck stages of regeneration, through the identification of loss factors (biotic and abiotic) that influence on natural regeneration success.

Methods

Study area characterization

The study was conducted from September 2012 to January 2018 in pure and mixed old-growth *Nothofagus* forests (> 250 years), without harvesting impact on at least the last

60 years, in southwest of Tierra del Fuego Island, Argentina (Fig. 1). Three *Nothofagus* forest types were considered according to their overstory composition: pure deciduous *N. pumilio* forests (Np), pure evergreen *N. betuloides* forests (Nb) and mixed *N. pumilio*–*N. betuloides* forests (M), with a similar proportion of deciduous and evergreen species in the canopy (Toro Manríquez et al. 2016, 2019a, 2020). Likewise, two geographic locations were selected, each of which comprised these three forest types: (i) marine coasts close to the Beagle Channel, and (ii) mountains areas toward the inner island. The coastal forests were located within the Tierra del Fuego National Park (50–100 m a.s.l.), where the estimated mean annual air temperature was 4.3 °C and the annual precipitation was 756 mm year⁻¹, with abundant snowfalls during winter. The mountains forests were in Garibaldi Pass (450 m a.s.l.), within the Andes Mountains,

where the estimated mean annual temperature was 3.1 °C, and the annual precipitation was 788 mm year⁻¹ (Fick and Hijmans 2017). In general, main soil type in both forest types for coasts and mountains locations is loam textured, with massive granular structures, low usable water capacity and moderate to slow internal and external drainage with a thick organic soil layer (Toro Manríquez et al. 2019a). However, coasts and mountains soils show some differences. For example, some soil properties (as pH and cation exchange capacity) change with the forest types (deciduous, evergreen), but others (as moisture, N and P content) are more strongly influenced by the geographic location (Toro Manríquez et al. 2019a). Pure and mixed forests vary in air and soil temperature (°C) and air relative humidity (%) according to the geographic location (Fig. 2). The highest mean air temperature occurs during January (8.5–9.5 °C) for the

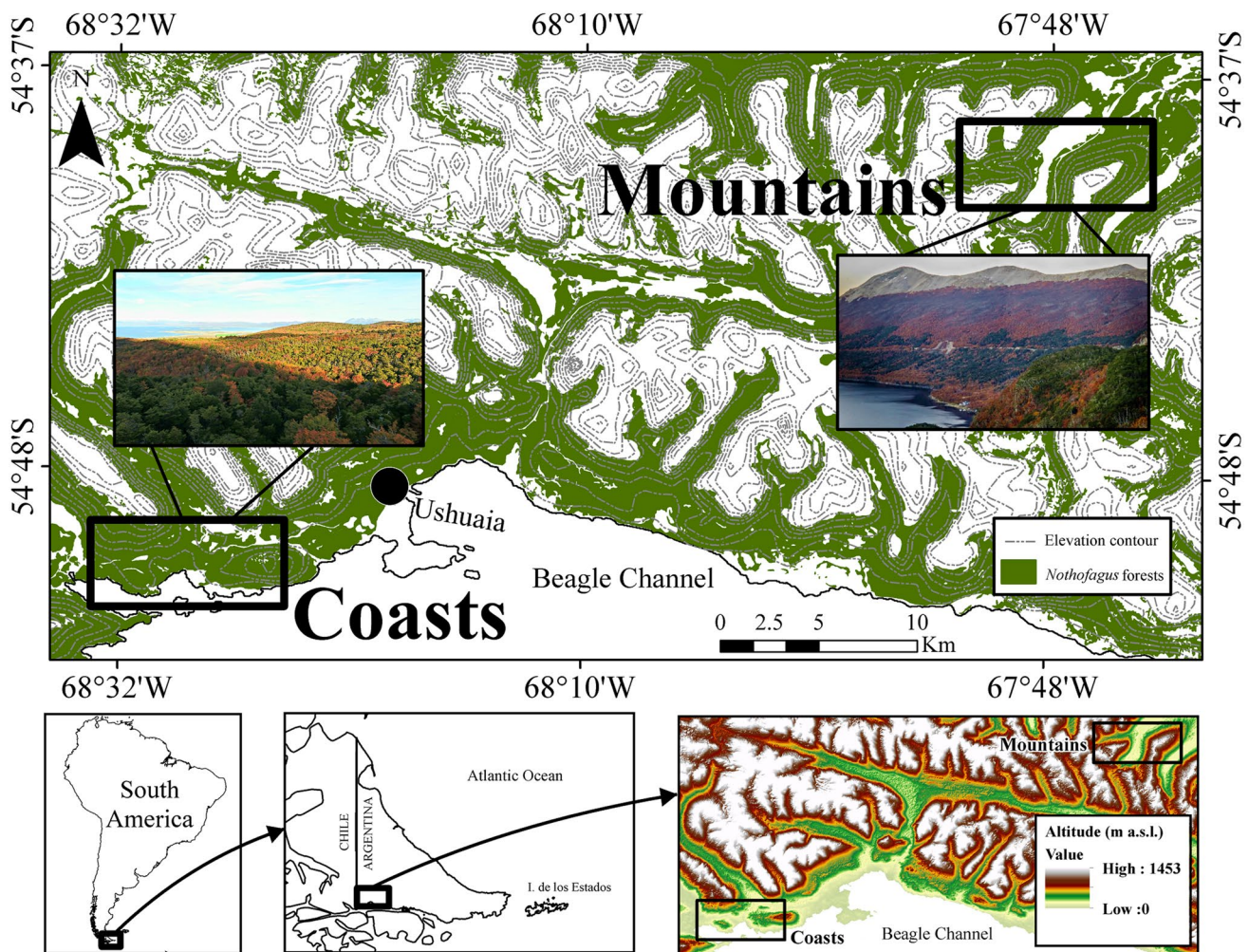
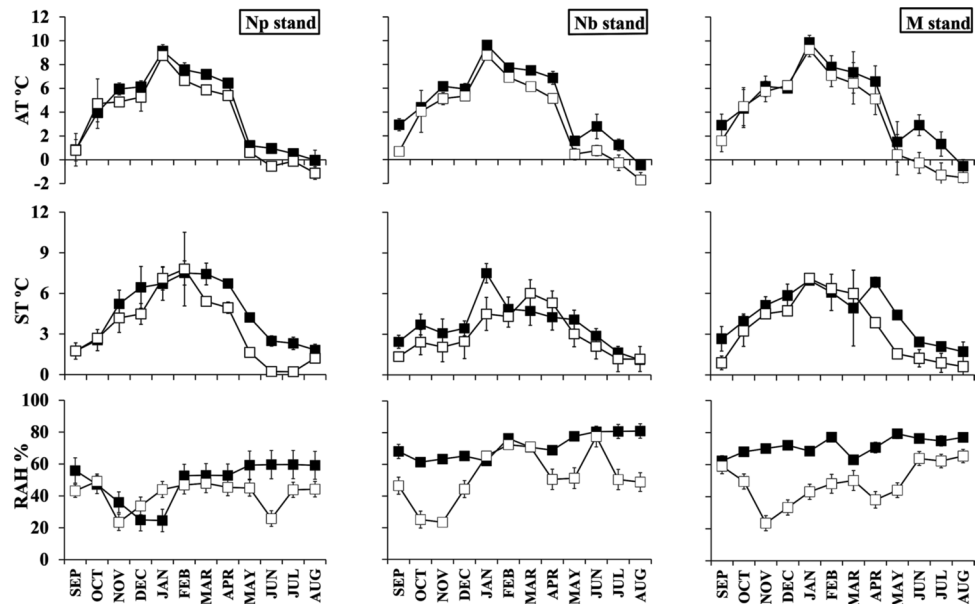


Fig. 1 Study area in southwestern Tierra del Fuego indicating contour lines and forest cover. Rectangles show the sampled geographical locations: (i) coasts along the Beagle Channel and (ii) mountains in the inner island. *Nothofagus* forest cover is shown in green, and photos next to the rectangles are views of each geographic location.

Altitude is presented in ranges (m a.s.l.). Adapted from “Forest canopy-cover composition and landscape influence on bryophyte communities in *Nothofagus* forests of southern Patagonia” by Toro Manríquez et al. (2020). Copyright 2020 by the Toro Manríquez et al.

Fig. 2 Mean monthly air (AT, °C) and soil (ST, °C) temperatures, and relative air humidity (RAH, %) in stands of pure and mixed *Nothofagus* forests of studied coasts (black square) and mountains (white square) locations, between September 2013 and August 2014. Vertical bars are standard error of the mean



three forest types and the two locations. However, mountains forests are colder in winter ($-0.7\text{ }^{\circ}\text{C}$ air and $1.0\text{ }^{\circ}\text{C}$ soil temperatures) than coasts forests ($1.0\text{ }^{\circ}\text{C}$ air and $2.1\text{ }^{\circ}\text{C}$ soil temperatures). Soil temperature reaches maximum values during January–February for the three forest types, but mixed forests show lower values on average ($5.3\text{ }^{\circ}\text{C}$) than evergreen and deciduous forests ($6.6\text{--}7.3\text{ }^{\circ}\text{C}$). Relative humidity (%) at forest interior remains constant throughout the year on the coasts ($\sim 70\%$), while in the mountains decreased sharply during spring and autumn ($\sim 40\%$). In general, the forest structure differs in forest types and geographic locations. For example, the basal area is higher in pure *N. betuloides* ($84.5\text{ m}^2\text{ ha}^{-1}$) than in mixed ($77.1\text{ m}^2\text{ ha}^{-1}$) and pure *N. pumilio* forests ($66.5\text{ m}^2\text{ ha}^{-1}$), as well as in the mountains ($80.7\text{ m}^2\text{ ha}^{-1}$) than in the coasts ($71.4\text{ m}^2\text{ ha}^{-1}$). Contrary, dominant height and diameter at breast height are higher in pure *N. pumilio* (21.1 m and 63.2 cm , respectively) than in mixed forests (17.6 m and 47.9 cm , respectively), than in pure *N. betuloides* forests (15.9 m and 37.5 cm , respectively) (for more details see Toro Manríquez et al. 2020).

Flower, fruit, and seed production

We used 20 randomly located, independent biomass traps (plastic recipients of 0.06 m^2 in area and 30 cm deep) for each forest type and geographic location ($N=3$ forest types $\times 2$ geographic locations $\times 20$ replicas = 120 biomass traps), which were perforated to allow rain and snow-water drainage. Fallen reproductive structures inside traps were monthly collected, starting in spring 2012 and ending in spring 2016, and associated to three consecutive different cohorts. Material was air dried and analysed in the laboratory. We identified reproductive structures associated to

different stages in the natural regeneration cycle (Fig. 3A): male flowers and abscised female flowers from October to December (spring), abscised and foraged (insects and birds) immature fruits during January and February (summer), and seeds during March–May (autumn). Classified plant material was oven dried at $70\text{ }^{\circ}\text{C}$ to constant weight and subsequently weighted ($\pm 0.0001\text{ g}$). Seeds were counted and classified as damaged (e.g., foraged, empty, non-viable) or sound seeds [for more details, see Toro Manríquez et al. (2016) and Toro Manríquez (2019)]. With these data, we quantified the number of female flowers derived in fruits, and the number of fruits derived in sound seeds. During the post-dispersal stage (June–October), we quantified the seed losses (e.g., foraged by birds and mice), and the viability losses during winter stratification by groups of marked seeds left in soil, inside and outside small cages. With these data, we estimated the number of seeds capable of generating a seedling [for more details, see Toro Manríquez et al. (2016) and Toro Manríquez (2019)].

Emerged and surviving seedlings

We established 10 randomly located, independent rectangular plots of 1 m^2 ($5.0 \times 0.2\text{ m}$) for each forest type and geographic location ($N=3$ forest types $\times 2$ geographic locations $\times 10$ replicas = 60 plots). In the mid-summer (late January), each recently germinated seed within each plot was individually identified using its position (x, y). The survival of each germinated seed was monitored along the two following seasons (ending the study of the third cohort in summer 2018). Thus, according with the last stage in the natural regeneration cycle (Fig. 3A) we determined as emerged seedlings to those germinated seeds with fully expanded

dead, from female flower to 2-year-old seedlings over a whole cycle (1–38 months). Each month was obtained from reproductive phenological records (following to Toro Manríquez et al. 2016). The mean time of survival from female flowers to each reproductive structure was: 3 months to fruits, 6 months to seeds, 11 months to sound seeds, 14 months to emerged seedlings, 26 months to 1-year survivors, and 38 months to 2-year survivors. We conducted log-rank (Mantel–Cox) tests to compare the survival time for each cohort, forest type and geographic location by species and it is similar to the Chi-square test for association ($p < 0.05$). The log-rank test statistic compares the observed with the “expected” number of failures and has an asymptotic distribution under the null hypothesis (Kartsonaki 2016). Complementarily, we conducted a Cox proportional hazards model regression (Cox 1972) to examine the effect of explanatory variables on survival times for *N. pumilio* and for *N. betuloides*, which assumes a multiplying relationship between predictor variables (cohort, forest type, geographic locations, and their interactions) and the hazard function among transitions (from flowering to 2-year survivors) (Kartsonaki 2016). Cox proportional hazards model regression allows several predictor variables to be considered and tests the independent effects of these predictor variables on the hazard of the event. The tested model for each tree species included: Cohort, forest type, and geographic location. The likelihood-ratio statistic ($-2 \text{ Log Likelihood}$) and the overall Chi-square ($p < 0.05$) were included. For each variable in the model, parameter estimates (β), standard errors, and Wald statistics ($p < 0.05$) were included. To understand the effects of individual predictors, Hazard Ratio (HR) is the predicted change in the hazard for a unit increase in the predictor. For this, the HR can be interpreted in a similar way to relative risk. It compares the risk of an event occurring in two groups (A/B) so, $\text{HR} = 1$: No effect, $\text{HR} < 1$: Reduction in the hazard, $\text{HR} > 1$: Increase in Hazard. The survival analyses and Cox proportional hazards model regression were conducted using SPSS Statistics version 25.0 (IBM Corporation Released 2017).

Differences between losses of reproductive structures corresponded to the sum of the proportion of losses (%) produced by the different factors in each stage (flowering, seeding, seedling emergence and survival) for three cohorts of *Nothofagus* species. The proportions of losses were analysed by one-way ANOVAs among cohorts, considering each geographic location separately. The regeneration losses included seedling mortality after 1 or 2 years. Mean comparisons for all the analyses were conducted using the Tukey honestly significant difference test ($p < 0.05$).

Results

General outcomes: reproductive structures at each cohort

From year 2012 to year 2015, we monitored 19,713 male flowers, 325 female flowers, 523 fruits, and 25,566 seeds. The number of reproductive structures was variable each year, differentiating between species, forest type and geographic location. For example, in the second year, we registered a total of 7347 seeds of *N. pumilio*, where the production of the mountains forests was 6 times higher than in the coasts. A similar trend occurred for *N. betuloides* during the second year, registering a total of 5484 seeds. This production was 5 times higher in the mountains than on the coasts. Regarding the seedlings, 584 newly installed seedlings (1 year) were recorded in 2014, monitoring their survival until 2018, and only 239 seedlings reached the age of 5 years. More details of all the reproductive structures and seedlings are shown in Tables S1 and S2 (mean value per m^2 and the sum of all traps per site). Moreover, the *N. pumilio* and *N. betuloides* species in pure and mixed forests showed strong cohort variation (Table S3). Male flower production of *N. pumilio* varied from 22.3 to 629.1 thousand m^{-2} per basal area, and 2.2 to 338.1 thousand m^{-2} for *N. betuloides*, with the maximum peak in the second cohort on the mountains for both species. The two species also presented inter-annual variations in the production of other reproductive structures, in both pure and mixed forests and in coasts and mountains (Figs. S1 and S2). For example, in pure *N. pumilio* forests on the coasts, mean number of flowers ranged from 20.1 ± 3.8 to 204.0 ± 19.5 thousand m^{-2} , fruits from 7.2 ± 3.8 to 86.0 ± 19.5 thousand m^{-2} , seeds from 0.26 ± 0.3 to 64.5 ± 3.1 thousand m^{-2} , and 2-year seedlings from 0.01 ± 0.01 to 1.15 ± 0.20 thousand m^{-2} .

Survival time for transitions in *Nothofagus pumilio* and *N. betuloides*

Survival analysis for the transitions from flowers to 2-year-old seedlings showed significant differences in *N. pumilio* species in each cohort (Chi-square = 365.3; $df = 2$; $p < 0.001$), forest type (Chi-square = 3.9; $df = 1$; $p = 0.048$) and geographic location (Chi-square = 83.1; $df = 2$; $p < 0.001$) (Table 1). Average survival time (estimate) was lower for cohort 1 (month 23, between emerged seedlings and 1-year survivors) than in cohorts 2 and 3 (month 35, between 1-year survivors and 2-year survivors). However, these differences were only slightly significant between forest types as the average survival time

Table 1 Kaplan–Meier survival estimated by means for survival time (transitions) for *N. pumilio* by cohorts (1, 2, 3), forest type (Np = pure *N. pumilio* forests, M = mixed forests) and geographic locations (coasts and mountains)

	Estimate	Transition	Standard Error	CI (95%)
Cohort				
1	23	SE–S1	0.67	21–24
2	35	S1–S2	0.45	34–36
3	35	S1–S2	0.44	35–36
	Log rank (Mantel–Cox): Chi-square = 365.3; $df=2$; $p < 0.001$			
Forest type				
Np	31	S1–S2	0.52	30–32
M	30	S1–S2	0.53	29–31
	Log rank (Mantel–Cox): Chi-square = 365.3; $df=2$; $p < 0.001$			
Geographic location				
Coasts	28	S1–S2	0.55	27–29
Mountains	33	S1–S2	0.45	32–31
	Log rank (Mantel–Cox): Chi-square = 365.3; $df=2$; $p < 0.001$			

Estimate = Average survival time (months), Transitions = SE (emerged seedlings), S1 = 1-year survivors, S2 = 2-year survivors. CI confidence interval at 95% (lower bound–upper bound). Log-rank test for equality of survival distributions by Chi-square, df degree free, p value at < 0.05

occurred between 1-year survivors and 2-year survivors. Among geographical locations, the average survival time was higher on the mountains (month 33) than on the coasts (month 28), occurring between 1-year survivors and 2-year survivors for both locations. Transition probabilities were described in more detail in Tables S4 and S5. In general, the highest probability of transition occurred in the mountains (0.719 ± 0.044 in mixed and 0.622 ± 0.046 in pure forests) than in coastal forests (0.399 ± 0.044 in pure and 0.168 ± 0.031 in mixed forests). Critical transition (where the percentage of transition was lower throughout all the structures) was from female flower to fruits (only 40.4% of the flowers became fruits in pure forests and 62.2% in mixed forests on the coasts; 63.5% in pure forests and 54.3% in mixed forests on the mountains). Another critical stage was from sound seeds to emerged seedlings (only 36.1% of the sound seeds became seedlings in pure forests and 10.3% in mixed forests on the coasts; 49.7% in mixed forests on the mountains) (Tables S4 and S5).

Survival analysis for the transitions from flowers to 2-year-old seedlings showed significant differences in *N. betuloides* species in each cohort (Chi-square = 33.8; $df=2$; $p < 0.001$), forest type (Chi-square = 16.2; $df=1$; $p < 0.001$), except between geographic locations (Chi-square = 0.1; $df=2$; $p = 0.715$) (Table 2). The mean survival time (estimate) was lower for cohort 1 (month 24, between the emerged seedlings and 1-year survivors) than in cohorts 2 and 3 (month 28, between the 1-year survivors and 2-year survivors), differing from *N. pumilio*. Furthermore, these differences were significant between forest types, although the mean survival time occurred between the 1-year survivors and 2-year survivors stages. Regarding the geographical

Table 2 Kaplan–Meier Survival Estimated by means for survival time (transitions) for *N. betuloides* by cohorts (1, 2, 3), forest type (Nb = pure *N. betuloides* forests, M = mixed forests) and geographic locations (coasts and mountains)

	Estimate	Transitions	Standard Error	CI (95%)
Cohort				
1	24	SE–S1	0.68	23–25
2	28	S1–S2	0.68	27–30
3	28	S1–S2	0.68	27–29
	Log rank (Mantel–Cox): Chi-square = 365.3; $df=2$; $p < 0.001$			
Forest type				
Nb	26	S1–S2	0.56	25–27
M	28	S1–S2	0.56	27–29
	Log rank (Mantel–Cox): Chi-square = 365.3; $df=2$; $p < 0.001$			
Geographic location				
Coasts	27	S1–S2	0.55	26–28
Mountains	26	S1–S2	0.57	25–27
	Log rank (Mantel–Cox): Chi-square = 0.1; $df=2$; $p = 0.715$			

Estimate = Average survival time (months), Transitions = SE (emerged seedlings), S1 = 1-year survivors, S2 = 2-year survivors. CI = Confidence interval at 95% (lower bound–upper bound). Log-rank test for equality of survival distributions by Chi-square, df degree free, p value at < 0.05

locations, the mean survival time was similar (1-year survivors to 2-year survivors) between coasts (month 27) and mountains (month 26). Transition probabilities were described in more detail in Tables S4 and S5.

The highest probability of transition occurred in the pure forest on the coasts (0.519 ± 0.046) followed by the mountains (0.231 ± 0.034 in pure and 0.344 ± 0.041 in mixed forests) and the mixed forest on the coasts (0.051 ± 0.016). Critical transition was from female flower to fruits (only 17.8% of the flowers became fruits in pure and 21.3% in mixed forests on the coasts; 20.8% in pure and 17.5% in mixed forests on the mountains). Similarly, to *N. pumilio*, the other critical stage was from sound seeds to emerged seedlings (only 7.9% of the sound seeds became seedlings in pure and 0.3% in mixed forests on the coasts; 32.7% in pure and 9.5% in mixed forests on the mountains). The transitions recorded in coastal forests for *N. betuloides* (sound seeds–emerged seedlings) was the most critical as it fell to 0, in cohort 1 and cohort 2 in the mixed forest). However, *N. betuloides* had a high probability of reaching 2-year survivor in mixed forest (100% of seedlings survive) (Tables S4 and S5).

The Cox proportional-hazards model showed significant differences when analysing all the predictor variables for both species (cohort, forest type, geographic locations and their interactions). The models generated were statistically significant for a good prediction both for *N. pumilio* ($-2 \text{ Log Likelihood} = 4499.79$, Chi-square = 464.79, $df = 11$, $p < 0.001$) and for *N. betuloides* ($-2 \text{ Log Likelihood} = 7636.63$, Chi-square = 194.96, $df = 11$, $p < 0.001$).

The Model for *N. pumilio* (Table 3) showed that the forest type had no statistical significance in the survival, whose Hazard ratio was close to 1 (0.990). The interactions were statistically significant, with some exceptions for some predictor variables, such as Cohort 2 (2/1) \times Geographic location (mountains/coasts), Forest type (M/Np) \times Geographic location (mountains/coasts), Cohort 2 (2/1) \times Forest type (M/Np) \times Geographic location (mountains/coasts). However, the model had significance in several predictor variables. For example, the hazard rate was 5% higher for cohort 1 compared to cohort 2 ($2/1 = 0.050$) and was 3% higher for cohort 1 compared to cohort 3 ($3/1 = 0.030$). Therefore, the cohorts had a reduced risk of 95% for cohort 2 and 97% for cohort 3, compared to cohort 1. For the geographic location, the hazard rate is 52.5% higher for coasts compared to mountains (mountains/coasts = 0.525). The Cohort 2 (2/1) \times Forest type (M/Np) interaction indicated that the hazard in cohort 2 and in mixed forest was 9.292 times higher than in cohort 1 and in pure forest. The Cohort 3 (3/1) \times Geographic location (mountains/coasts) interaction indicated that the hazard in cohort 3 and in the mountains was 7.623 times higher than in cohort 1 and on the coasts.

The model for *N. betuloides* (Table 4) showed that most of the predictor variables and the interactions among them were statistically significant. Forest type significantly influenced

Table 3 Parameter estimates for Cox proportional-hazards models for transitions in *N. pumilio*

Predictor variables	β	Standard Error	Wald	df	p	Hazard ratio (eb)	CI (95%)
Cohort			76.27	2	<0.001		
Cohort 2 (2/1)	- 3.006	0.458	43.04	1	<0.001	0.050	0.020–0.122
Cohort 3 (3/1)	- 3.517	0.586	36.03	1	<0.001	0.030	0.009–0.094
Forest type (M/Np)	- 0.01	0.141	0.01	1	0.944	0.990	0.751–1.305
Geographic location (mountains/coasts)	- 0.645	0.170	14.45	1	<0.001	0.525	0.376–0.732
Cohort \times Forest type			27.96	2	<0.001		
Cohort 2 (2/1) \times Forest type (M/Np)	2.229	0.492	20.56	1	<0.001	9.292	3.546–24.352
Cohort 3 (3/1) \times Forest type (M/Np)	1.907	0.635	9.02	1	0.003	6.733	1.940–23.375
Cohort \times Geographic location			9.28	2	0.010		
Cohort 2 (2/1) \times Geographic location (mountains/coasts)	- 9.387	67.437	0.02	1	0.889	0.000	0.000–2.118E+53
Cohort 3 (3/1) \times Geographic location (mountains/coasts)	2.031	0.667	9.26	1	0.002	7.623	2.061–28.197
Forest type (M/Np) \times Geographic location (mountains/coasts)	- 0.323	0.255	1.6	1	0.206	0.724	0.439–1.194
Cohort \times Forest type \times Geographic location			7.36	2	0.025		
Cohort 2 (2/1) \times Forest type (M/Np) \times Geographic location (mountains/coasts)	- 1.896	95.37	0	1	0.984	0.150	0.000–2.266E+80
Cohort 3 (3/1) \times Forest type (M/Np) \times Geographic location (mountains/coasts)	- 2.268	0.836	7.36	1	0.007	0.104	0.020–0.533

The model includes the cohort (1, 2, 3), forest type (Np=pure *N. pumilio* forests, M=mixed forests) and geographic locations (coasts and mountains). Next to each predictor variables, the analysed level in relation to the reference level defined by the model is indicated in parentheses

β parameter estimates, Wald tests for statistical significance, df =degree of freedom, p value at <0.05 , Hazard Ratio (eb)=Hazard ratio (or odds ratio); ratio > 1 it is associated with a higher hazard of transition. CI95% interval for Hazard Ratio

Table 4 Parameter estimates for Cox proportional-hazards model for transitions in *N. betuloides*

Predictor variables	β	Standard error	Wald	df	<i>p</i>	Hazard ratio (eb)	CI (95%)
Cohort			13.956	2	0.001		
Cohort 2 (2/1)	0.973	0.285	11.692	1	0.001	2.647	1.515–4.625
Cohort 3 (3/1)	0.345	0.317	1.183	1	0.277	1.412	0.758–2.628
Forest type (M/Nb)	1.699	0.264	41.507	1	<0.001	5.471	3.262–9.174
Geographic location (mountains/coasts)	1.655	0.265	39.116	1	<0.001	5.235	3.116–8.795
Cohort \times Forest type			15.481	2	<0.001		
Cohort 2 (2/1) \times Forest type (M/Nb)	-1.052	0.322	10.694	1	0.001	0.349	0.186–0.656
Cohort 3 (3/1) \times Forest type (M/Nb)	-1.381	0.376	13.472	1	<0.001	0.251	0.120–0.525
Cohort \times Geographic location			43.813	1	<0.001		
Cohort 2 (2/1) \times Geographic location (mountains/coasts)	-2.061	0.311	42.181	2	<0.001	0.127	0.047–0.201
Cohort 3 (3/1) \times Geographic location (mountains/coasts)	-2.327	0.368	39.872	1	<0.001	0.098	0.237–0.964
Forest type (M/Nb) \times Geographic location (mountains/coasts)	-0.739	0.358	4.255	1	0.039	0.478	0.069–0.234
Cohort \times Forest type \times Geographic location			15.037	2	0.001		
Cohort 2 (2/1) \times Forest type (M/Nb) \times Geographic location (mountains/coasts)	0.763	0.508	2.258	1	0.133	2.144	0.793–5.797
Cohort 3 (3/1) \times Forest type (M/Nb) \times Geographic location (mountains/coasts)	1.742	0.450	15.012	1	<0.001	5.711	2.366–13.789

The model includes the cohort (1, 2, 3), forest type (Nb = pure *N. betuloides* forests, M = mixed forests) and geographic locations (coasts and mountains). Next to each predictor variables, the analysed level in relation to the reference level defined by the model is indicated in parentheses β estimated parameter, Wald tests for statistical significance, *df* degree of freedom, *p* value at <0.05, Hazard Ratio (eb)=Hazard ratio (or odds ratio); ratio > 1 it is associated with a higher hazard of transition. *CI*=95% interval for Hazard Ratio

survival, where the Hazard ratio for M/Nb was 5.471. The cohorts also significantly influenced survival, since the hazard ratio was 2.647 times greater in cohort 2 than in cohort 1. However, the interactions with the cohorts showed that the Hazard ratio is reduced in Cohort 2 (2/1) \times Forest type (M/Nb)=0.349 and Cohort 3 (3/1) \times Forest type (M/Nb)=0.251 and in Cohort 2 (2/1) \times Geographic location (mountains/coasts)=0.127 and Cohort 3 (3/1) \times Geographic location (mountains/coasts)=0.098. This suggests that *N. betuloides* had a higher Hazard ratio in the mixed forest in cohort 1 and on the coasts, as indicated by the Kaplan–Meier survival analysis.

Cumulative probabilities of transition and influence of loss factors along the whole cycle

The losses along with the reproductive cycle influenced on the probability of transitions of *N. pumilio*, where reproductive capacity significantly varied among the studied forest types, mainly in cohorts 2 and 3 (Fig. S3). For *N. betuloides*, reproductive losses were quite similar between pure and mixed forests. However, reproductive losses were quite variable among the different cohorts for coasts and mountains (Fig. S4). In the cohorts 1 and 2, the seedling emergence of *N. betuloides* completely failed in mixed forests at the coasts location, while in the mountains, there were no losses in seedling emergence (100% survival) during cohort 1.

Figure 4 shows the mean cumulative probabilities of successful transition for each *Nothofagus* species and cohorts at different forest type and geographic locations. In general, probabilities were much higher for the flowers and fruits in the tree canopy than for seeds and seedlings in the understory. The cumulative probabilities of transition for *N. pumilio* varied between 0.3–46.2% in pure and 1.4–30.2% in mixed forests, but only cohort 3 reached a similar probability at both forest types. *N. betuloides* varied between 2.8–24.4% in pure and 0.0–6.5% in mixed forests. Both *Nothofagus* species showed better performance in mountains (15.9–46.2% Np and 3.8–24.8% Nb) than in coasts (0.3–16.1% Np and 2.8–5.3% Nb). However, *N. pumilio* had a higher overall probability transition for all cohorts in the mountains than in the coasts. While *N. betuloides* in mountains resulted in a higher probability of transition in cohort 2 and 3 in pure and mixed forests, the probability in cohort 1 and 2 was 0.0% at mixed forests in the coasts. Pre-dispersal losses were in turn higher for fruits than for flowers, in each forest type and geographic location in all cohorts. Percentages of female flower loss were consistently low for all cohorts and species in each forest type and geographic location. For example, in cohort 1 for the pure forest of *N. pumilio*, of 100% of female flowers, 19.5% was lost by abscised female flowers and then 53% was lost by female flowers derived in empty fruits. Once on the forest floor, seeds suffered from foraged similarly in all cohorts and species in each forest type and

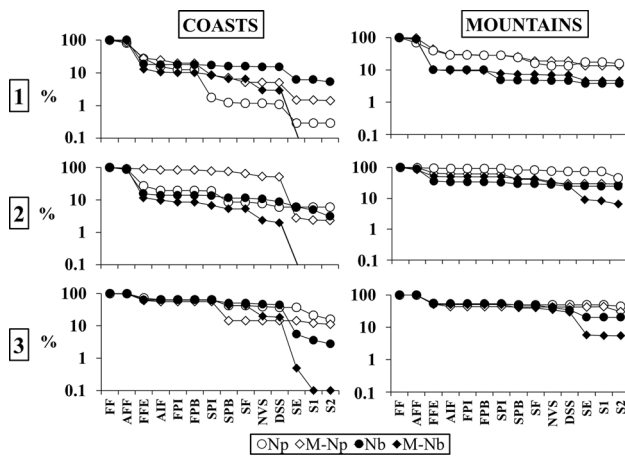


Fig. 4 Mean cumulative probabilities (%) of transition between reproductive structures resulting from the incidence of loss factors on *N. pumilio* in pure (Np) and mixed (M–Np) forests, and on *N. betuloides* in pure (Nb) and mixed (M–Nb) forests, in coasts and mountains locations and each cohort (1, 2, and 3). Percentages refer to the initial number of female flowers (FF). Axis Y is on a logarithmic scale. Lines crossing the horizontal axis drop to zero values. FF female flowers. Losses factors: AFF abscised female flowers, FFE female flowers derived in empty fruits, AIF abscised immature fruits, FPI fruits predated by insects, FPB fruits predated by birds, SPI seeds predated by insects, SPB seeds predated by birds, SF seeds foraged in the forest floor (mice + birds), NVS non-viable seeds, DSS dead seeds during winter stratification, SE emerged seedlings, S1 1-year survivors, S2 2-year survivors

geographic location, while winter stratification seed losses exceeded those from foraged especially in cohorts 1 and 2 for *N. betuloides* in the mixed forests in coasts. Overall, losses at the seed process were quantitatively similar to those in the flower and fruit process.

Emerged seedlings was by far the most critical stages, accounting for greater losses in all cohorts and species in each forest type and geographic location. Drop in recruitment potential at this stage were much more severe in mixed forests in coastal location. Within mixed forests, *N. betuloides* species suffered the greatest losses in emerged seedlings, thus leading to virtually no recruitment in the latter. Concerning seedling survival, values were around or below 9% in all cases, except in pure *N. pumilio* and *N. betuloides* forests in the mountains location (about 20%). Survival from 1 to 2 years was consistently lower in all cohorts and species in each forest type and geographic location.

Discussion

Influence of forest type and geographic locations in early life stage transitions

We have considered early stages of regeneration to detect the main bottlenecks in pure and mixed forests, in processes ranging from flowering to the installation and survival of seedlings. Through the integrated approach of the reproductive cycle and how the forest type and three cohorts influenced, we found multiple pathways for tree regenerations, e.g., from seedling emergence failure, extremely poor fruiting years, to high rates of female flowers forming 2-year-old seedlings. However, performance of the species was strongly determined by forest type and geographic location, principally for *N. betuloides* (according to the Cox proportional-hazards models). In concordance with previous studies in *Nothofagus* species (e.g., Soler et al. 2013), the most critical stages in the whole natural regeneration cycle considered in this study were from female flower to fruit and from the sound seeds to emerged seedlings for all forests type on the coasts and mountains. The loss of individuals during the natural regeneration cycle is mainly driven by biotic interactions but probably, also by resource competition with other tree plants, or neighbouring vegetation (Messaoud and Houle 2006), although it is unknown for *Nothofagus* species. The abrupt decrease in the transition from female flowers to fruits could be related to: (i) an unfavourable development of the female flower due to the high energy cost demanded by this process (Pulido et al. 2010), or (ii) also to the attack of pathogens and insects, whose abundance is greater in unmanaged *Nothofagus* forests (Martínez Pastur et al. 2013). It should be noted that these forests have not been managed in the last 60 years or more. Another cause could be the effect of wind speed and rainfall that lead to pollination failures forming empty fruits, as has already been seen in other primary *Nothofagus* forests (Martínez Pastur et al. 2013; Soler et al. 2013). Regarding emerged seedlings, resource competition is considered a main determinant of plant survival and growth and, consequently, of species coexistence during the regeneration stage (Nelson and Wagner 2014). Temperature, radiation, and soil humidity are key factors affecting the seedling emergence and survival in southern forests (Heinemann et al. 2000; Toro Manríquez et al. 2019b). Seedling emergence may also be limited by the availability of seeds or suitable microsites for seed germinations and growth (Clark et al. 1999). Rey and Alcántara (2000) indicate that there may be a decoupling of different selective forces that act on seeds and seedlings, or due to ontogenetic changes (development phases) in resource requirements and stress

in various microenvironments. Forest structure (i.e., canopy cover) and microsites mainly determine the spatial context in which the forest is located (Martínez Pastur et al. 2011; Toro Manríquez et al. 2019b).

Results of our study showed a determining role of geographic location on the seedling emergence related to the inter-annual variation of seeds production (number and quality). Spatial and temporal heterogeneity in seedling emergence is a common characteristic among other *Nothofagus* species (Bahamonde et al. 2011; Soler et al. 2013), where the effective seedling emergence is influenced by cyclical and intermittent seeds production (synchronized at a regional scale) along with inter-annual climate variability (Martínez Pastur et al. 2013; Soler et al. 2013). Regarding the seedling survival, this characteristic is mainly affected by abiotic factors, mainly those related to the soil (e.g., soil moisture), which are more favourable in mountains forests (Toro Manríquez et al. 2020).

Within mixed forest, where both *Nothofagus* species coexist and potentially compete by resources, the deciduous *N. pumilio* showed better recruitment performance (highest transition probabilities among reproductive structures) than the evergreen *N. betuloides*. The evergreen species failed to recruit in the mixed coastal forests for two of the three cohorts analyzed, which implies an advantage of *N. pumilio* over *N. betuloides* that must be further examined. However, if we focus on forest type and geographic location factors (not interannual variability), the results showed that survival can be 100% in *N. betuloides* 2-year seedlings in mixed coastal forests. In *Nothofagus* mixed forests, we expected some advantages in reproductive performance mainly for the deciduous species, because at canopy level, the evergreen species have greater availability of light during a part of the year, which does not happen in pure evergreen forests. According to Pretzsch (2014), the multiple crowns overlap in a mixed forest to maximize the space filling, drawing additional advantages in resource utilization. In our mixed forests, the highest probability of transition was for *N. pumilio* compared with *N. betuloides*, both on the coasts and mountains. This would indicate that the seedling bank is neither stable nor permanently mixed, and that the greater reproductive success and recruit of the deciduous species foster the dominance of such species in the understory, at least during early years after seeding (e.g., masting years). Therefore, the semi-open condition of mixed canopies infers an improvement in the environmental conditions for the deciduous species.

General factors that can influence along the whole cycle

Strong variability in annual seed production and occurrence of years with exceptionally large seeding is a common

feature of trees in the Fagaceae family (Kelly 1994; Kelly and Sork 2002; Espelta et al. 2009; Kelly et al. 2013; Soler et al. 2017). Previous studies related masting events to climatic drivers. Torres et al. (2015) demonstrated the relevance of precipitation in the seeds production of *Nothofagus* in Tierra del Fuego. Richardson et al. (2005) demonstrated that cold, wet summers produce higher seeds number in the forests of *Nothofagus solandri* in New Zealand. On the other hand, Kon et al. (2005) demonstrated the correlation between seed production and the minimum temperatures of the previous spring for *Fagus crenata*, demonstrating that such production is sensitive to changing climatic conditions based on its specific ecophysiological traits.

Although we did not detect exceptional seeding years, variability in seed production had consequences for the recruitment in mixed forests, as was observed in the years with high proportion of *N. pumilio* seeds, when great foraging occurred in post-dispersal, because these attract more predators, causing less availability of viable seeds for installation. On the contrary, in other Fagaceae species, it was observed that the production of seeds is inversely related to foraging: the lower the production the greater the foraging (Pulido et al. 2010). There are also some other studies (involving larger seeds), which have demonstrated that foraging and predation are key in the installation of seedlings (Jordano 2000; García Castaño et al. 2006).

Seeding fluctuations could lead to a meta-stable situation of mixed canopy or instability, with alternation of dominance between the two conforming species, mainly caused by its relationship with the climate. For example, alternating wet and dry years frequently might determine years with high seedling survival and good seed production. For some mixed forests, this alternation of dry and wet years makes the regeneration process occur as pulses, although these establishment pulses do not occur with a regular frequency (White 1979). The alternation of dominance phenomenon has been studied in European forests (Roženbergar et al. 2007), but no for *Nothofagus* in the southern hemisphere. The alternation in the dominance of the species could explain the greater dominance of *N. pumilio* over *N. betuloides* regeneration in the three cohorts studied. In general, *N. betuloides* presents a persistent and permanent bank of older plants than *N. pumilio*, with higher probabilities of survival over medium or long time. It can be due to the tolerance to shading conditions of *N. betuloides*, which could indicate a subsequent dominance when microclimatic conditions change and favour growth (e.g., gap opening due to the fall of a large tree), accompanied by these pulses of seed (Toro Manríquez 2019). After longer periods in such understory, shade-tolerant tree species will probably dominate the tree regeneration at the understory level (Löf et al. 2018).

Due to the dependency of seeding on climatic conditions, as well as its repercussion on predation and alternation of

dominance, climatic change could be a strong threat to mixed forests. Complementary, the evaluation of the stability of mixed forests against climatic change would only be possible through long-term studies of the seed, installation, and survival stages, accompanied by climatic data at various scales. According to climate change models in Southern Patagonia, it is predicted that temperature and precipitation would increase, which would favour regional productivity (Kreps et al. 2012), but not the predominance of species sensitive to high temperatures and low humidity.

Reproductive performance in coasts and mountains forests: two contrasting stability trends

The coasts and mountains location differ principally in topographic conditions (Toro Manríquez et al. 2019a). Any modification in these environmental parameters could modify the stability (proportion of deciduous and evergreen in the canopy) of the mixed forests towards the predominance of such species boosted by such changes. According to our results, the probabilities of transition were generally higher in the pure forests and in the mountains than in the coasts for *N. betuloides* in mixed forests, but with great variations between cohorts. This demonstrates a clear effect of the landscape location and the inter-annual variability in how the limiting factors intervene in the reproductive performance, seeding and seedling emergence. Even the same species in pure forests displayed differences in the transitions between reproductive structures for both coasts and mountains location. Although both species reached the lowest reproductive success on the coasts, it was more noticeable for *N. betuloides* in mixed forests as it only recruited 2-year-old individuals only in one of the three cohorts studied. For the pure *N. pumilio* forests, 1-year seedling survival on the coasts was a critical stage, probably due to driest soil conditions in the coasts than in the mountains (Toro Manríquez et al. 2019a), or other not studied factors that may occur at this critical stage (e.g., insect or fungal attacks on seedlings, soil nutrient lacks).

In the mountains, *N. pumilio* had a greater loss during seedling emergence in mixed forests compared to the pure ones. This could be related to less amount of effective precipitation reaching the forest floor of the mixed forests (e.g., more water interception under partial evergreen canopy) than in the pure deciduous forests, and therefore, the upper centimetres of soils, where the radicles develop were much drier. In addition, the pure forests of *N. pumilio* in the mountains, have greater forbs cover in the understory (Mestre et al. 2017), which benefit the retention of relative air humidity near the soil that avoid apex desiccation and, therefore, improve seedling development as was demonstrated by previous studies (Martínez Pastur et al. 2011).

Conclusion

This study highlights the importance of evaluating early stages of regeneration to detect the main bottlenecks in pure and mixed *Nothofagus* forests, in aspects ranging from flowering to the installation and survival of seedlings. Through the integrated approach of the reproductive cycle in different forest types, geographic locations and cohorts, our results provide quantitative evidence for multiple pathways for tree regenerations. Nevertheless, the performance of the species (hazard ratio) is strongly determined by the forest type and the geographic location in *N. betuloides*, and for the geographic location in *N. pumilio*. However, *N. betuloides* in the pure forest presented a better transition probability than other forest type on the coasts. Although variable, the most critical stage detected in this study were from female flower to fruits and the emerged seedling in all forests for coasts and mountains forests. Within mixed forest, the deciduous *N. pumilio* shows better recruitment performance (highest transition probabilities among reproductive phases and seedling survival) than the evergreen *N. betuloides*, which completely fails some years. However, *N. betuloides* species had a higher probability of survival than *N. pumilio* at 2-year survivors. This implies differential advantages of both species (e.g., *N. pumilio* had a greater number of propagules and a better transition probability and *N. betuloides* had greater seedling survival at 2 years), and that mixed forests tend to be unstable but rather dynamic, depending on the installation pulses, which do not always coincide with both species mainly on the coasts. Medium and long-term studies are essential to determine if the dominance of deciduous species over the evergreen persists over-time.

Author contribution statement MDRTM: conceptualization, ideas, methodology, validation, formal analysis, investigation, data curation, writing—original, writing—review and editing, visualization, and project administration. RS: methodology, investigation, writing—review and editing, and supervision. AHH: investigation, writing—review and editing. MVL: writing—review and editing, supervision. AP: writing—review and editing. APB: investigation. GMP: conceptualization, ideas, resources, writing—review and editing, and supervision.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-021-02195-8>.

Acknowledgements We want to thank the support of Centro Austral de Investigaciones Científicas (CADIC-CONICET, Ushuaia-Argentina) and Tierra del Fuego National Park (PNTDF) by the Administración de Parques Nacionales, Ushuaia, Argentina, through the project "Ciclo de regeneración natural en bosques mixtos de *Nothofagus pumilio* y *N. betuloides*: ¿Son bosques estables o dinámicos? DRPA

N° 19 (2013–2018)", whose research was part of the doctoral thesis of MDRTM supported by CONICET doctoral scholarships.

Funding This work was supported by CONICET doctoral scholarships for Latin American students (2014–2019) and was conducted with funds provided by PICT2016–1968 ANPCyT-Argentina (Monitoreo y evaluación de plantas vasculares, artrópodos y aves en ambientes de Patagonia Sur para la identificación de bioindicadores de actividades agroforestales y el desarrollo de estrategias de conservación).

Declarations

Conflict of interest The authors have declared that no competing interests exist.

References

- Ali A, Lin SL, He JK, Kong FM, Yu JH, Jiang HS (2019) Tree crown complementarity links positive functional diversity and above-ground biomass along large-scale ecological gradients in tropical forests. *Sci Total Environ* 656:45–54. <https://doi.org/10.1016/j.scitotenv.2018.11.342>
- Bahamonde HA, Peri PL, Monelos LH, Martínez Pastur G (2011) Aspectos ecológicos de la regeneración por semillas en bosques nativos de *Nothofagus antarctica* en Patagonia Sur, Argentina. *Bosque* 32:20–29. <https://doi.org/10.4067/S0717-92002011000100003>
- Bewick V, Cheek L, Ball J (2004) Statistics review 12: survival analysis. *Crit Care* 8(5):1–6. <https://doi.org/10.1186/cc2955>
- Bogdziewicz M, Fernández-Martínez M, Bonal R, Belmonte J, Espelta JM (2017) The Moran effect and environmental vetoes: phenological synchrony and drought drive seed production in a Mediterranean oak. *Proc Biol Sci* 284(1866):20171784. <https://doi.org/10.1098/rspb.2017.1784>
- Burgos A, Grez AA, Bustamante RO (2008) Seed production, pre-dispersal seed predation and germination of *Nothofagus glauca* (Nothofagaceae) in a temperate fragmented forest in Chile. *For Ecol Manag* 255(3–4):1226–1233. <https://doi.org/10.1016/j.foreco.2007.10.032>
- Chen Y, Chen G, Yang J, Sun W (2016) Reproductive biology of *Magnolia sinica* (Magnoliaceae), a threatened species with extremely small populations in Yunnan, China. *Plant Divers* 38(5):253–258. <https://doi.org/10.1016/j.pld.2016.09.003>
- Clark JS, Beckage B, Camill P, Cleveland B, Hilleris Lambers J, Lichten J, McLachlan J, Mohan J, Wyckoff P (1999) Interpreting recruitment limitation in forests. *Am J Bot* 86:1–16
- CONAF Corporación Nacional Forestal (2011) Catastro de los recursos vegetacionales nativos de Chile. In: Monitoreo de cambios y actualizaciones. Período 1997-2011, Corporación Nacional Forestal, Santiago, Chile, 28 p
- Cox DR (1972) Regression models and life-tables. *J R Stat Soc* 34(2):187–202
- Crone EE, Ellis MM, Morris WF, Stanley A, Bell T, Bierzychudek P, Ehrlén J, Kaye TN, Knight TM, Lesica P, Oostermeijer G, Quintana-Ascencio PF, Ticktin T, Valverde T, Williams JL, Doak DF, Ganesan R, McEachern K, Thorpe AS, Menges ES (2013) Ability of matrix models to explain the past and predict the future of plant populations. *Conserv Biol* 27(5):968–978. <https://doi.org/10.1111/cobi.12049>
- Espelta JM, Cortés P, Molowny-Horas R, Retana J (2009) Acorn crop size and pre-dispersal predation determine inter-specific differences in the recruitment of co-occurring oaks. *Oecologia* 161:559–568. <https://doi.org/10.1007/s00442-009-1394-x>
- Fick SE, Hijmans RJ (2017) World Clim 2: new 1km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37(12):4302–4315. <https://doi.org/10.1002/joc.5086>
- Fischelli N, Vor T, Ammer C (2014) Broadleaf seedling responses to warmer temperatures “chilled” by late frost that favors conifers. *Eur J for Res* 133:587–596. <https://doi.org/10.1007/s10342-014-0786-6>
- Frangi JL, Barrera MD, Puig De Fábregas J, Yapura PF, Arambarri AM, Richter L (2005) Ecología de los bosques de Tierra del Fuego. In: Goya JF, Frangi JL, Arturi MF (eds) Investigación en bosques nativos de Argentina. Universidad Nacional de La Plata, Buenos Aires
- García Castaño JL, Kollmann J, Jordano P (2006) Spatial variation of post-dispersal seed removal by rodents in highland microhabitats of Spain and Switzerland. *Seed Sci Res* 16:213–222. <https://doi.org/10.1079/SSR2006245>
- Heinemann K, Kitzberger T, Veblen T (2000) Influences of gap micro heterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. *Can J for Res* 30:25–31
- IBM Corporation Released (2017) IBM SPSS Statistics for Windows, Version 25.0. Armonk, New York
- Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) Seeds: the ecology of regeneration in natural plant communities. Commonwealth Agricultural Bureau International, Wallingford, pp 125–166
- Kartsonaki C (2016) Survival analysis. *Diagn Histopathol* 22(7):263–270. <https://doi.org/10.1016/j.mpdhp.2016.06.005>
- Kelly D (1994) The evolutionary ecology of mast seeding. *Trends Ecol Evol* 9:465–470. [https://doi.org/10.1016/0169-5347\(94\)90310-7](https://doi.org/10.1016/0169-5347(94)90310-7)
- Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? *Ann Rev Ecol Syst* 33:427–447. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095433>
- Kelly D, Geldenhuis A, James A, Holland EP, Plank MJ, Brockie RE, Cowan PE, Harper GA, Lee WG, Maitland MJ, Mark MF, Mills JA, Wilson PR, Byrom AE (2013) Of mast and mean: differential temperature cue makes mast seeding insensitive to climate change. *Ecol Lett* 16:90–98. <https://doi.org/10.1111/ele.12020>
- Kon H, Noda T, Terazawa K, Koyama H, Yasaka M (2005) Proximity factors causing mast seeding in *Fagus crenata*: the effects of resource level and weather cues. *Can J Bot* 83(11):1402–1409. <https://doi.org/10.1139/b05-120>
- Kreps G, Martínez Pastur G, Peri PL (2012) Cambio climático en Patagonia sur. Escenarios futuros en el manejo de los recursos naturales. In: INTA (ed) Santa Cruz, Argentina
- Leishman MR, Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed size. In: Fenner M (ed) Seeds: the ecology of regeneration in natural plant communities. CABI Publishing, Wallingford, pp 125–166
- Löf M, Ammer C, Coll L, Drössler L, Huth F, Madsen P, Wagner S (2018) Regeneration patterns in mixed species stands. In: Bravo-Oviedo A, Pretzsch H, del Río M (eds) Dynamics, silviculture and management of mixed forests. Managing forest ecosystems, vol 31. Springer, Cham, pp 103–130. https://doi.org/10.1007/978-3-319-91953-9_4
- Martínez Pastur G, Lencinas MV, Peri PL, Cellini JM (2008) Flowering and seeding patterns in unmanaged and managed *Nothofagus pumilio* forests with a silvicultural variable retention system. *Forstarchiv* 79:60–65
- Martínez Pastur G, Cellini JM, Lencinas MV, Barrera M, Peri PL (2011) Environmental variables influencing regeneration of *Nothofagus pumilio* in a system with combined aggregated and dispersed retention. *For Ecol Manag* 261:178–186. <https://doi.org/10.1016/j.foreco.2010.10.002>

- Martínez Pastur G, Soler Esteban R, Pulido F, Lencinas MV (2013) Variable retention harvesting influences biotic and abiotic drivers of regeneration in *Nothofagus pumilio* southern Patagonian forests. For Ecol Manag 289:106–114. <https://doi.org/10.1016/j.foreco.2012.09.032>
- Menges ES (2000) Population viability analyses in plants: challenges and opportunities. Trends Ecol Evol 15:51–56. [https://doi.org/10.1016/S0169-5347\(99\)01763-2](https://doi.org/10.1016/S0169-5347(99)01763-2)
- Messaoud Y, Houle G (2006) Spatial patterns of tree seedling establishment and their relationship to environmental variables in a cold temperate deciduous forest of eastern North America. Plant Ecol 185:319–331
- Mestre L, Toro-Manríquez M, Soler R, Huertas-Herrera A, Martínez Pastur G, Lencinas MV (2017) The influence of canopy-layer composition on understory plant diversity in southern temperate forests. For Ecosyst 4:6. <https://doi.org/10.1186/s40663-017-0093-z>
- Moles AT, Leishman MR (2008) The seedling as part of a plant's life history strategy. In: Allesio Leck M, Parker VT, Simpson RL (eds) Seedling ecology and evolution. Cambridge University Press, pp 217–238. <https://doi.org/10.1017/CBO9780511815133.012>
- Nelson AS, Wagner RG (2014) Spatial coexistence of American beech and sugar maple regeneration in postharvest northern hardwood forests. Ann for Sci 71:781–789. <https://doi.org/10.1007/s13595-014-0376-2>
- Pillay R, Hua F, Loïsele BA, Bernard H, Fletcher RJ Jr (2018) Multiple stages of tree seedling emergence are altered in tropical forests degraded by selective logging. Ecol Evol 8(16):8231–8242. <https://doi.org/10.1002/ece3.4352>
- Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For Ecol Manag 327:251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>
- Pulido F, García E, Obrador JL, Moreno G (2010) Multiple pathways for tree regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. J Appl Ecol 47:1272–1281. <https://doi.org/10.1111/j.1365-2664.2010.01865.x>
- Ramírez C (1987) El Género *Nothofagus* y su importancia en Chile. Bosque 8(2):71–76
- Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J Ecol 88:622–633
- Richardson SJ, Allen RB, Whitehead D, Carswell FE, Ruscoe WA, Platt KH (2005) Climate and net carbon availability both determine seed production in a temperate tree species. Ecology 86: 972–981. www.jstor.org/stable/3450850. Accessed 15 Sept 2020
- Riveros M, Parades MA, Rosas MT, Cardenas E, Armesto J, Arroyo MTK, Palma B (1995) Reproductive biology in species of the genus *Nothofagus*. Environ Exp Bot 35:519–524. [https://doi.org/10.1016/0098-8472\(95\)00022-4](https://doi.org/10.1016/0098-8472(95)00022-4)
- Roženbergar D, Mikac S, Anic I, Diaci J (2007) Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech—fir forest reserves in South East Europe. Forestry 80(4):431–443. <https://doi.org/10.1093/forestry/cpm037>
- Soler R, Martínez Pastur G, Peri PL, Lencinas MV, Pulido F (2013) Are silvopastoral systems compatible with forest regeneration? An integrative approach in southern Patagonia. Agrofor Syst 87:1213–1227. <https://doi.org/10.1007/s10457-013-9631-z>
- Soler R, Espelta JM, Lencinas MV, Peri PL, Martínez Pastur G (2017) Masting has different effects on seed predation by insects and birds in antarctic beech forests with no influence of forest management. For Ecol Manag 400:173–180. <https://doi.org/10.1016/j.foreco.2017.06.014>
- Toro Manríquez M (2019) Bosques Mixtos de *Nothofagus pumilio* y *N. betuloides*: ¿Son Estables? Aproximación basada en el estudio de las primeras etapas de su ciclo de regeneración natural. PhD Thesis. Universidad Nacional de La Plata. Buenos Aires (Argentina). <https://doi.org/10.35537/10915/73602>
- Toro Manríquez M, Mestre L, Lencinas MV, Promis Á, Martínez Pastur G, Soler R (2016) Flowering and seeding patterns in pure and mixed *Nothofagus* forests in southern Patagonia. Ecol Process 5:21–33. <https://doi.org/10.1186/s13717-016-0065-1>
- Toro Manríquez M, Soler R, Lencinas MV, Promis A (2019a) Canopy composition and site are indicative of mineral soil conditions in Patagonian mixed *Nothofagus* forests. Ann for Sci 76:117. <https://doi.org/10.1007/s13595-019-0886-z>
- Toro Manríquez MDR, Cellini JM, Lencinas MV, Peri PL, Peña Rojas KA, Martínez Pastur GJ (2019b) Suitable conditions for natural regeneration in variable retention harvesting of Southern Patagonian *Nothofagus pumilio* forests. Ecol Proc 8:e18. <https://doi.org/10.1186/s13717-019-0175-7>
- Toro Manríquez M, Ardiles V, Promis Á, Huertas Herrera A, Soler R, Lencinas MV, Martínez Pastur G (2020) Forest canopy-cover composition and landscape influence on bryophyte communities in *Nothofagus* forests of southern Patagonia. PLoS ONE 15(11):e0232922. <https://doi.org/10.1371/journal.pone.0232922>
- Torres AD, Cellini JM, Lencinas MV, Barrera MD, Soler R, Díaz-Delgado R, Martínez Pastur G (2015) Seed production and recruitment in primary and harvested *Nothofagus pumilio* forests: influence of regional climate and years after cuttings. For Syst 24:s2.0-84930831436. <https://doi.org/10.5424/fs/2015241-06403>
- Traveset A, Tur C, Trøjelsgaard K, Heleno R, Castro-Urgal R, Olesen JM (2016) Global patterns of mainland and insular pollination networks. Glob Ecol Biogeogr 25:880–890. <https://doi.org/10.1111/geb.12362>
- Villalide JM, Corely JC (2008) The role of stand composition on pre-dispersal seed predation in *Austrocedrus chilensis* (Cupressaceae) in north-west Patagonia. Rev Chil Hist Nat 81:387–393. <https://doi.org/10.4067/S0716-078X2008000300007>
- Wesołowski T, Rowiński P, Maziarz M (2015) Interannual variation in tree seed production in a primeval temperate forest: does masting prevail? Eur J for Res 134(1):99–112. <https://doi.org/10.1007/s10342-014-0836-0>
- White PS (1979) Pattern, process, and natural disturbance in vegetation. Bot Rev 45 (3): 229–299. <https://www.jstor.org/stable/4353953>. Accessed 30 Oct 2020
- Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J Ecol 100(3):742–749. <https://doi.org/10.1111/j.1365-2745.2011.01944.x>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Authors and Affiliations

Mónica D. R. Toro-Manríquez^{1,2}  · Rosina Soler³  · Alejandro Huertas Herrera^{1,2}  · María Vanessa Lencinas³  · Álvaro Promis⁴  · Ana Paula Blazina³ · Guillermo Martínez Pastur³ 

¹ Ulterarius Consultores Ambientales y Científicos Ltda, Río de Los Ciervos 5862, Loteo D, km 6 ½ Sur, 6200000 Punta Arenas, Chile

² Departamento de Ciencias Agropecuarias y Acuícolas, Universidad de Magallanes, Av. Bulnes 01855, 6210427 Punta Arenas, Chile

³ Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas

(CONICET), Houssay 200, 9410 Ushuaia, Tierra del Fuego, Argentina

⁴ Departamento de Silvicultura y de La Conservación de La Naturaleza, Universidad de Chile, Av. Santa Rosa 11315, 9206 La Pintana, Santiago, Chile