

Contrasting climate influences on *Nothofagus pumilio* establishment along elevational gradients

Valeria Aschero (✉ vaschero@mendoza-conicet.gob.ar)

CONICET Mendoza <https://orcid.org/0000-0003-3865-4133>

Ana M Srur

CONICET Mendoza

Claudia M Guerrero

Universidad Nacional de la Patagonia Austral

Ricardo Villalba

CONICET Mendoza

Research Article

Keywords: germination, seedlings, mortality, elevation range, fruit rain

Posted Date: June 28th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-636169/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Plant Ecology on January 13th, 2022. See the published version at <https://doi.org/10.1007/s11258-021-01211-8>.

Abstract

Predicted warmer temperatures and more frequent extreme climatic events in the southern Andes will affect the dynamics of the Patagonian forests. These environmental changes may differentially alter the probability of *Nothofagus pumilio* establishment across its altitudinal range of distribution. We monitored fruit rain, seedling emergence and survival at the lower and upper elevation boundaries of *N. pumilio* forests in Santa Cruz (49° 22'S – 72° 56' W), Argentina. From 2012 to 2018, recruitment and mortality were evaluated biannually in the field. Seedling establishment was tested in relation to drought, based on the SPEI (Standardized Precipitation Evapotranspiration Index), and changes in elevation. Fruit rain was consistently higher at low elevation and the abundance of fruits was not affected by drought intensity. Seedling emergence was ~ 11 to 19 times larger at the upper forest boundary, in particular during years characterized by warm-dry climatic conditions in spring-early summer. In contrast, seedling abundance was ~ 3 times larger at low elevations during relatively cold-wet growing seasons. Over the period 2012 to 2018, dominated by dry-warm spring and summers, survival probability curves for seedlings and juvenile trees were higher at upper than lower elevations. Our results show contrasting effects of climate on tree establishment at the elevation limits, with positive and negative drought effects at high and low elevations, respectively. Predicted increase of extreme drought events during the XXI century could be detrimental for *N. pumilio* establishment at dry, low-elevation forests.

Introduction

Understanding the consequences of climate change on mountain's forests requires a comprehensive view of tree life stages and species-specific processes along their ranges of distribution. At large-spatial scale, cold temperature is usually recognized as the limiting factor modulating plant performance at the upper-elevation limits, whereas at the lower and warmer borders of distribution, water supply, indirectly regulated by temperature, is the main forcing of plant growth (Hampe and Petit 2005). Therefore, the consequences of climate warming on plant vital rates are expected to differ spatially for tree species with wide elevation ranges. Empirical knowledge on the performance of montane at elevation boundaries could help us to understand plant responses to climate changes before the potential expansion or contraction of their range occurs (Harsch et al. 2009, Harsch and Bader 2011, Cagnacci et al. 2020). Demographic information provides the basis to predict future population performance, as well as changes in distribution and in turnover rates within populations. Seedling emergence and survival are the stages in the trees' life cycle most vulnerable to climatic change (Hampe and Petit 2005, Engelbrecht 2007, Tercero Bucardo et al. 2007, Peter et al. 1996, Grubb 1977).

Minor variations in environmental conditions at the elevational limits of the forest can induce changes in tree establishment and mortality patterns, but may affect to a lesser degree demographic processes at intermediate sites with lower environmental stress (Kullman 2007; Kirilyanov et al., 2012). While air temperature decreases along the elevation gradient with indirect effects on environmental humidity, atmospheric pressure gradually decreases and solar radiation increases with elevation (Körner and Paulsen 2004, Körner 2007a). Lower temperatures at higher elevations induce a shortening of the

growing season, and in most cases, a reduction in the supply of nutrients from the soil, negatively impacting the growth rates with increasing elevations (Coomes and Allen 2007; Körner 2007b). In addition, trees at high elevation are more exposed to wind and experience longer persistence of snow cover than trees at lower elevation. In contrast, the increment in temperature at the lower forest boundary increases evapotranspiration, which in turn reduces soil water availability for tree establishment and growth (Sánchez-Salguero et al. 2015). In this context, there is a greater possibility that environmental fluctuations on plant performance will manifest earlier at the extreme forest boundaries (Doak and Morris 2010), justifying the importance of conducting demographic studies in these focal locations.

The *Nothofagus* (southern beech) forests in the Patagonian Andes from South America comprise one of the most singular and large mountain ecosystems in the planet (Bryant et al. 1997, Donoso 1993). This genus dominates the upper treeline in the highest hostile Andean environment and their species are widely distributed throughout the region, from Central Chile (33.5°S) to Tierra del Fuego (56°S; Veblen et al., 1996). The *Nothofagus pumilio* ([Poepp. & Endl.] Krasser) forests are important as timber producers, regulators of Andean runoff, and other ecosystem services to populations, like tourism and recreation, on both slopes of the Patagonian Andes (Ramírez et al. 1997, Martínez Pastur et al. 2000, Bava and Rechene 2004).

Seed production and dispersal are prerequisites for successful recruitment in the forest. A continuous decrease in seed production with increasing elevation has been reported for *Nothofagus* species, including *N. solandri* var. *cliffortioides* in New Zealand (Wardle 1980; Allen and Platt 1990) and *N. pumilio* in Southern Patagonia (Barrera et al. 2000; Cuevas 2000; Cuevas 2002). Fruit rain, seed viability and seedling emergence in *N. pumilio* decrease with increasing elevation, suggesting that tree regeneration at high elevation is regulated by two bottlenecks: seed production and seedling emergence (Cuevas 2000). In addition to seed production and germination, tree establishment could also be limited by seedling survival. The highest mortality rate of trees occurs during the first years of establishment since seedlings are extreme sensitivity to variations in environmental factors (Maher and Germino et al. 2006, Cagnacci et al. 2020). Seedling mortality can be caused by desiccation, overheating, freezing, diseases or herbivory (Stevens and Fox 1991; Piper et al. 2006; Danby and Hik 2007). In addition, mortality can be also induced by competitive interactions between plants (Olofsson 2004). At the low-elevation *Nothofagus* forests in the ecotone with the Patagonian steppe, climate warming could impose an increased drought stress, limiting the survival of *N. pumilio* seedlings and trees. Conversely, the survival and consequent establishment of seedlings at higher elevations could benefit from the increase in temperature associated with the extension of the growing season and the stress reduction due to heavy snow accumulation (Daniels and Veblen 2004; Piper et al. 2013; Srur et al. 2016, 2018).

Based on the analysis of instrumental and proxy records, temperature in southern Patagonia has increased during the past century with a marked positive trend in the past few decades (Villalba et al. 2003; Falvey and Garreaud 2009; Masiokas et al. 2008, 2009; Lopez et al. 2010; Garreaud et al. 2013). According to Magrin et al (2014), precipitation has decreased in southern Chile and Argentina since the 1960s concurrent with a warming trend close to 0.1°C per decade. We hypothesize that temperature and

precipitation variations differentially modulate tree recruitment at high- versus low-elevation boundaries in the southern Andes. Therefore, in this study we evaluate how tree regeneration and seedling survival at upper and lower elevations vary in relation to climate in southern Patagonia. We postulated that warmer climate would ameliorate the harsh environmental conditions for tree recruitment imposed by high elevations, but intensified water stress (drought and overheating) for seedlings at lower elevation forests. We test this hypothesis by comparing fruit rain, seedling emergence and survival in *N. pumilio* forest at low and high elevations over 6 years of changing climate in the southern Andes. Finally, we describe and analyzed the temperature and precipitation variations during the years of our study (2012–2018) in order to relate the tree establishment patterns to climate variability at the elevational of *N. pumilio* distribution.

Materials And Methods

Study Area

The study area is located in the Río de las Vueltas basin (42° S – 72° W), Santa Cruz, Argentina (Fig. 1a). All the area is under the influence of strong winds from the west throughout the year. At regional scale, temperature decreases with elevation, while precipitation increase in the east-west direction (Villalba et al. 2003). Meteorological data from El Chaltén, indicates a total annual precipitation of 450 mm, evenly distributed throughout the year, and a mean annual temperature of 7° C (data provided by Los Glaciares National Park). Data provided by Los Huemules meteorological station, in the central sector of the precipitation gradient, indicates a total annual precipitation over 1000 mm and a mean annual temperature of 6° C. *N. pumilio* is the dominant subalpine tree, endemic to the Patagonian Andes of Chile and Argentina (Veblen et al. 1996). The *N. pumilio* forests belong to the Sub-Antarctic phytogeographical province, a district of the deciduous forest vegetation in southern South America (Cabrera 1976). In the study area, *N. pumilio* forms a monospecific forest belt covering the eastern slopes of the southern Andes from ~ 500 to 1100 m elevation. Trees grows to a height of up to 20 m, and trunk diameter up to 1.5 m. Leaves are deciduous, elliptic, 2–4 cm long with regular lobed margins. The fruit is a small nut (4–7 mm) dispersed by wind in early spring. Seeds do not form a persistent soil bank, but after germination during spring and summer they persist as seedling for many years until canopy opens (Donoso 1993).

Data collection

From 2012 to 2018, tree regeneration and survival were biannually registered within plots located at the upper and lower elevational boundaries in the *N. pumilio* forests (Fig. 2a). All plots were located in old-growth, multi-aged forests without recent evidence of natural or anthropic disturbances (e.g. livestock grazing, fire or logging). Plots were located along the east-to-west precipitation gradient in private and national protected areas (Los Glaciares National Park, Estancia Los Huemules, and Estancia Río Toro). Ten plots (five at each elevation boundary) including 50 live individuals larger than 5 cm diameter at breast height (DBH) (Srur et al. 2008) were delimited in 2012 (Fig. 1b). All trees and seedlings were initially tagged with plastic numbers to follow individual fate. Inside each plot, 10 regeneration sub-plots (1 x 1 m) were established to mark and follow biannually seedling's fate. In each plot 10 seed traps

(diameter 25 cm wide and 35 cm in depth, Fig. 1c) were installed and annually monitored from February 2014 to February 2018 in order to estimate fruit rain. Due to accessibility limitations, census were conducted in Ea. Río Toro for the years 2014 and 2018, in Ea. Los Huemules for 2014, 2016 and 2018, and in Los Glaciares National Park for the years 2016 and 2018.

Data analysis

Drought characterization

To identify the drought events in our study area, we used a multiscale drought index based on instrumental climatic data. The Standardized Precipitation Evapotranspiration Index (SPEI) was developed combining the sensitivity of the Palmer Drought Severity Index (PDSI) to accounts for evaporation demand and the robustness of the multi-temporal Standardized Precipitation Index (McKee et al. 1993 and Paulo et al. 2012). The SPEI was calculated using the SPEI package version 1.7 (Beguería et al. 2017) of the free programming language R (R Core Team 2020). The time period analyzed was 2006–2020, using the temperature and precipitation records from Cerro Torre (49° 19'S – 73° 05'W) and Estancia Los Huemules, respectively. We calculate the SPEI6 that considers the months of October-March for the common period of the seasons (2006–2020).

Statistical models

Fruit rain and seedling emergence in relation to elevation and climate were tested by applying Generalized Linear Models (GLMs) assuming a quasi Poisson distribution for errors to remedy overdispersion (Crawley 2005). In these models, the response variable was the annual number of fruits collected in each trap or the number of seedlings/m² counted in each census (recruited during last two years), while the explanatory variables were elevation (high/low) and spring-late summer SPEI. Given that fruit traps were monitored every year (in February) between 2015–2018, we used data from October of the previous year and census year when analyzing fruit rain. Seedling emergence and survival instead was registered every 2 years. Therefore, we used the average SPEI of previous growing season and the current season of the census to characterize each period when analyzing seedling emergence and survival. For example, seedling emergence registered in 2014 was explained by elevation and the SPEI estimated by the mean of October 2012-March 2013 and October 2013-March 2014. Interactions between fixed factors were considered and included if required for empirical support in each model.

Survival package in R (Therneau and Grambsch 2000; Therneau 2015) was used to test for differences in survival of marked seedlings and juvenile trees in the forests. We used the Kaplan-Meier non-parametric estimator to create survival function with our censoring data splitted by elevation. Finally, the log-rank test was used to test statistical differences in survival curves at both boundaries of elevation. We also analyzed the probability of seedling survival with elevation and SPEI using Hazard-Cox regressions, which similarly to the Kaplan-Meier estimator, construct survival functions but allow the incorporation of covariates.

Results

The study period was characterized by large climatic variability in terms of monthly temperature and precipitation (Fig. 2). Growing-season temperature and precipitation deviations, in relation to the period 2006–2018, were 0.17°C and – 71.2 mm in 2014, 0.47°C and – 74.1 mm in 2016, but 0.06 C and 72.5 mm in 2018.

Fruit rain was consistently more abundant at low- than at high-elevations (Fig. 3a) between 2015–2018 but the magnitude of this difference was variable between years. There was no interaction between elevation and time period to explain fruit rain. Fruit production showed the lowest record at both elevations in 2016 and the maximum in 2017 (Fig. 3).

Seedling emergence was explained by elevation interacting with SPEI, reflecting the importance of water deficit in spring-summer during the previous year for regeneration. Under spring-summer seedling emergence was larger at the upper forest during but on the wet cold period abundance of emerged seedlings was similar at both elevation boundaries (Fig. 4). Therefore, seedling emergence was more abundant at high-elevation forests in 2014 and 2016, but lower in 2018. Between the first biannual censuses, the estimated density of newborn seedlings was ~ 11 to 19 times higher at high- than at low-elevation plots. In contrast, during the latest monitoring period (2016–2018), seedling abundance was ~ 3 times larger at the low elevation boundary.

Seedling survival in relation to time was lower in the lower than in the upper forest boundary (Log rank test, $Chisq = 14.2$ on 1 d.f., $p = 2e-04$; Fig. 5). From 2012 to 2014, the survival probability of seedlings initially marked at the low and high altitude sites was 84 % (95% CI 82–86) and 92 % (90–93), from 2014–2016 was 82 % (95% CI = 80–85) and 88 % (95% CI = 86–89), and during 2016–2018 was 65 % (95% CI = 62–69) and 71 % (95% CI = 68–74).

Conclusions And Discussion

Our study reports different tree regeneration responses to climate variability at contrasting elevation boundaries of Patagonian mountain forests. Although seed supply was consistently larger at lower than at higher elevations, seedling establishment varied over time, particularly in relation to drought conditions during the growing season. Density of seedling emergence was higher at the upper elevation in periods with negative SPEI, consistent with dry and warm climatic anomalies during the spring and summer (October-March).

Across our study area, seedling survival probabilities were larger in the upper boundary of elevation. These findings contradict previous studies showing scarce tree recruitment at high-elevation erect *N. pumilio* forests (Barrera et al. 2000) in Tierra del Fuego (latitude ~ 54 °S) or indistinctly along the elevation gradient at 40 °S in northern Patagonia (Cagnacci et al. 2020). The different results between these and our studies could be associated with differences in the climatic conditions prevailing in each study during the monitoring period of establishment and survival. In our region, the biannual periods

2012–2014 and 2014–2016 were characterized by a dry and warm spring-summer climate conditions, while abundant rainfall was recorded in the period 2016–2018. Consistent with this climatic pattern, seedling emergence was less abundant at the higher forest boundary during the most recent wet period, suggesting that *N. pumilio* germination in high-elevation forests is favored by warm and dry climatic anomalies. In contrast, wet conditions favor regeneration in the lower elevations. Our observations indicate that establishment and survival patterns are strongly modulated by climatic variability. Therefore, differences with Barrera et al (2000), could be due to the specific climate conditions during the seedling monitoring, the shorter monitoring time and the more humid environments at the sampling sites in Tierra del Fuego.

Seedling survival probabilities were 7 to 10 % larger at high- than low-elevation forest boundary. The concept of increasing reproductive capacity in *N. pumilio* forests with increasing elevation was early suggested by Rush (1993), who noted that although shorter growing seasons at high elevation limit tree productivity, recruitment is benefited by more abundant precipitations that mitigate soil water deficit. Consistent with Rush (1993) observations, the main cause of seedling mortality at low-elevation forest appears to be summer desiccation, as typified by the orange colouration of the seedling first leaves or cotyledons observed in the field. Most monitored seedlings in our study were from sexual reproduction since they were initially tagged with the presence of cotyledons. In seed-bearing plants, cotyledons are embryonic leaves, whereas plants from asexual sprouts do not shown them. Our results support the untested hypothesis from Rush's (1993), indicating that larger seedling survival probability can explain higher seedling density at high- than at low-elevation boundary.

Extreme climatic events, rather than the mean climate, seem to be more important for terrestrial ecosystem dynamics (Holmgren et al. 2007; Suarez and Kitzberger 2008; Amoroso et al. 2012). Extreme dry-warm summers between 2013 and 2016 at our study area exacerbated the recorded differences in recruitment at both elevation extremes. Cagnacci et al. (2020) showed, with an experimental approach, that seedling mortality was regulated by air temperature during the first year of growth, but for relative air humidity during the second year of their experiments. Therefore, consistent with our results, Cagnacci et al. (2020) showed that establishment is largely dependent on climate conditions, and emphasize the need of long-term monitoring to properly characterize regeneration dynamics. In ecological studies, the use of a stationary temporal assumption could limit the applicability of results beyond the monitoring range. In turn, it has recently been emphasized that climate change is introducing unprecedented non-stationary changes that should be considered for forecasting the dynamics of biological systems (Wolkovich et al. 2014). Our findings highlight the benefits of long-term monitoring over time to understand the responses of forest species to changes in climate along elevational gradients.

Detrimental effects of climate warming for the conservation of plant populations at low elevation, called rear edges, has been reported (Peñuelas and Boada 2003) in Europe. Our results support the rear edge hypothesis for forests at the lower elevation boundary in Southern Patagonia, particularly under recent prevalent warm-dry springs and summers. A challenge for future research is to monitor with a life-cycle

approach how population dynamics of this Patagonian endemic tree would respond if climatic extremes increase their frequency as predicted for the near future.

Declarations

I here confirm that the authors declare no competing interests for the preprint submission "Contrasting climate influences on *Nothofagus pumilio* establishment along elevational gradients".

Acknowledgements

Our project was partially financed by THEMES-CONICET project funded by the BNP Paribas Foundation in the frame of its 'Climate Initiative' program", PIP 2012–2014 and PICT 2018–03691. The authors thank Reinhardt Brand, Mariano Guzmán, Alberto Ripalta, Marcela Tonello, Gonzalo Sottile, Lidia Ferri-Hidalgo, Jorge Gonnet and Milagros Rodriguez-Cantón, who contributed to collect field data. We also thank to the administration of Parque Nacional Los Glaciares, Ea. Los Huemules and Ea. Río Toro for helping us with logistic for field sampling and authorization for data collection inside their properties.

References

- Allen RB and Platt KH (1990). Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* 57: 199-206.
- Amoroso MM, Suarez ML, Daniels LD (2012). *Nothofagus dombeyi* regeneration in declining *Austrocedrus chilensis* forests: Effects of overstory mortality and climatic events. *Dendrochronologia* 30:105–112.
- Bava J O & Rechene DC (2004). Dinámica de la regeneración de Lengua (*Nothofagus pumilio* (Poepp. et Endl) Krasser) como base para la aplicación de sistemas silvícolas in *Ecología y Manejo de los Bosques de Argentina* Arturi MF, Frangi JL, Goya JF (eds.). Editorial de la Univ. Nacional de La Plata, Argentina, pp 1–22.
- Barrera MD, Frangi JL, Richter LL, Perdomo MH, Pinedo LB (2000). Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *J Veg Sci* 11:179–188.
- Cabrera AL (1976). Regiones fitogeográficas argentinas. *Encicl Argentina Agric y Jard* II:1–85.
- Coomes DA, Allen RB (2007). Effects of size, competition and altitude on tree growth. *J of Ecol* 95: 1084-1097.
- Crawley MC (2005). *An Introduction using R*. John Wiley & Sons, UK. 335 pp.

- Cuevas JG (2000). Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *Ecology* 88:840–855.
- Cuevas JG (2002). Episodic regeneration at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *J Ecol* 90:52–60.
- Danby RK and Hik DS (2007a). Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Global Change Biology*, 13, 437–451.
- Daniels LD and Veblen TT (2004). Spatiotemporal influences of climate on altitudinal treeline in Northern Patagonia. *Ecology* 85:1284–1296.
- Donoso C (1993). Bosques templados de Chile y Argentina. Variación, Estructura y Dinámica. Editorial Universitaria, Santiago, Chile. 488 pp.
- Doak DF and Morris WF (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature* 467: 959–962.
- Engelbrecht MJ, Comita IS, Condit R, Kursar TA, Tyree MT, Turner BL and Hubbell SP (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447: 80-83.
- Falvey M and Garreaud RD (2009). Regional cooling in a warming world: recent temperature trends in the southeast Pacific and along the west coast of subtropical South America (1979–2006). *J Geophys Res* 114: 1–16. doi: 10.1029/2008JD010519
- Garreaud R, Lopez P, Minvielle M and Rojas M (2013). Large-scale control on the Patagonian climate. *J Clim* 26:215-230.
- Grubb P (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. *Bio Rev* 52: 107-145.
- Hampe A and Petit RJ (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8: 461–467.
- Harsch MA, Hulme PE, McGlone MS and Duncan RP (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol Lett* 12:1040–1049.
- Harsch MA and Bader MY (2011). Treeline form—a potential key to understanding treeline dynamics. *Global Ecology and Biogeography* 20:582-596.
- Holmgren M, Stapp P, Dickman CR, Gracia C, Graham S, Gutiérrez JR, Hice C, Jaksic F, Kelt DA, Letnic M, Lima M, López BC, Meserve PL, Milstead WB, Polis GA, Previtali MA, Richter M, Sabaté S, Squeo FA (2007) Extreme climatic events shape arid and semiarid ecosystems. *Front Ecol Environ* 4:87–95.

- Körner C and Paulsen J (2004). A world-wide study of high altitude treeline temperatures. *J Biogeogr* 31:713–732.
- Körner C. (2007a). The use of “altitude” in ecological research. *Trends in Ecology and Evolution* 22: 569-574.
- Körner C (2007b). Climatic treelines: conventions, global patterns, causes (Klimatische Baumgrenzen: Konventionen, globale Muster, Ursachen). *Erdkunde* 61: 316-324.
- Kullman L (2007). Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. *Journal of Ecology*, 95: 41–52.
- Kirdyanov AV; Hagedorn F; Knorre AA; Fedotova EV; Vaganov EA; Naurzbaev MM, Moiseev PA and Rigling A (2012). 20th century tree-line advance and vegetation changes along an altitudinal transect in the Putorana Mountains, northern Siberia. *Boreas* 41(1): 56-67.
- Lopez P; Chevallier P; Favier V; Pouyaud B; Ordenes F and Oerlemans J (2010). A regional view of fluctuations in glacier length in southern South America. *Global Planet Change* 71:85–108.
- Martínez Pastur G; Cellini JM; Peri PL; Vukasovic RF; Fernández MC. 2000 Timber production of *Nothofagus pumilio* forests by a shelterwood system in Tierra del Fuego (Argentina). *For. Ecol. Manage* 134:153–162.
- Magrin GO, Marengo JA, Boulanger JP, Buckeridge MS, Castellanos E, Poveda G, et al. (2014). “Central and South America,” in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge, UK; New York, NY: Cambridge University Press), pp 1499–1566.
- Maher EL and Germino MJ (2006) Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience*, 13, 334–341.
- Masiokas MH, Luckman BH, Villalba R, Delgado S, Skvarca P and Ripalta A (2009). Little ice age fluctuations of small glaciers in the Monte Fitz Roy and Lago del Desierto areas, South Patagonian Andes, Argentina. *Palaeogeogr Palaeoclimatol Palaeoecol* 281: 351–362. doi: 10.1016/j.palaeo.2007.10.031
- Masiokas MH, Villalba R, Luckman BH., Lascano ME, Delgado S and Stepanek P (2008). 20th-century glacier recession and regional hydroclimatic changes in northwestern Patagonia. *Glob Planet Change* 60: 85–100. doi: 10.1016/j.gloplacha.2006.07.031.
- McKee T B., Doesken NJ and Kleist J (1993). The relationship of drought frequency and duration to the time scales. In *Proceedings of the 8th Conference on Applied Climatology*; Anaheim, USA.

- Olofsson J (2004). Positive and negative plant–plant interactions in two contrasting arctic-alpine plant communities. *Arct Antarct Alp Res*, 36: 464–467.
- Paulo AA, Rosa RD and Pereira LS (2012). Climate trends and behavior of drought indices based on precipitation and evapotranspiration in Portugal. *Nat Hazards Earth Syst Sci* 12: 1481–1491.
- Peñuelas J and Boada M (2003). A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob Chang Biol* 9:131–140.
- Piper FI, Cavieres LA, Reyes-Díaz M and Corcuera LJ (2006). Carbon sink limitation and frost tolerance control performance of the tree *Kageneckia angustifolia* D. Don (Rosaceae) at the treeline in central Chile. *Plant Ecology*, 185: 29–39.
- Piper FI, Fajardo A and Cavieres LA (2013). Simulated warming does not impair seedling survival and growth of *Nothofagus pumilio* in the southern Andes. *Perspect Plant Ecol Evol Syst* 15: 97–105. doi: 10.1016/j.ppees.2013.02.003
- Peter FK and Ronald R (1996). High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. *Tree Physiol*, 16: 665-672.
- Petit RJ and Hampe A (2006). Some evolutionary consequences of being a tree. *Annu Rev Ecol Evol Syst* 37: 187–214.
- Ramírez C, San Martín C, Oyarzún A, Figueroa H (1997). Morpho-ecological study on the South American species of the genus *Nothofagus*. *Plant Ecol* 130:101–109.
- Rusch, VE (1993). Altitudinal variation in the phenology of *Nothofagus pumilio* in Argentina. *Rev Chil His Nat* 66: 131-141.
- Sánchez Salguero R, Camarero JJ, Hevia A, Madrigal-González J, Linares JC, Juan A Ballesteros-Canovas JA, Sánchez-Miranda A, Raquel Alfaro-Sánchez R, Sangüesa-Barreda G, Galván JD, Emilia Gutiérrez E, Mar Génova M, Rigling A (2015). [What drives growth of Scots pine in continental Mediterranean climates: drought, low temperatures or both?](#) *Agricultural and Forest Meteorology* 206: 151-162.
- Stevens GC and Fox JF (1991). The causes of treeline. *Ann Rev Ecol and Sys* 22: 177–191.
- Srur AM, Villalba R, Villagra PE, Hertel D (2008). Influencia de las variaciones climáticas y la concentración de CO₂ en el crecimiento y la eficiencia en el uso del agua de *Nothofagus pumilio* a lo largo de un gradiente altitudinal en la Patagonia. *Rev Chil Hist Nat* 81: 239–256.
- Srur AM, Villalba R, Rodríguez-Catón M, Amoroso MM, Marcotti E (2016). Establishment of *Nothofagus pumilio* at Upper Treelines Across a Precipitation Gradient in the Northern Patagonian Andes. *Arctic, Antarct Alp Res* 48, 755–766.

Srur AM, Villalba R, Rodríguez-Catón M, Amoroso MM and Marcotti E (2018). Climate and *Nothofagus pumilio* Establishment at Upper Treelines in the Patagonian Andes. *Front Earth Sci*, 6: 57.

Suarez ML and Kitzberger T (2008). Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Can J For Res* 38: 3002–3010.

Therneau TM, Grambsch PM (2000). *Modeling Survival Data: Extending the Cox Model*. Springer, New York.

Therneau TM (2015). A Package for Survival Analysis in S. R package version 2.38-7, <http://CRAN.R-project.org/package=survival>.

Veblen TT, Donoso C, Kitzberger T, Rebertus AJ (1996). Ecology of Southern Chilean and Argentinean forests. In: Veblen TT, Hill RS, Read J (eds) *The ecology and biogeography of Nothofagus forests*. Yale University Press, Chelsea, Michigan, USA, pp 293–353

Villalba R, Lara A, Masiokas M, Delgado S, Aravena JC, Roig FA, Schmelter A, Wolodarsky A, Ripalta A (2003). Large-scale temperature changes across the southern andes: 20th-century variations in the context of the past 400 years. *Clim Change* 59:177–232.

Wardle P (1980). Ecology and distribution of silver beech (*Nothofagus menziesii*) in the paringa district, South Westland, New Zealand. *New Zealand Journal of Ecology*, 3: 23-36 .

Wolkovich EM, Cook BI, McLauchlan KK, Davies TJ (2014). Temporal ecology in the Anthropocene. *Ecol Lett* 17:1365-1379.

Figures

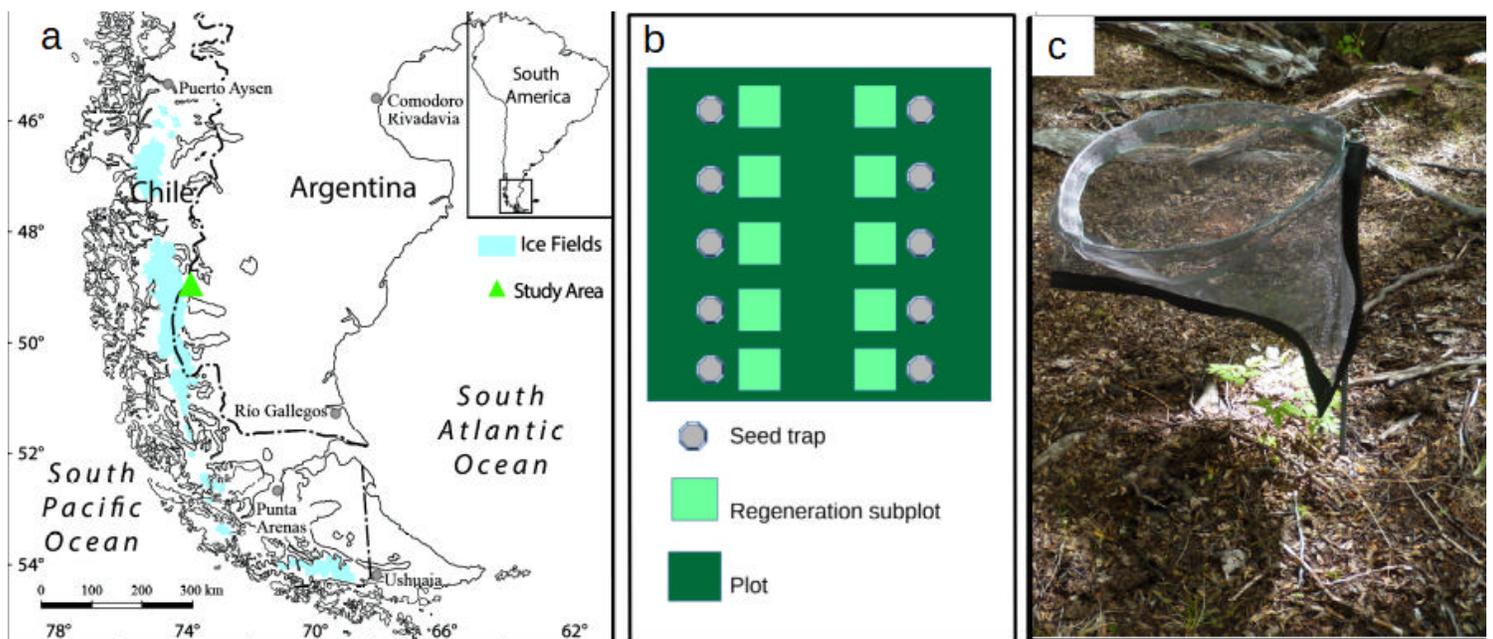


Figure 1

(a) Map of location of the study area in Southern Patagonia, Argentina. (b) Diagram of the field design to record *N. pumilio* demographic changes at the extremes of the elevation range. At high and low elevation forest boundaries, 10 plots (1m²) for monitoring the regeneration were located inside an area with 50 adult trees. All saplings and seedlings were tagged and seedling emergence and survival was monitored every 2 years from 2012 to 2018. (c) Inside each area, 10 seed traps were used to quantify fruit rain.

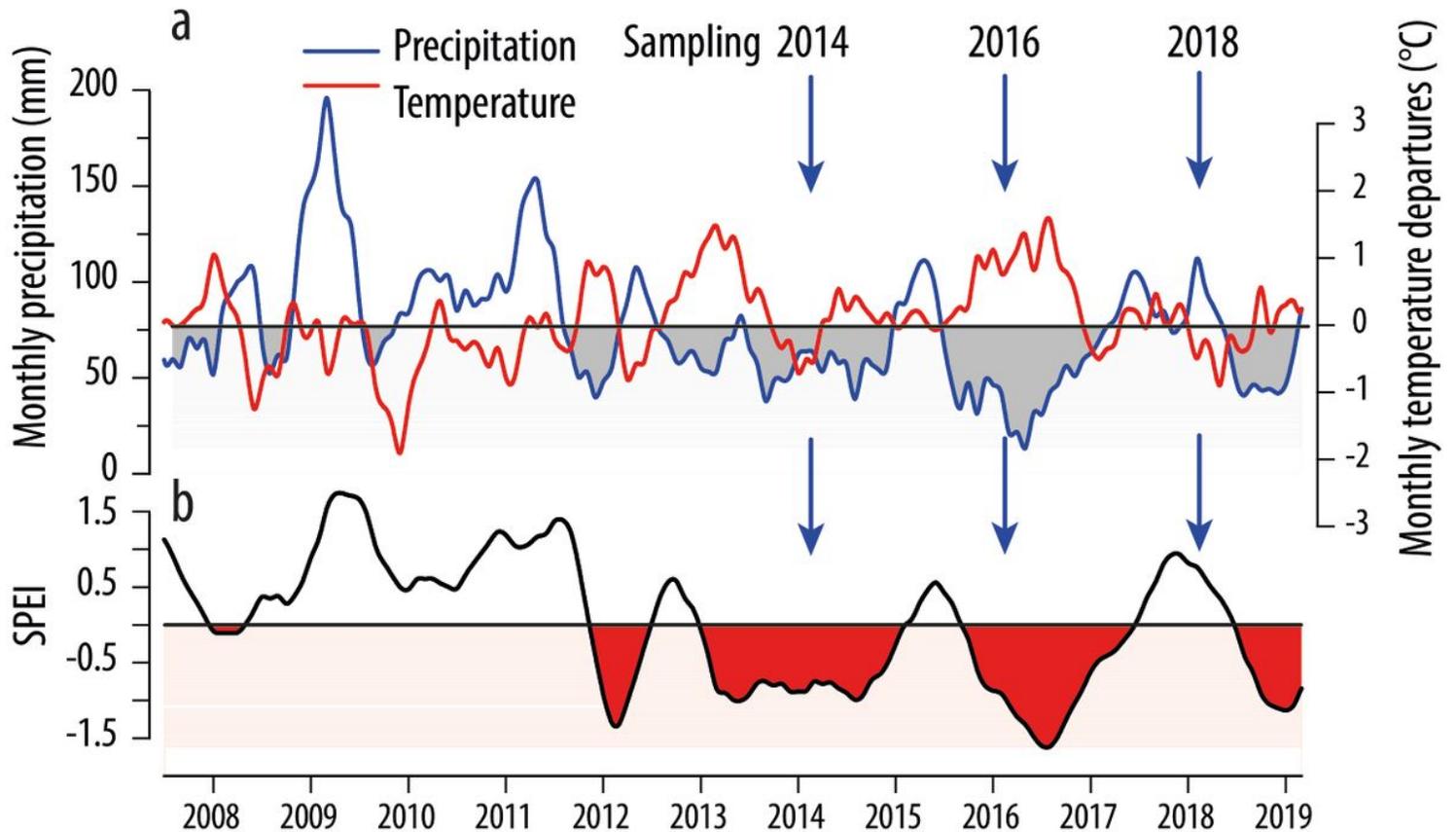


Figure 2

(a) Monthly variations of precipitation and temperature deviations (in relation to the period of 2006-2018) from Los Huemules meteorological station, southern Patagonia, Argentina. To emphasize the long-term climate fluctuations, variations in precipitation (blue) and temperature (red) are shown as 5-month moving averages. (b) Long-term (5-month moving averages) monthly variations of SPEI (black). Long-term dry periods (SPEI < 0) are highlighted in red. The initial experimental setting was conducted in January 2012 and followed by periodic samplings in January 2014, 2016 and 2018.

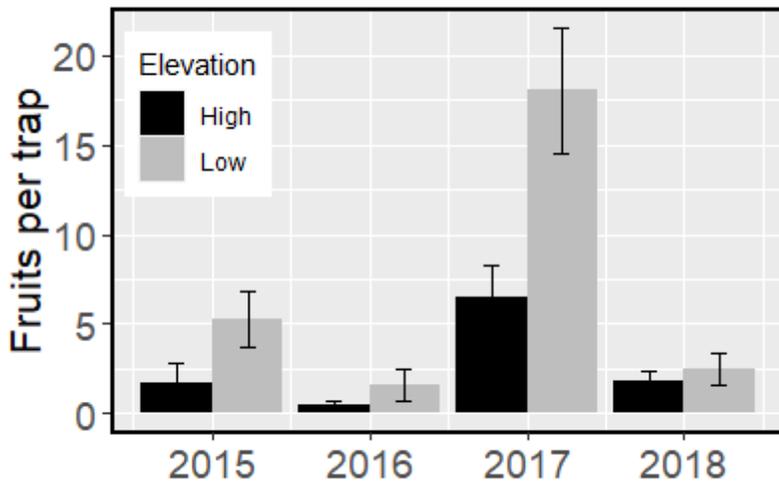


Figure 3

Fruit rain during the study in *N. pumilio* forest , mean \pm SE by elevation using 2015-2018 annual data. Large interannual variability in the amount of fruit production was recorded over the interval 2015-2018, with a maximum in 2017.

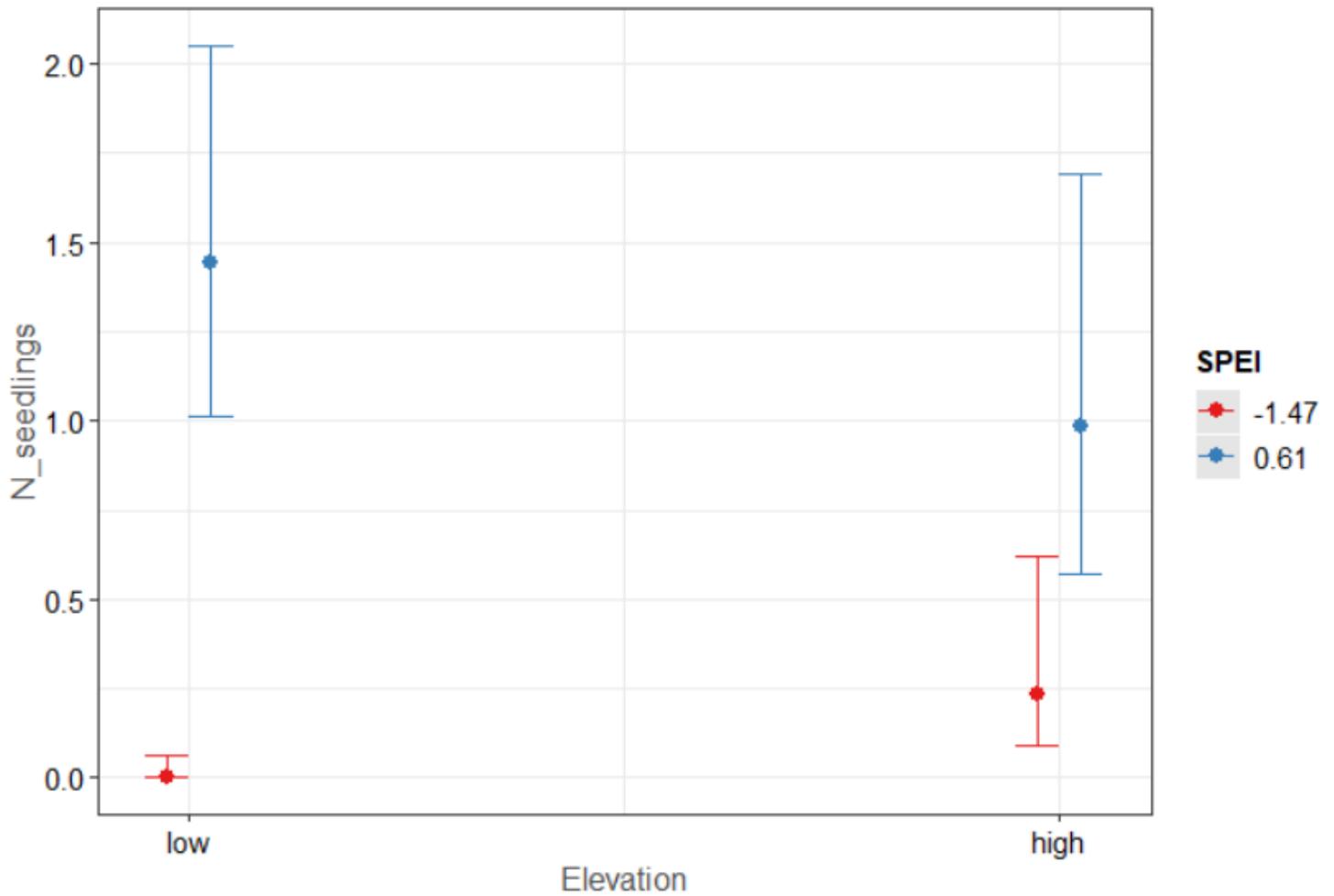


Figure 4

Elevation and climate (SPEI) interaction to explain seedling emergence. In periods of drought (SPEI < -0.5) seedling emergence was higher at the upper elevation boundary of *N. pumilio* forest, but differences in establishment were null in the absence of drought during the spring-early summer period. These climatic anomalies are consistent with SPEI of -1.47 and 0.61 for spring-summer 2016 and 2018, respectively.

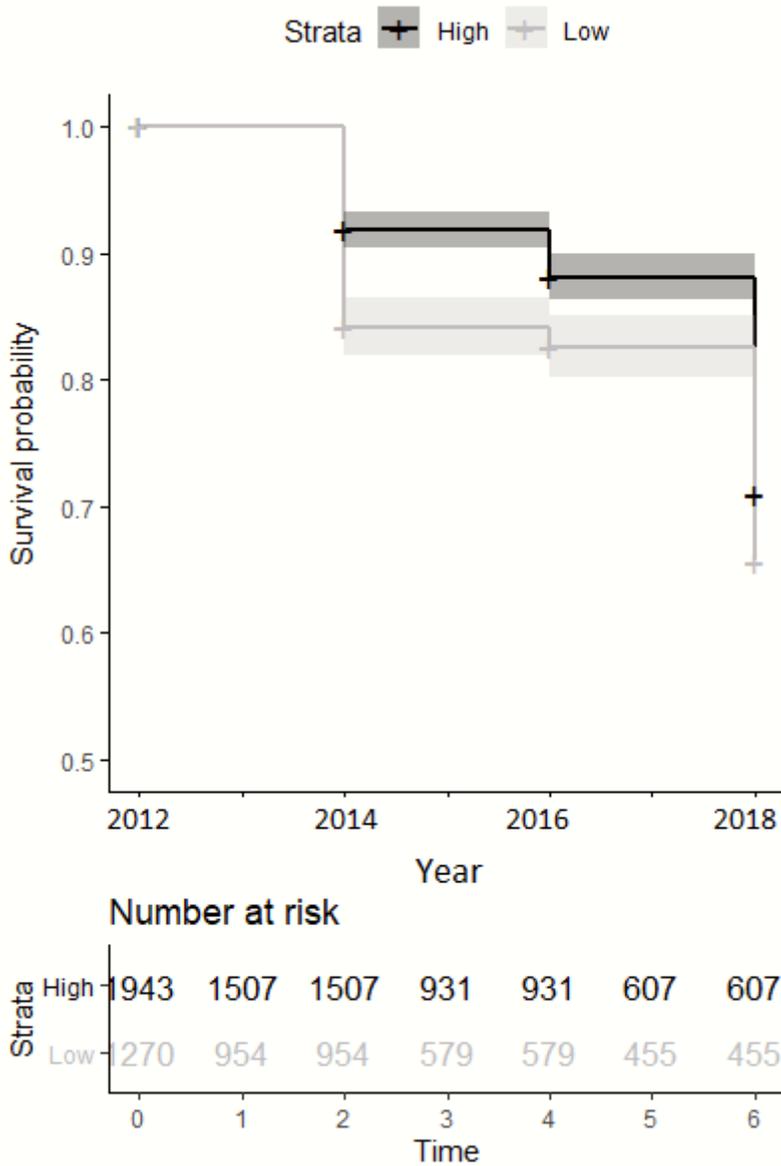


Figure 5

Survival curve at each elevation boundary using Kaplan-Meier estimator and log-rank assess for differences between both elevations. The risk of death in seedlings was associated with elevation and SPEI in the two previous spring-summer (Hazard Cox Wald test= 173.2, 2 df, $p < 2e-16$). Taking high elevation as reference, drought conditions increased the risk of death for seedlings at low elevation.