Interactions among patch area, forest structure and water fluxes in a fog-inundated forest ecosystem in semi-arid Chile

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Summary

1. The area or size of an ecosystem affects the acquisition, storage and redistribution of energy and matter. Patch size reduction due to natural or anthropogenic habitat loss will not only modify species distribution and patch structure but also affect the ecosystem processes that are, in part, responsible for patch persistence.

2. In a fog-dependent forest ecosystem, trees and their architectures play essential roles in capturing and redistributing water from collection surfaces. In this paper, we address the question of how forest patch size and structure interact to determine fog water inputs and storage in a fog-inundated, coastal ecosystem in semi-arid Chile (30°S).

3. Six forest patches ranging in area from 0·2 to 36 ha on a coastal mountaintop of Fray Jorge National Park were characterized using 0·1 ha plots laid down at the centre of each forest patch. In each patch, we assessed tree basal area as a measure of forest structure, recorded daily air temperature and humidity, measured water influx from stemflow and throughfall (water that has passed through the forest canopy). Soil and litter gravimetric water contents were used as a measure of storage.

4. Total tree basal area per hectare was positively related to patch area, despite some variation at the species level. Mean and maximum air temperatures inside the patches were inversely related to patch size, with maximum temperatures differing by 2 °C on average. Annual fog water capture by trees within forest patches (net throughfall) was estimated in 296·1 mm after rain flux (about 122 mm) was subtracted. Throughfall volume and patch area were uncorrelated, but stemflow volume, soil and litter water contents scaled positively with patch area, showing a functional link between water interception and ecosystem retention.

5. Our study shows that ecosystem area in this mosaic of fog-dependent temperate forest patches can modify water fluxes and storage capacity of the ecosystem. This finding has important consequences for fragmented landscapes, where large continuous forests are fragmented into smaller patches, affecting not only the persistence of species but also the continuity of critical ecosystem processes.

Key-words: patch size, fog, ecosystem function, water cycle, temperate forest, habitat fragmentation

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Introduction

It is well known that the size of a biological system affects its rates of acquisition, storage and redistribution of energy and matter (e.g. West, Brown & Enquist 1997). At the ecosystem level, changes in area can affect ecosystem functions such as nutrient acquisition (Polis, Anderson & Holt 1997) and redistribution (Spencer & Warren 1996), microbial activity and decomposition rates (Wardle *et al*. 1997). However, only a handful of studies have addressed the consequences of the generalized decline of ecosystem area resulting from natural or anthropogenic processes on ecosystem functions (Wardle *et al*. 1997; Weathers, Cadenasso & Pickett 2001; Ewing *et al*. 2009; Ponette-González, Weathers & Curran 2009). For instance, forest clearing, road building, farming and urban expansion have led to major alterations to hydrological and nutrient cycles in remnant forest patches (Lovett, Weathers & Sobcak 2000; Diaz, Bigelow & Armesto 2007), to the point of altering regional and global climate and causing water and soil pollution problems (Chase *et al*. 2000; Webb *et al*. 2006).

Shrub and tree species have significant influences on the hydrological cycle, mainly through the regulation of hydrological inputs, outputs and redistribution within ecosystems (Dawson 1998; Oliveira *et al*. 2005; Bradshaw *et al*. 2007). This is achieved at two levels. First, shrub and tree canopies intercept rain and fog, hence determining how much water reaches the ground and infiltrates to deep soil layers (Ewing *et al*. 2009). Secondly, trees and shrubs return water to the atmosphere through evapotranspiration from exchange surfaces, which is one of the main predictors of ecosystem productivity (Chapin, Matson & Mooney 2002). In addition, while the forest canopy intercepts a substantial portion of total precipitation, the remaining fraction is conducted to the soil via throughfall and stemflow (Hutley *et al*. 1997; Ponette-González, Weathers & Curran 2009). Given the importance of plants for maintaining ecosystem water balance, the massive loss of tree biomass and canopy leaf area as a consequence of a reduction in ecosystem area, through habitat fragmentation, can lead to important alterations in the hydrological cycle (Weathers 1999; Bradshaw *et al*. 2007; Diaz, Bigelow & Armesto 2007).

In Mediterranean-climate and semi-arid regions, coastal fogs are a significant source of moisture, especially during dry summers and extended droughts. In these ecosystems, water from fog deposition may account for 28–66% of the total water used by woody species (Dawson 1998; Corbin *et al*. 2005). In these cases, plant architecture can substantially enhance water influx to a forested watershed by capturing and channelling fog and rain to the soil (Hutley *et al*. 1997; Ponette-González, Weathers & Curran 2009). Accordingly, changes in forest structure (e.g. leaf area, vertical stratification, branching patterns, crown biomass) could significantly alter water inputs, especially from passing clouds and fog (Weathers *et al*. 2006). Moreover, such changes can affect other ecosystem functions, as rain and fog may deliver essential nutrients from the atmosphere to the soil and plants, having a direct impact on other biogeochemical cycles (Weathers & Likens 1997; Weathers *et al*. 2000; Perakis & Hedin 2002).

A striking example of a fog-inundated ecosystem occurs in semi-arid Chile (30°S), where regionally dominant xerophytic vegetation receives a mean annual rainfall of only 147 mm (López-Cortés & López 2004). Here, fog inputs are essential to the persistence on coastal mountaintops of a mosaic of rain forest patches surrounded by dry shrublands (del-Val *et al*. 2006; Gutierrez *et al*. 2008). These fog-dependent rain forest outliers are strongly dominated by the evergreen broad-leaved tree *Aextoxicon punctatum* (del-Val *et al*. 2006), the only member of the endemic family Aextoxicaceae. Floristically these rain forest patches are markedly similar to Valdivian rain forests (0·2 Jaccard Index, Villagrán *et al*. 2004) located more than 1000 km south, in areas receiving more than 2000 mm of rain per year.
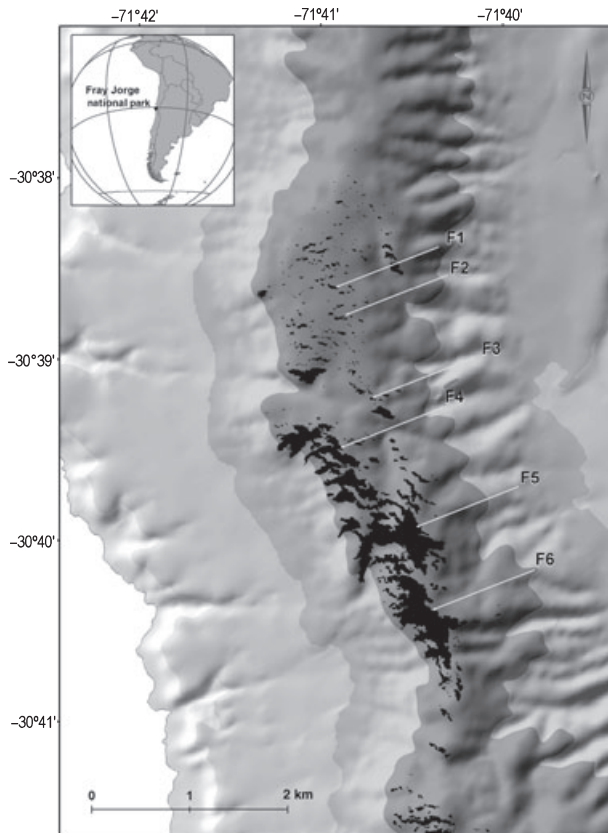
Here we evaluated how forest patch size in this fog-dependent forest mosaic can influence patch structure (measured as tree basal area per hectare), thereby altering ecosystem water capture and storage. In particular, we assessed four key ecosystem components in six forest patches of different areas: (i) tree basal area as a proxy of crown size and fog intercepting surfaces; (ii), stemflow and throughfall water inputs, as well as overall fog water inputs outside forest patches; (iii) soil and litter gravimetric water contents as a measure of ecosystem water storage; and (iv) microclimatic variables such as air temperature and relative humidity. Given that ecosystem size affects overall tree biomass (Echeverría *et al*. 2007) and tree biomass affects hydrological vectors and microclimate, our working hypothesis is that water influx and storage will scale with patch size, in relation to tree basal area.

Materials and methods

STUDY SITE

Our study was conducted in Fray Jorge National Park (FJNP, 30°40′S, 71°30′W), where the northernmost patches of Chilean temperate rain forests occur on a fog-inundated coastal terrace from 450 to 660 m elevation. A mosaic of 370 rain forest patches, ranging in size from 0·1 to 36 ha, interspersed within a matrix of xerophytic shrubland (Fig. 1), is presumably the legacy of past silvo-agricultural use (CONAF 1992) and wetter periods during the Pleistocene (Villagrán *et al*. 2004; del-Val *et al*. 2006). These rain forest patches are isolated by about 1000 km from their main range in south-central Chile.

The regional climate is Mediterranean-arid (Di Castri & Hajek 1976). The mean annual temperature recorded at 150 m elevation is 13·6 °C with a mean annual rainfall of 147 mm (years 1983–2003; data from Fray Jorge LTSER weather station and López-Cortés & López 2004), falling predominantly (> 95%) in winter (June–August). There is substantial inter-annual variability in rainfall (CV = 81%) with wetter periods every 3–5 years, associated with positive phases of ENSO and drier ones associated with negative phases (Montecinos & Aceituno 2003; López-Cortés & López 2004). Fog is a nearly permanent feature of the landscape above 400 m elevation, especially during spring and summer months

period (austral winter 2004) did not exceed the average value for the last 20 years.

In addition to the canopy dominance by *A. punctatum* (Aextoxicaceae), these forest patches contain other broad-leaved evergreen trees that are characteristic of temperate rain forests of south-central Chile, namely *Myrceugenia correifolia* (Myrtaceae), *Drimys winteri* (Winteraceae), *Rhaphithamnus spinosus* (Verbenaceae) and *Azara microphylla* (Flacourtiaceae). Woody vines such as *Griselinia scandens*, and epiphytic ferns (e.g. *Polypodium feullei*) are frequent components of the forest canopy (Squeo, Arancio & Novoa-Jerez 2004). Understorey plants are generally small herbaceous species, sometimes epiphytes, ferns and a sparse shrub cover (see Gutierrez *et al.* 2008 for a detailed description). In the larger patches, tree trunks and soils are covered by a dense coat of mosses, lichens and liverworts, which are absent from areas outside the patches.

SAMPLING DESIGN

To assess the effect of forest ecosystem size (hereafter patch size), on ecosystem function, we concentrated our sampling inside one 0·1 ha plot set up at the centre of each patch. We used this approach to focus primarily in the effects of patch size on: (i) the main characteristics of vegetation structure away from edges and (ii) the proportional influence of edge effects in patches of different sizes.

Patch structure and microclimate

To capture the entire range of size variation in the local forest mosaic, we selected six forest patches, between 0·2 and 36 ha, thus encompassing almost the entire range from the very small to the largest patches found (Table 1). According to the positive relationships found between tree basal area with crown length, stem, branch and leaf biomass (Bartelink 1997), we assessed structural changes associated with patch area, using tree basal area as a proxy of crown size and fog-intercepting surfaces. For this, we sampled all trees > 5 cm stem diameter (at 1·3 m from the base, or dbh) found within the 0·1 ha plots (50 × 20 m). Each tree rooted within

Fig. 1. Location of the study area showing the mosaic of rain forest patches in Fray Jorge National Park, Chile, at 30°S. The prevailing climate is semi-arid and forest patches are located on costal mountaintops.

(Cereceda & Schemenauer 1991; del-Val *et al.* 2006). Although the study period corresponded to a positive ENSO phase, following Trenberth's (1997) criteria, average rainfall during the sampling

Table 1. Forest patch characterization and mean values for microclimatic and water flux variables for our study site (further patch description can be found in Gutierrez *et al.* 2008)

Patch area (ha)	0·21	0·28	1·35	4·3	23·76	36·08
P/A ratio (m ha^{-1})	1322·16	861·66	469·14	496·28	300·5	299·04
Altitude (m)	529	566	495	566	639	635
Slope (%)	1	11	35	10	38	42
Patch ID	F2	F1	F3	F4	F6	F5
Tree basal area (m^2 ha^{-1})	61·64	49·41	46·69	90·37	102·61	125·12
Median dbh (cm)	13	10·2	10·8	11·6	14·5	10·3
Stem density (N ha^{-1})	1520	2270	1490	3590	2520	3610
Tree species in canopy	4	4	5	5	5	5
Throughfall (mm)	31·10 ± 21·31	49·91 ± 43·16	35·49 ± 15·67	23·32 ± 11·86	37·38 ± 22·55	29·56 ± 18·05
Stemflow (mm)	0·10 ± 0·06	0·25 ± 0·06	0·16 ± 0·14	0·55 ± 0·59	1·00 ± 0·99	0·69 ± 1·07
Soil water content (gH$_2$O g^{-1} soil)	0·28 ± 0·14	0·30 ± 0·19	0·55 ± 0·63	0·50 ± 0·24	0·84 ± 0·37	1·17 ± 1·03
Litter water content (gH$_2$O g^{-1} litter)	0·49 ± 0·40	0·36 ± 0·29	0·51 ± 0·36	0·84 ± 0·55	1·18 ± 0·85	1·12 ± 0·88
Mean temperature (°C)	11·80 ± 1·60	11·46 ± 1·75	11·62 ± 1·41	11·04 ± 1·52	11·29 ± 1·51	10·95 ± 1·42
Max. temperature (°C)	15·35 ± 1·83	15·09 ± 2·15	14·44 ± 1·43	13·69 ± 1·63	13·53 ± 1·57	13·32 ± 1·41
Min. temperature (°C)	9·45 ± 1·57	9·08 ± 1·62	9·67 ± 1·58	9·10 ± 1·57	9·65 ± 1·58	9·15 ± 1·54
Mean relative humidity (%)	91·33 ± 4·00	94·98 ± 3·04	96·14 ± 5·28	NA	95·96 ± 3·73	95·12 ± 4·63
Max. relative humidity (%)	99·09 ± 0·90	99·61 ± 0·41	99·50 ± 1·01	NA	99·54 ± 0·75	99·61 ± 0·46
Min. relative humidity (%)	74·31 ± 6·31	82·25 ± 6·17	85·54 ± 13·00	NA	87·96 ± 5·92	83·60 ± 10·74

P/A, perimeter area ratio.

the plot was identified to species and basal area per patch was calculated by adding the basal areas calculated for all individual trees in the plot.

Air temperature (°C) and relative air humidity (%RH) were recorded every 15 min and monthly averaged from September 2003 to August 2005, using one data logger (HOBO Pro RH/Temp; Onset Computer Corporation), per patch. Each sensor was attached to the trunk of a tree (*A. punctatum*) at 1·5 m above the ground to represent the conditions of the interior of the patch.

Water fluxes

We measured water influx via canopy drip (throughfall, TF) and stemflow (SF) using six collectors per patch. All measurements were made within the 0·1 ha central plot in each patch, using six PVC funnels of 22 cm diameter connected to 10–20 L drums. Funnels were placed 1 m above the ground and directly below the crown of randomly selected *A. punctatum* trees with a dbh > 25 cm and an emergent position in the forest canopy. Monthly, water drip volume was recovered from TF collectors (Stogsdill *et al.* 1989; Diaz, Bigelow & Armesto 2007) in each forest patch. The water volume (litres per TF collector per month) was converted to millimetres of precipitation equivalents (mm) by dividing the water volume collected by the area of the upper opening of the funnel (0·038 m^2). SF was measured by attaching rubber collars around the bark of the same six focal trees. Water running down the main stem of each tree was collected in a 15-L high-density, polyethylene-lidded storage bucket. Every month we recovered water from each SF collector. The volume of water collected (litres per SF collector per month) was converted to mm by dividing it by the crown area (m^2) of each tree, estimated using the formula of an ellipse. SF and TF volumes were collected on the last day of each month from September 2003 to August 2005, and more frequently when rain events occurred. We calculated net throughfall (NTF) from fog interception as: NTF = TF − R, where TF is throughfall and R is rainfall. TF values recorded during the rainy season (May–August) are considered to be rain, and during the rest of the year (September–February) TF in excess of bulk collections (NTF) is exclusively the product of canopy drip from fog (Ewing *et al.* 2009).

Water inputs from fog (and rain) outside forest patches were estimated using passive fog collectors (hereafter fog collectors) on a subset of four forest patches. Fog collectors were placed in the windward edge of patches F1, F2, F3 and F5, 3 meters from the edge, and away from tree crowns to exclude dripping (after del-Val *et al.* 2006). Water volume was converted to mm by dividing the volume collected by the fog collector's capturing-surface area (see description in Del-Val *et al.* 2006). When fog was sparse or not present (primarily between May and August), the volume of water collected was converted to mm by dividing the volume collected by the fog collector's funnel area (excluding the mesh designed to collect horizontally driven droplets) in order to calculate the input of rain. Water volume from fog collectors in the windward edge of patches did not differ between locations (linear regression, $P = 0·263$), indicating that these sampled forest patches sit in a similar fog regime and that any relation between water influx and patch size is not a product of patch location.

During the first year of our study, soil and litter water content was determined gravimetrically every season following methods in Robertson *et al.* (1999). For soil, six random samples of the first 20 cm (horizons O and A) were taken from the central plot in

each forest patch using PVC plastic cores of 15 cm length × 4·5 cm diameter, taken in sealed polyethylene bags and oven dried (70 °C) in the laboratory until constant weight was achieved. Litter water content was estimated for five random samples of fresh litter taken from the centre of each plot and processed as with soil samples. Soil and litter water content were determined as the mass difference between fresh and dry samples (divided by dry weight) and used as a measure of water storage in the ecosystem.

STATISTICAL ANALYSES

Forest structure and microclimate

To characterize the relationship between forest patch area and forest structure we used linear regressions, with patch area (hectares) as the independent predictor of total tree basal area (m^2 ha^{-1}) per plot. We evaluated patch size–basal area relationships for the three most abundant tree species in the patches, *A. punctatum*, *M. correifolia* and *D. winteri*. Basal area was analysed at the species level and the patch level (all tree species pooled) and data were log$_{10}$ transformed to fulfil normality assumptions.

We calculated mean, maximum and minimum monthly air temperatures (°C) within forest patches, as well as mean, maximum and minimum monthly relative air humidity (%RH). For %RH we excluded patch F4 (4·3 ha) due to repeated failures in the sensor during our study period. The effects of area and season on microclimatic variables were analysed using linear models (ANCOVA) averaging both years, as there were no significant differences between years. Only minimum adequate models (Crawley 2002) are presented.

Water fluxes

Water input vectors and ecosystem storage values (TF, SF, soil and litter water content) were analysed using a linear mixed modelling approach to evaluate the effect of area while taking into account the nested structure of our sampling design (i.e. six samples per forest patch). We started with a saturated specified structure for the model, adding the fixed effects of as many covariates as possible (i.e. area × season) and we evaluated whether or not to keep the interaction in the model (West, Welch & Galecki 2007). Since at present the best way to calculate the appropriate number of degrees of freedom in mixed models is unclear, hypothesis testing for fixed effects was carried out in two different ways (Baayen 2008). First, we used Likelihood Ratio Tests (LRT) of nested models based on Maximum Likelihood estimation. The asymptotic null distribution of the test is a chi-square with degrees of freedom equal to the difference in the number of parameters between the two models (West, Welch & Galecki 2007). Secondly, we used a Markov chain Monte Carlo (MCMC) sampling, where each MCMC sample contains one number for each of the parameters in the model (Baayen 2008). We created 10 000 samples from which we obtained the posterior distribution of the parameters. From these distributions *P*-values and 95% highest posterior density intervals were estimated. In all cases results from LRT did not differ from MCMC, and thus we present the former. All variables were log$_{10}$ transformed to meet normality assumptions. Note that we decided not to evaluate the effect of the perimeter/area ratio, in addition to the direct effect of area, as both variables were – as expected – highly correlated ($r_P = -0·95$, $P < 0·001$; Quinn & Keough 2002). We performed all the statistical analyses using R (R Development Core Team, 2008).

Results

PATCH AREA, FOREST STRUCTURE AND MICROCLIMATE

Forest structure, defined by total basal area, differed significantly among the forest patches sampled (Table 1). Total basal area scaled positively with patch area ($R^2 = 0.75$, $b = 0.16 \pm 0.04$ SE, $t_{(4)} = 3.521$, $P = 0.024$) and values ranged from $46.7 \, m^2 \, ha^{-1}$ in smaller patches up to $125 \, m^2 \, ha^{-1}$ in larger ones. The scaling relationship differed among the main tree species. For the dominant tree species in all patches, *A. punctatum*, total basal area showed a positive but nonsignificant trend with patch area ($P = 0.113$). For *M. correifolia,* the second most frequent species, especially in small patches, basal area scaled negatively with patch area ($R^2 = 0.85$, $b = -0.87 \pm 0.16$ SE, $t_{(4)} = 5.372$, $P = 0.005$). Finally, *D. winteri*, which was only present in patches larger than 4 ha, basal area showed a significant positive relationship with patch size ($R^2 = 0.88$, $b = 1.2 \pm 0.22$ SE, $t_{(4)} = 5.399$, $P = 0.005$).

Regardless of size, differences in mean air temperatures between forest patches and the surrounding semi-arid matrix averaged 2·3 °C, with a maximum of 3·6 °C cooler in forest patches during summer. Mean air temperature inside patches (Table 1; see Fig. S1 in Supporting Information) was significantly affected by patch area ($b = -0.294 \pm 0.09$ SE, $F_{1,19} = 10.49$, $P = 0.004$) and season ($F_{3,19} = 53.60$, $P < 0.001$). Forest patch area affected maximum air temperature, with differences of 2 °C between the largest and smallest patch sampled. This effect was dependent on season, although in all cases the relationship was negative, with larger patches having lower maximum air temperatures (area × season: $F_{3,16} = 4.46$, $P = 0.019$). Minimum air temperature inside patches (Table 1) was not affected by patch area ($F_{1,19} = 0.07$, $P = 0.799$) but it was affected by season ($F_{3,19} = 73.71$, $P < 0.001$). All air temperature variables (mean, maximum and minimum) differed between seasons (Table 1), but interestingly spring temperature was always the lowest.

Mean values of %RH (Table 1; see Fig. S2) were positively (but marginally) affected by forest patch area ($b = 1.060 \pm 0.51$ SE, $F_{1,15} = 4.32$, $P = 0.055$) and season ($F_{3,15} = 17.16$, $P < 0.001$). Maximum %RH values were not affected by area ($F_{1,15} = 1.33$, $P = 0.268$) but they were affected by season ($F_{3,15} = 12.93$, $P < 0.001$). Minimum %RH values were affected by area ($b = 3.36 \pm 1.34$ SE, $F_{1,15} = 6.25$, $P = 0.025$) and season ($F_{3,15} = 9.79$, $P < 0.001$). Differences in %RH between small and large forest patches were about 10%. For the air humidity variables, summer and spring were the wetter seasons.
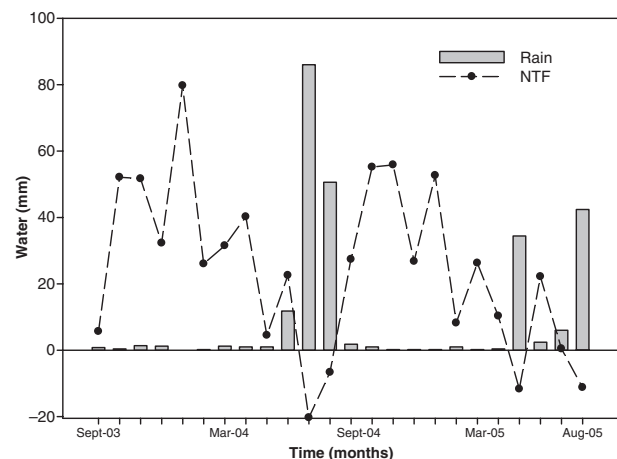
WATER FLUXES

Rainfall recorded during our study period (September 2003–August 2005) averaged 122·9 ± 21·4 mm. Total water influx to forest patches (TF + SF, including both precipitation and

fog capture; Table 1) was 480 and 357 mm respectively during the first and second year of the study, averaging 419 mm for the 2-year period. On the other hand, NTF on average for all patches combined was 324·7 mm for the first and 267·5 mm for the second year, averaging 296·1 mm for the whole study period. These estimates of NTF (Fig. 2) are greater than the average annual rainfall for the last 20 years.

On average, forest patches received 34·5 mm of water monthly delivered by direct drip, with highest TF volumes measured during the austral spring (42·2 mm; September–November). Spring months represent the foggiest period in the area (del-Val *et al.* 2006; Garreaud *et al.* 2008). The relationship between patch area and monthly TF was nonsignificant ($b = -0.0003 \pm 0.04$, $\chi^2_{[1]} = 0.0001$, $P = 0.991$; SE) and was independent of season, so the final model for TF included the fixed effects of area and season but not their interaction ($\chi^2_{[3]} = 0.244$, $P = 0.970$). The amount of water entering the forest ecosystems via TF was lower in autumn (March–May) than in the other three seasons (Fig. 3a) regardless of the fact that some rain events were recorded during autumn (see Fig. 2) ($\chi^2_{[3]} = 11.342$, $P = 0.010$).

As expected (Hutley *et al.* 1997), SF volumes were lower than TF (i.e. the average monthly volume collected was 0·45 mm) The relationship between patch area and stemflow was positive ($b = 0.298 \pm 0.10$ SE; $\chi^2_{[1]} = 7.037$, $P = 0.008$) and linear on a $\log_{10}$ scale. This relationship was unaffected by season, so the final model for this variable included the fixed effects of area and season but not their interaction ($\chi^2_{[3]} = 1.320$, $P = 0.724$). Although the water influx via SF was higher in spring than in autumn, its overall effect was nonsignificant ($\chi^2_{[3]} = 5.355$, $P = 0.148$; Fig. 3b).

Soil water content (Table 1) was affected by forest patch area showing a positive linear relationship on a $\log_{10}$ scale

Fig. 2. Main water influxes in Fray Jorge ecosystem: total monthly NTF in mm within forest patches (average values from the six forest patches), shown in dashed line for the study period (September 2003–August 2005) and rainfall averages from Fray Jorge National Park meteorological station in grey bars. Throughfall water fluxes that are greater than rain fluxes to an adjacent open area are assumed to be fog (after Ponette-González, Weathers & Curran 2009). Dispersion measures for these mean values are not displayed for graph simplicity.
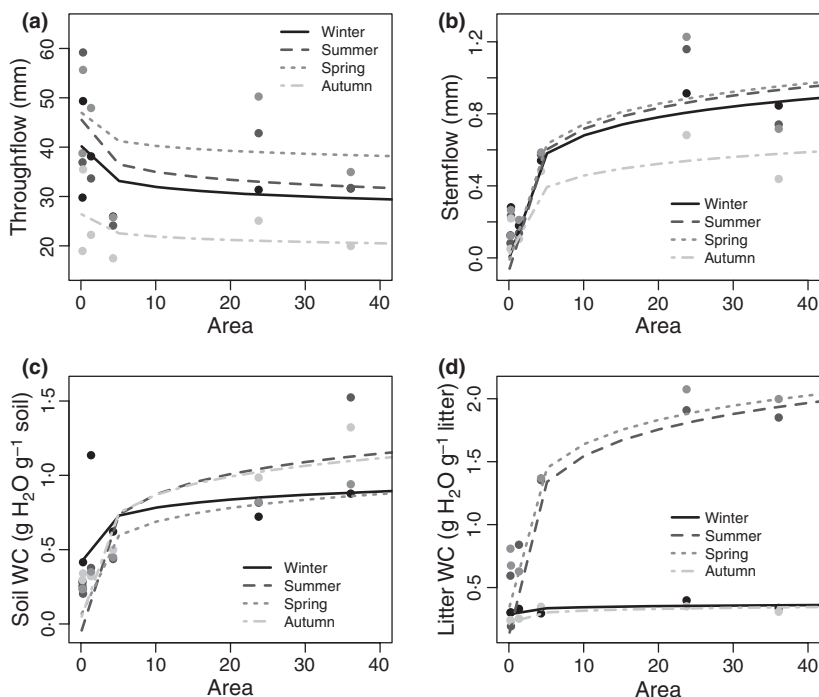
Fig. 3. Scaling relationship of ecosystem area (hectares) on water influxes and storage per season: Throughfall (a), stemflow (b), soil water content (c) and litter water content (d). Points are mean values for each patch and curves are fitted values from a linear model.

($b = 0.244 \pm 0.02$ SE; $\chi^2_{[1]} = 22.378$, $P < 0.001$; Fig. 3c), independent of season ($\chi^2_{[3]} = 6.889$, $P = 0.076$). Furthermore, season had no significant effect on soil moisture ($\chi^2_{[3]} = 4.691$, $P = 0.196$), but the effect of area on litter water content (Table 1) was dependent on season, so the final model for this variable included the fixed effects of area, season and their interaction ($\chi^2_{[3]} = 50.603$, $P < 0.001$). The relationship between patch area and litter moisture content was positive in summer and spring but not in autumn and winter (Fig. 3d).

Discussion

FOREST PATCH SIZE, STRUCTURE AND MICROCLIMATE

Forest structure (expressed as tree basal area) and microclimate differed greatly across patches of different areas, suggesting that the combination of abiotic and biotic conditions found in small patches may not be suitable for continuous regeneration of all tree species (del-Val *et al.* 2006). However, this pattern may be recent (i.e. last 90 years) given that, historically, we have not found recruitment differences between patches (i.e. trees have similar ages throughout all patches; Gutierrez *et al.* 2008).

The dominant tree species, *A. puncatum*, achieved similar basal areas per plot in all forest patch sizes suggesting it may be less sensitive to patch area than the other tree species. The positive and negative scaling relationship of *D. winteri* and *M. correifolia* respectively (see also del-Val *et al.* 2006) may be the consequence of their differential sensitivity to desiccation. This is also reflected in their differential sclerophylly index (leaf carbon : nitrogen ratio of 47.3 for *M. correifolia*

and 43.9 for *D. winteri*, Pérez 1994) where higher ratios are product of greater leaf mass, higher crude fibre contents, greater leaf hardness and result in lower rates of water loss (Loveless 1961).

The lower tree basal area of the small patches may be a direct consequence of their size and resultant greater perimeter/area ratio (i.e. edge effects). Here, edge effects have an important influence on three interdependent ecosystem components: (i) tree regeneration, (ii) tree mortality and (iii) microclimate. First, smaller patches have lower tree regeneration associated with higher rates of insect and mammal herbivory (del-Val *et al.* 2006, 2007) and unsuitable microclimatic condition (see below). This is reflected in the positive scaling of total tree basal area and patch area, which is a product of higher tree size and density. In large forest patches, there are more trees that can reach larger sizes on average (Gutierrez *et al.* 2008), and this pattern is not exclusively related to the presence of an additional species in larger patches (i.e. *D. winteri*), but to all tree species in the patch. Secondly, it has been shown that tree mortality can be higher along patch edges due to canopy damage and tree falls caused by wind turbulence (Ferreira & Laurance 1997; Laurance *et al.* 2000). A similar pattern of mortality may be occurring in our forest mosaic, where smaller patches of rather elongated shapes have half of the basal area per hectare of larger patches. Furthermore, mortality can be strongly associated with the leeward edge of patches due to fog shadow effects (del-Val *et al.* 2006). Thirdly, higher overall air temperature in small forest patches is common to other fragmented forests (Kapos 1989; Saunders, Hobbs & Margules 1991; Laurance *et al.* 2002; Cadenasso *et al.* 2003). The fact that small patches show higher thermal amplitude (greater difference between maximum and minimum air temperatures) implies

that these patches are more exposed to climatic fluctuations that characterize the semi-arid matrix. Nevertheless, the nearly constant presence of fog in coastal mountaintops during spring and summer seems to provide an effective physical buffer against temperature fluctuations, lowering evapotranspiration (Ewing *et al.* 2009).

WATER INPUTS AND STORAGE

Our results highlight the importance of canopy trees for channelling water from passing fog into forest patches. The presence of trees as water conveyors more than tripled the hydrological flow into these forest ecosystem outliers, when compared with water interception outside the forest (derived primarily from rainfall). Water fluxes that are greater than rain fluxes to an adjacent open area are assumed to be fog (after Ponette-González, Weathers & Curran 2009), so our values of NTF during the main fog season (September–March, Fig. 2) clearly show that the increase in hydrological flow is a consequence of the fog drip generated by interception on canopy surfaces inside forest patches. Accordingly, trees behave as ecosystem engineers in fog-inundated ecosystems (Jones, Lawton & Shachak 1994) by channelling water in excess to their demands and hence proving moist habitats to other hygrophilous species. We also show that the semi-arid matrix differs greatly from forest patches in %RH, as records outside patches show on average 20% less %RH (data from Fray Jorge LTSER weather station). The fact that fog is present primarily during spring and summer months in this area (Cereceda & Schemenauer 1991; del-Val *et al.* 2006; Garreaud *et al.* 2008; Gutierrez *et al.* 2008) combined with rainfall events during winter (that in 'El Niño' years may be up to 325 mm), results in a relatively even water supply all-year long for forest trees and herbs inside the patches. Although further work is needed, we hypothesize that this largely aseasonal pattern of moisture availability enables this rain forest outlier to persist in this semi-arid landscape.

Throughfall inputs, although not significantly affected by patch size, were the main component of water influx to forest patches. Hydrological models indicate that TF may account for *c.* 60% of the total volume of water that effectively reaches the soil (Gash, Wright & Lloyd 1980; Diaz *et al.* 2007) and usually this percentage increases with decreasing canopy surface area in areas where rainfall is the main water input (Ponette-González, Weathers & Curran 2009). Given the positive relationship between patch area and tree basal area observed in this forest we expected a negative relationship between TF and patch area. However, we found no relationship between area and TF. A major reason for such discrepancy with the theoretical prediction may be that canopy drip in our system is predominantly fog driven and the amount of fog captured and redistributed by trees exceeds the amount of water effectively intercepted and evaporated by tree surfaces. This idea is supported by our NTF values (Fig. 2) that show how trees channel fog drip into the forest floor. In fog-dependent ecosystems, adult trees are the only vertical structures that are tall and wide enough to intercept significant

quantities of fog (e.g. Dawson 1998; Weathers 1999). TF patterns are not only complex and dependent on vertical and horizontal deliveries (Ewing *et al.* 2009) but also on factors such as stem density, tree height, leaf area index, crown volume and epiphyte loadings among others (Ponette-González, Weathers & Curran 2009). Even though these variables were not assessed in our patches, we do know that larger patches are structurally more complex (Gutiérrez *et al.* 2008).

On the other hand, SF, although generally assumed to be less important as a hydrological vector (Hutley *et al.* 1997), was greater in larger than in smaller forest patches. Given that SF volume is strongly dependent on canopy interception surface (Stogsdill *et al.* 1989), patches with higher basal area are more likely to show this positive relationship. SF values were orders of magnitude smaller than TF values and we believe the thick coats of mosses and other epiphytes may directly take up a large proportion of fog water impacting the stems and branches, thus reducing our estimates of total stemflow. It is important to note that that in addition to patch size and structure, TF and SF inputs may be influenced by factors related to landscape heterogeneity, such as slope, altitude and wind currents (Weathers *et al.* 2000, 2006). Although we did not measure these factors, they might not differ greatly between our sampled patches given that we collected similar values of water in the windward edge of them (i.e. outside patches; see Materials and methods).

Interestingly, even though patches received roughly similar amounts of water during our study period based on TF and precipitation, the ability of each patch to retain water in the soil and litter was different. Soil water content increased markedly with patch area, which is consistent with other studies that have shown greater desiccation rates in forest patches with large perimeter to area ratio (Camargo & Kapos 1995; Laurance *et al.* 2000, 2002; Ewing *et al.* 2009). Although we do not have data to support this assertion, we consider that differences in soil water content are not a consequence of differential average water influx to patches, but are more likely due to differential rates of evapotranspiration from canopy surfaces. Hydrological losses are likely to increase in smaller patches subject to stronger edge effects, which are a direct consequences of patch size (Weathers, Cadenasso & Pickett 2001; Laurance *et al.* 2002). The positive scaling effect of litter water content with patch size was dependent on season showing no pattern during autumn and winter. A potential reason for this may be due to the effect of rainfall, which saturates litter and soil equally in all patches, thus homogenizing humidity patterns (Ewing *et al.* 2009).

ECOSYSTEM FUNCTIONING AND PATCH SIZE

The relationship between patch area and patch structure and its connection to the processes responsible for fog water interception, use and storage are complex. Our results show that patch area affected forest structure, through changes in tree basal area, microclimatic conditions within patches, and the efficiency and distribution of water storage compartments

(e.g. soil, litter). As shown in Fig. 3a,b functions involving water capture and storage tend to stabilize after patch size has reached 5 ha. According to studies of landscape structure in Fray Jorge National Park (Necochea 2008), we know that for nearly 470 patch units identified, the mean patch size is only 0·36 ha with a median of 0·04 ha. This suggests that many forest patches in this area may be well under the minimal conditions to sustain ecosystem functions related to hydrological balance, imposing serious constraints for potential management practices. Unfortunately, our small sample size (i.e. only six patches) together with the great variation in size our patches have (i.e. patches were specifically chosen to capture the entire range of size variation in this forest, and thus we did not sample enough in the 2–10 ha range), prevents us from drawing definitive conclusions.

Several studies have shown that land use change, forest clearing, replacement of diverse vegetation by monocultures, and the proliferation of forests edges can seriously affect water inputs and cycling within ecosystems (Weathers *et al.* 2000, 2006; Weathers, Cadenasso & Pickett 2001; Diaz *et al.* 2004); however, this is one of the first quantitative demonstration of how forest patch size affects the magnitude of hydrological vectors in a strongly fog-dependent ecosystem. In a similar manner as island area affects major ecosystem processes (Polis, Anderson & Holt 1997; Wardle *et al.* 1997), here we show that patch area in this mosaic of temperate forest patches within a semi-arid matrix can significantly modify water fluxes and water storage capacity of the ecosystem. This finding has meaningful consequences for the functioning of ecosystems, where large continuous forests have been fragmented into smaller patches, affecting not only the persistence of species but also through changes in structure effect the continuity of critical ecosystem processes.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article.

Figure S1. Scaling relationship of ecosystem area and mean, minimum and maximum air temperature.

Figure S2. Scaling relationship of ecosystem area and mean, minimum and maximum relative humidity.

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