**Dwarf shrub and grass vegetation resistant to long term experimental warming while microarthropod abundance declines on the Falkland Islands**

*Running title: Empetrum* and grass resistant to warming

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**Abstract**

Dwarf shrubs are a dominant plant type across many regions of the Earth and have a large impact on carbon and nutrient cycling rates. Climate change impacts on dwarf shrubs have been extensively studied in the Northern Hemisphere and there appears to be large variability in response between ecosystem types and regions. In the Southern Hemisphere far less is available despite dwarf shrub vegetation being a dominant feature of southern South America and mountainous regions of the Southern Hemisphere. Here we present the response of an *Empetrum rubrum* dwarf shrub and a grass community to 12 y of experimental climate manipulation achieved using open top chambers on the Falkland Islands, a cold temperate island group in the South Atlantic. The dwarf shrub and grass vegetation did not significantly change in cover and biomass over the 12 y period in response to climate warming scenarios of up to 1 °C, reflecting annual warming levels predicted in this region for the coming decades. The soil microarthropod community however, responded with declines in abundance (37 %) under warming conditions in the grass community, with higher temperatures and increased evaporation as likely drivers. Overall, these results indicate that dwarf shrub communities are resistant to climate warming in the southern South America region and will therefore remain a dominant driver of local ecosystem properties.

Keywords: *Azorella*; *Empetrum*; Mites; Springtails; Warming

**Introduction**

Dwarf shrub vegetation dominates many natural ecosystems across various biomes. Common heather (*Calluna vulgaris*) and crowberry (*Empetrum nigrum*) are two of the most abundant species in montane and heathland ecosystems in the Northern Hemisphere, with a strong influence on ecosystem properties, such as through the build-up of recalcitrant soil organic matter with a low pH which slows the decomposition process (Aerts 1995; Aerts and Chapin 2000; Tybirk, Nilsson et al. 2000). Due to its vegetative horizontal growth *Empetrum* sp*.* can quickly cover large areas and, by producing allelopathic substances in their leaves, the soil-litter layer often limits the establishment of other plant species (Nilsson and Zackrisson 1992; Nilsson 1994; Wardle, Nilsson et al. 1998). As climate warming appears to promote the poleward spread of shrubs in the Northern Hemisphere, large changes may occur in these ecosystems with potential feedback to the global climate (Myers-Smith, Forbes et al. 2011; Ylänne, Stark et al. 2015). However, very limited information is available on the contemporary success and growth of such dwarf shrub communities in the Southern Hemisphere. Given that these dwarf shrubs are key ecosystem drivers and that their response to climate warming in the Northern Hemisphere is far from consistent across different regions (van Wijk, Clemmensen et al. 2004; Elmendorf, Henry et al. 2012), there is a pressing need to expand our knowledge on their responses to contemporary climate and environmental changes.

Some climate manipulation studies on *Empetrum* sp*.*-dominated ecosystems report shifts with warming in bud phenology, increased shoot growth and reproductive output in alpine (Suzuki and Kudo 1997; Suzuki and Kudo 2000; Wada, Shimono et al. 2002; Kudo and Suzuki 2003), sub-Arctic (Arft, Walker et al. 1999), and temperate regions (Buizer, Weijers et al. 2012), while there was little to no response in a sub-Arctic *Sphagnum* peatbog (Dorrepaal, Aerts et al. 2006). There also appears to be high inter-annual variability in the responses recorded (Shevtsova, Haukioja et al. 1997; Hartley, Neill et al. 1999). Even where changes in *Empetrum* shoot growth do occur this does not always lead to overall plant community or cover changes (Richardson, Press et al. 2002; Keuper, Dorrepaal et al. 2011). This latter observation suggests that there could be a response to climate warming at the individual shoot level, but that this may not translate to changes in the plant community or ecosystem processes. Quantifying plant community changes often requires longer-term manipulative warming studies, as the responses noted during the initial years may not be indicative of longer term patterns (Chapin, Shaver et al. 1995; Bokhorst, Convey et al. 2016).

Plants have a large impact on the soil fauna and microbiota, and *vice versa* (van der Putten, Vet et al. 2001; Wardle, Bardgett et al. 2004; Yergeau, Bokhorst et al. 2007; Sabais, Eisenhauer et al. 2012). Changes in the plant community, due to climate and other environmental changes, are therefore also likely to have an impact on the soil fauna (Bokhorst, Wardle et al. 2014). The response of soil microarthropods such as springtails (Collembola) and mites (Acari) to warming is, like the vegetation, often dependent on location, and the duration and intensity of warming (Coulson, Hodkinson et al. 1996; Hodkinson, Webb et al. 1998; Webb, Coulson et al. 1998; Convey, Pugh et al. 2002; Bokhorst, Huiskes et al. 2008). In addition, specific characteristics or traits of microarthropods can play a role in their response to climate warming manipulations, with smaller and deeper-living species often being more vulnerable to the imposed warmer and usually drier micro-climate (Makkonen, Berg et al. 2011; Bokhorst, Phoenix et al. 2012).

Current climate warming predictions for southern South America indicate mean annual warming of 0.7 °C to 2.7 °C by 2100, and winter precipitation in Tierra del Fuego is likely to increase (IPCC 2013). Simulation of such warming predictions can be achieved by passive warming chambers such as open top chambers (OTCs), while precipitation changes require active manipulations (Bokhorst, Huiskes et al. 2013). Here we report on the response of an *Empetrum rubrum* dwarf shrub and a *Poa* *annua* grass community on the Falkland Islands to 12 y of experimental climate manipulation using OTCs. Based on initial observations during the first 2 y of the manipulation (Bokhorst, Huiskes et al. 2007), we here test the hypothesis that the grass community would further deteriorate under the longer-term warming conditions of the OTCs while the dwarf shrub community would be resistant. We further predicted that the microarthropod fauna would decline in tandem with the vegetation in the grass community, with little or no change expected in the dwarf shrub soil faunal community.

**Materials and Methods**

The study site was at Saladero Farm, south-west of Brenton Loch (near the settlement of Goose Green on East Falkland) (51° 17’ S 59° 10’ W). Annual soil temperature is around 7 °C and precipitation 575 mm yr-1 (data obtained from the Department of Agriculture, Falkland Islands Government). The Falkland Islands vegetation is treeless and dominated by grasses and dwarf shrubs due to exposure to typically high winds and low precipitation (Moore 1968). The two communities chosen for sampling and manipulation were a dwarf shrub heath and a grass-dominated community. The dwarf shrub community was dominated by the evergreen shrub *Empetrum rubrum* Vahl ex Willd and is underlain by a 30–50 cm layer of peat. The grass community was co-dominated by *Festuca magellanica* Lam., *Poa annua* L. and *P. pratensis* L. A 0.5-1 cm layer of soil above the rocky base layer (mainly sandstone) underlies this vegetation.

Warming of the vegetation and soil was achieved by using open top chambers (OTCs) based on the ITEX six-sided model (Molau and Molgaard 1996). OTCs have been shown to increase mean summer temperature by 1 °C on the Falkland Islands (Bokhorst, Huiskes et al. 2007) which is in line with the current predictions of warming for the coming decades of southern South America (IPCC 2013). Further microclimatic changes induced by OTCs include increases in degree day sums (9 %) and the maximum temperature experienced, but reductions in photosynthetically active radiation (PAR; -7 %). While soil moisture declined in OTCs (-12 %) this was not significantly different from control plots (Bokhorst, Huiskes et al. 2007; 2013). Three paired plots (2 m × 4 m) were established in the grass community, each containing a control plot and an OTC, and nine such paired plots were established in the dwarf shrub community, during November 2003. To monitor the impact of OTCs on environmental conditions sensors were placed in three paired plots of each community. Canopy temperature at 5 cm and soil temperature (5 cm depth) were measured using thermocouples (Copper constantan), soil moisture (Water Content Reflectometer CS616, Campbell Scientific UK) and PAR (SKP215 Campbell Scientific UK) were recorded. Due to the shallow nature of the substratum, we were unable to place a soil moisture probe in the grass community. Data were recorded (CR10X Storage module Campbell Scientific, Shepshed, UK) every hour for the duration of the study. Environmental impacts of these OTCs during the initial years of the experiment have been reported previously (Bokhorst et al.,(2007; 2011; 2013), and we here report data from 2007 and 2008 as data from 2010-2015 were impaired due to sensor damage, providing limited replication of environmental data. The overall warming pattern for 2010-2015 were in line with the warming of the earlier periods.

*Vegetation surveys*

To quantify changes in vegetation composition associated with the OTC deployment we measured the abundance of all plant species in a fixed quadrat (30 cm × 30 cm) in each plot using the point-intercept method. Point counts (n = 121) were made at 2.5 cm intervals of the vegetation in each quadrat by counting the number of times a vertical pin touched plant parts. Cryptogams were counted as present or absent while vascular plants could be hit more than once by each vertical pin. For *E. rubrum*, only shoots were counted rather than every leaf hit, in order to avoid overrepresentation due to the high number of tightly packed needle-like leaves. We used the point intercept hit data to calculate plant biomass from linear regressions between point intercept hits and oven dry mass plant mass (Jonasson 1988). These measurements were made at the start of the growing season (November) during 2003 and 2015. *Azorella* species (*A. caespitosa*, *A. filamentosa A. lycopodioides*) were grouped together, as the individual species were not consistently present across all 24 plots. The same approach was used for the grasses. Species cover was calculated from the presence of each species at each of the 121 point counts. In addition, we calculated species richness and diversity (Shannon diversity H’) for each plot.

*Normalized differentiated vegetation index*

 To quantify the overall greenness of the vegetation we measured the NDVI (Normalized differentiated vegetation index) using a digital camera modified to a handheld passive proximal sensor (Bokhorst, Tømmervik et al. 2012); this was a Maxmax-modified Canon camera (LDP LLC, Carlstadt, NJ, USA) where an infrared sensor replaced the normal sensor (the blue channel records the visible light and the red channel the near infrared). NDVI of the experimental plots was calculated as follows: NDVI = (NIR – RED) / (NIR + RED) with the reflectance values of NIR (near-infrared 0.73–1.10 mm) and RED (red 0.58–0.68 mm).

*Microarthropod community*

To quantify the abundance and species richness of microarthropods in the OTCs and control plots we collected a soil sample (5 cm diameter, 5 cm deep) from each plot and extracted these in a modified Tullgren extractor (van Straalen and Rijninks 1982) for 4 d. Springtails (Collembola) were identified to species level following various keys, as there is no comprehensive identification key for the Falkland Islands. We used a key for South America springtails (Heckman 2001) and one for New Zealand (Salmon 1940) and generic keys from the Palaearctic (Fjellberg 1998; Potapov 2001; Thibaud, Schulz et al. 2004; Fjellberg 2007). Mites (Acari) were grouped into major orders: Astigmata-Prostigmata, Oribatida and Mesostigmata, and only Oribatida were further identified to family or genus level following Weigmann (2006).

*Calculations and statistical analyses*

The OTC impacts on environmental variables were calculated for seasonal means (summer: December–February, autumn: March–May, winter: June–August and spring: September–November) and included: mean temperature within the canopy and in the soil, the number of freeze-thaw cycles, degree day sums (above 0°C), soil moisture and PAR levels. To identify changes in environmental variables, plant cover and biomass, we used repeated-measures ANOVA with treatment (OTC vs. control plots) within a plot as a within-subject factor. To compare the present day differences between OTCs and control plots in NDVI, microarthropod abundance, species richness and diversity (H’) we used one-way ANOVA. All statistical analyses were carried out using R studio 3.3.0 (RCoreTeam 2015).

**Results**

*Microclimate effects of the OTCs*

Mean seasonal temperature increases in the OTCs at canopy height ranged from 0.2 to 1.2 °C (Table 1). In the soil, temperature increases ranged from 0.3 to 1.3 °C. Degree day sums increased up to 11 % in the canopy and 14 % in the soil. The number of freeze-thaw cycles was not affected by the OTCs. Maximum soil temperatures ranged from 25.9 °C to 27.1 °C in the control plots and from 29.1 °C to 34.7 °C in the OTCs over the grass vegetation during 2008. In the dwarf shrub vegetation soil temperatures reached maxima of 18.6-21.5 °C in the control plots and 20.3-29.0 °C in the OTCs in 2008, with similar range differences measured during 2007 for both vegetation types. Soil moisture in the dwarf shrub community was decreased in the OTCs compared to control plots, ranging from 7.3 % to 18.5 % during different seasons. PAR levels were on average 6 % lower inside OTCs compared to control plots during summer months.

*Vegetation responses to climate warming*

There were no changes in species-specific plant cover in the dwarf shrub community after 12 y of warming (Table 2). Biomass of *E. rubrum* decreased by 28 % (±SE: 13.1) in the control plots and increased by 18 % (±22) in the OTCs between 2003 and 2015 but this did not lead to significant biomass changes in the OTCs (Fig. 1a). Biomass of *Azorella* species increased by 58 % (±32) in the control plots but decreased by 34 % (±21) in the OTCs. Grasses and *Oxalis enneaphylla* decreased in both the OTCs and control plots (Fig. 1). *Olsynium filifolium* and *Pernettya pumila* were no longer present in any of the plots during 2015. The vegetation in the grass community was not affected by the environmental impacts of the OTCs (Table 2). However, grasses declined by 25 % (±10) and 23 % (±15) in the control plots and OTCs respectively between 2003 and 2015 (Fig. 1b). There was no consistent change in the total cover and biomass of *Azorella* species between control plots and OTCs. Species richness and diversity (H’) were not affected by the OTCs (3.7 ±0.3 and 0.3 ±0.1) compared to the controls (4.1 ±0.5 and 0.5 ±0.1) in the dwarf shrub community. The species richness and diversity (H’) also did not differ between OTCs (3.3 ±0.3 and 0.8 ±0.2) and control plots (3.7 ±0.3 and 0.8 ±0.1) in the grass community. NDVI values also did not differ between OTCs and control plots in either community during 2015.

*Micro-arthropod responses to climate warming*

Twelve years of manipulation with OTCs had no effect on the total abundance of microarthropods, taxon-specific abundances, taxonomic richness or diversity (H’) in the dwarf shrub community (Fig. 2, Table 3). In contrast, total microarthropod abundance was 37 % lower (F1,4 = 13.1, *P* < 0.05) in the OTCs compared to the control plots of the grass community. This decline resulted from overall, though non-significantly, lower micro-arthropod abundances (Table 3). Only the springtail *Tomocerura conjugens* had a 10 times lower abundance (F1,4 = 24.6, *P* < 0.01) in the OTCs compared to the control plots. Taxonomic richness was halved (F1,4 = 8.9, *P* < 0.05) in the OTCs (4.7 ±1.3) compared to the control plots (9.7 ±0.6) but diversity (H’) did not differ between treatments. Taxonomic richness losses from the OTCs included springtails (*Xenylla maritima*, *Lepidocyrtus* sp*. (lanuginosus* or *nigrosetosus),* an unidentifiedIsotomidae) and Oribatida (Oppiidae, Nothroidae and *Scheloribates* sp*.*).

**Discussion**

The dwarf shrub and grass vegetation of the Falkland Islands appeared very resistant to the environmental changes induced by the OTCs while, below-ground, the micro-arthropods showed a strong decline in the grass community but no response in the dwarf shrub community. Counter to our first hypothesis, there was no continued decline in vegetation cover and species richness of the grass community in response to OTC warming. During the first years of this warming study we recorded large declines and species losses (*Festuca magellanica, Poa annua* and *Aira pracox*) in the OTCs (Bokhorst, Huiskes et al. 2007), but these changes appear to have been transient over time as differences were no longer detectable after 12 y of manipulation and some species reappeared (*P. annua* and *A. pracox*). The plants in the dwarf shrub community, however, were consistently resistant against the OTC treatment. We observed a percentage increase in *E. rubrum* biomass in the OTCs, in line with responses found for *E. nigrum* shoot growth in the Northern Hemisphere (Buizer, Weijers et al. 2012; Barrett and Hollister 2016), but this response was not significantly different from the changes in control plots and it also did not lead to significant changes in total biomass. These responses are in line with long-term warming studies performed in the Netherlands (52° N) and the Arctic (Buizer, Weijers et al. 2012; Elmendorf, Henry et al. 2012; Barrett and Hollister 2016), indicating that *Empetrum*-dominated communities are stable, in terms of vegetation cover, in response to this level of manipulation. Further support is provided by the similarity in NDVI values between OTC and control plots, indicating that there were no apparent differences in plant health or physiological activity (Bokhorst, Tømmervik et al. 2012). Although we did not measure season growing length (phenology), shoot growth or reproductive output, which are plant variables often affected in OTCs (Arft, Walker et al. 1999; Aerts, Cornelissen et al. 2004; Buizer, Weijers et al. 2012; Barrett and Hollister 2016), these factors, if affected at all during 12 y of warming, did not allow *E. rubrum* to increase in cover or biomass in the study plots on the Falkland Islands.

The soil microarthropod community showed a strong decline in response to OTC-induced changes in the grass community but not in the dwarf shrub community. These microarthropod responses were most likely driven by the changed microclimatic conditions as there were no consistent plant cover and biomass changes in the OTCs. Changes in litter quality, due to warming, can affect microarthorpods but this often requires large changes in the overall litter composition or quality driven by change in the overall plant community (Krab, Berg et al. 2013; Bokhorst, Wardle et al. 2014). The contrasting response of the microarthropods between vegetation types observed here was probably a reflection of the canopy structure, with the dwarf shrub community soil being more closed and therefore thermally buffered, limiting strong evapotranspiration, while the open grass vegetation experienced the opposite. In a multivariate environmental manipulation experiment near Palmer Station (64° S), reduced water availability linked with warmer microhabitat temperatures was identified as a significant negative driver of abundance of springtails and prostigmatid mites (Convey et al. 2002). A similar microarthropod response to a 16 y manipulation in northern Sweden (68° N) (Makkonen *et al.* 2011) was also correlated with moisture stress. The overall higher mean and maximum soil temperature impacts of OTCs in the grass compared to the dwarf shrub vegetation (Table 1) are likely also to be an indication of increased evaporative water loss and water stress.

As the microarthropod decline in the OTCs was apparent across almost all taxonomic groups, with although limited significant changes for individual species, it appears that all were somewhat vulnerable to the microclimatic changes induced by the OTCs. These declines in micro-arthropods are consistent with the findings of other warming and drying experiments (Coulson, Hodkinson et al. 1996; Convey, Pugh et al. 2002; McGeoch, Le Roux et al. 2006; Briones, Ostle et al. 2009), although other studies have identified no response (Webb, Coulson et al. 1998; Bokhorst, Huiskes et al. 2008; Kardol, Reynolds et al. 2011; Bokhorst, Convey et al. 2016). Differences between studies may also reflect the large between-year and between-site variations that often exist in microarthropod population densities (Usher and Booth 1984), which could themselves outweigh the effects of experimental manipulations (Hodkinson, Webb et al. 1998), but longer-term studies should eventually overcome such variability. Indeed, Makkonen *et al.* (2011) reported declines in microarthropod abundance (51 %) and species richness following 16 y manipulation using OTCs in the sub-Arctic, indicating that at least some longer-term studies (>10 y) do point in the same direction. The microarthropod response to the OTC treatment observed in the current study probably results from a combination of factors including reduced moisture availability and increased exposure to temperature maxima (Makkonen, Berg et al. 2011; Bokhorst, Phoenix et al. 2012; 2013).

Overall our results indicate that the grass and dwarf shrub vegetation studied, which are widespread on the Falkland Islands and in Patagonia (Moore 1968; Henriquez and Lusk 2005), appear resistant to climate warming scenarios of up to 1 °C, reflecting annual warming levels predicted in this region for the coming decades (IPCC 2013). The presence of these species, or close relatives, in milder climates than those typical of the Falkland Islands (Buizer, Weijers et al. 2012) and their presence in southern South America over the last several thousand years (Chambers, Mauquoy et al. 2007; Federico, Maria et al. 2011) suggests that these vegetation types are likely to survive and thrive under much warmer climate change scenarios. This in contrast to some of the endemic upland species on the Falkland Islands which are expected to lose suitable habitats due to climate warming (Upson, Williams et al. 2016). The soil microarthropod community however, responded with declines under warming conditions in the grass community. The longer-term impacts of such declines are hard to predict, but could include changes in the plant community and carbon and nutrient cycling rates of these grassland ecosystems (Sabais, Eisenhauer et al. 2012). This study has also provided further evidence that initial ecosystem responses to experimental warming may in fact be artefactual, and not indicative of longer-term changes and patterns (Chapin, Shaver et al. 1995; Convey and Wynn-Williams 2002). This study reinforces the necessity for long-term experimental studies and monitoring in order to understand the impacts of climate change on ecosystems.

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Table 1 Effect of Open Top Chambers (OTC) on canopy and soil temperature, degree day sums and number of freeze-thaw cycles in a dwarf shrub and grass community. The differences between variables measured in OTCs and control plots are shown. Temperature data are mean of n = 3 plots \* *P*<0.05, \*\* *P*<0.01. FT: Freeze-thaw

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **OTC-effect** |  |  |  |  |  | **OTC-effect** |  |  |  |  |
|  | Temperature (°C) | Degree day sums | FT-cycles (nr) |  | Temperature (°C) | Degree day sums | FT-cycles (nr) |
|  | 2007 | 2008 | 2007 | 2008 | 2007 | 2008 |  | 2007 | 2008 | 2007 | 2008 | 2007 | 2008 |
| **Canopy** | **Dwarf shrub community** |  |  |  |  | **Grass community** |  |  |  |
| Spring | 0.7 | 0.6 | 504 | 409 | -0.9 | -1.4 |  | 0.8 | 0.9 | 610 | 651 | -0.3 | -0.2 |
| Summer | 0.8 | 0.9 | 576 | 633 | -0.1 | -0.4 |  | 1.0 | 1.2 | 735 | 906 | -0.2 | -0.1 |
| Autumn | 0.4 | 0.4 | 263 | 265 | -1.3 | -0.4 |  | 0.5 | 0.6 | 362 | 414 | -1.1 | -1.3 |
| Winter | 0.2 | 0.2 | 141 | 122 | -1.4 | -0.9 |  | 0.3 | 0.3\* | 184 | 200\* | -0.6 | 0.4 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Soil** |  |  |  |  |  |  |  |  |  |  |  |  |
| Spring | 0.6 | 0.5 | 412 | 337 | 0.0 | 0.0 |  | 0.8\* | 0.9\* | 593\* | 673\* | 0.0 | 0.0 |
| Summer | 0.7 | 0.7 | 476 | 481 | 0.0 | 0.0 |  | 1.1 | 1.3 | 787 | 939 | 0.0 | 0.0 |
| Autumn | 0.4 | 0.4 | 276 | 293 | 0.1 | 0.0 |  | 0.6\* | 0.6\* | 444\* | 469\* | -0.1 | 0.3 |
| Winter | 0.3\*\* | 0.3 | 195\*\* | 195 | 0.4 | 0.3 |  | 0.2\* | 0.3\* | 186\* | 219\* | 0.1 | 1.0 |

Table 2 ANOVA statistics of changes in plant cover and biomass after 12 y of experimental manipulation on the Falkland Islands. *Azorella* species and various grass species were grouped as the individual species were not consistently present across all 24 plots. Analyses were based on nine and three paired plots for the dwarf shrub and grass community respectively with data recordings from 2003 and 2015.

|  |  |  |  |
| --- | --- | --- | --- |
|   |   | Change in cover | Change in biomass (%) |
|   |   | F (1,8) | *P* | F (1,8) | *P* |
| Dwarf shrub community |  |  |  |  |
| *Azorella* species | 2.1 | 0.181 | 7.9 | 0.023 |
| *Blechnum penna-marina* | 0.9 | 0.374 | 0.5 | 0.510 |
| *Empetrum rubrum* | 4.0 | 0.082 | 14.6 | 0.005 |
| *Oxalis enneaphylla* | 0.8 | 0.392 | 1.6 | 0.242 |
| Grasses |  | 1.2 | 0.298 | 0.2 | 0.682 |
|  |  |  |  |  |  |
| Grass community |  |  |  |  |
| *Azorella* species | 0.2 | 0.671 | 0.4 | 0.608 |
| Grasses |   | 0.0 | 0.940 | 0.9 | 0.436 |

Table 3. Microarthropod abundance in a dwarf shrub and a grass community following 12 y of manipulation with open top chambers (OTCs) in the Falkland Islands. Values are individuals m-2 with significant (*P* < 0.05) abundance differences between OTCs and control plots (C) indicated by \*

|  |  |  |  |
| --- | --- | --- | --- |
|   | Dwarf shrub community  | Grass community  |   |
|   | C | OTC | se | se | C | OTC | se | se |
| *Cyrptopygus sp.* | 9970  | 6768 | 5524 | 2286 | 20886 | 6792 | 8560 | 3827 |
| *Isotomidae sp.* | 873 | 364 | 426 | 146 | 849 | 0 | 612 | 0 |
| *Lepidocyrtus sp.* (*lanuginosus/nigrosetosus*) | 582 | 364 | 422 | 146 | 1019 | 0 | 778 | 0 |
| *Tomocerura conjugens* | 73 | 0 | 73 | 0 | 3906 | 340\* | 1114 | 170 |
| *Xenylla maritima* | 146 | 364 | 94 | 364 | 340 | 0 | 340 | 0 |
| *Dinaphorura sp. (pefauri/spinosissima)* | 1383 | 2038 | 454 | 676 | 1358 | 1019 | 679 | 1019 |
| Total springtail abundance | 13027 | 9897 | 6589 | 2635 | 28358 | 8151 | 9527 | 3891 |
|  |  |  |  |  |  |  |  |  |
| Astigmata-Prostigmata | 15137 | 22560 | 6885 | 6083 | 22584 | 12736 | 5736 | 5302 |
| Oppiidae | 2693 | 1674 | 1732 | 1132 | 170 | 0 | 170 | 0 |
| Nothroidae | 146 | 0 | 94 | 0 | 340 | 0 | 170 | 0 |
| Phthiracaridae (Hoplophthiracarus) | 3202 | 1092 | 1201 | 451 | 0 | 0 | 0 | 0 |
| Scheloribatidae  | 73 | 291 | 73 | 151 | 1189 | 679 | 679 | 679 |
| *Scheloribates sp.* | 1092 | 218 | 724 | 103 | 509 | 0 | 509 | 0 |
| *Chamobates sp.* | 0 | 0 | 0 | 0 | 1528 | 2377 | 1282 | 1891 |
| Camissidae | 73 | 0 | 73 | 0 | 2377 | 1868 | 2377 | 1868 |
| Mesostigmata | 2693 | 4003 | 1414 | 1045 | 3396 | 1868 | 1390 | 1390 |
| Total mite abundance  | 25107 | 29838 | 9548 | 7834 | 32094 | 19528 | 5673 | 7290 |
|  |  |  |  |  |  |  |  |  |
| Total microarthropods | 38134 | 39735 | 15852 | 7595 | 60452 | 27679\* | 3917 | 6130 |

**Figures**

Figure 1. Mean plant biomass of a dwarf shrub (a) and grass (b) community at the start of observations in 2003 and after 12 y of manipulation with open top chambers (OTCs) on the Falkland Islands. Panels c and d show the percentage change in point intercept hits between 2003 and 2015 for the OTCs and control plots respectively. Bars are means of 9 and 3 replicate plots for the dwarf shrub and grass community respectively, with SE as error bars. \* denote significant differences (*P* < 0.05) between years (a-b) or control plots (C) and OTCs (c-d).

Figure 2. Microarthropod abundances in a dwarf shrub (a) and grass (b) community warmed by open top chambers (OTCs) in the Falkland Islands. Bars are means of seven and three replicate soil samples for the dwarf shrub and grass community, respectively, with SE as error bars. \* denote significant differences (*P* < 0.05) between control plots (C) and OTCs.

Figure 1



Figure 2

