

VIERAEA	Vol. 33	41-50	Santa Cruz de Tenerife, diciembre 2005	ISSN 0210-945X
---------	---------	-------	--	----------------

Ecological data of isopods (Crustacea: Oniscidea) in laurel forests from the Western Canary Islands

ERIK ARNDT* & DIRK MATTERN**

* *Anhalt University of Applied Sciences, Department LOEL,
Strenzfelder Allee 28,
D-06406 Bernburg, Germany. Correspondence address.*
***Ahornweg 15, D-99867 Gotha, Germany.*

ARNDT, E. & D. MATTERN (2005). Datos ecológicos de isópodos (Crustacea: Oniscidea) en bosques de laurisilva de las islas canarias occidentales. *VIERAEA* 33: 41-50.

RESUMEN: Se examinó la fauna de isópodos en diferentes bosques de laurisilva de La Gomera, El Hierro y La Palma (Canarias Occidentales), con datos obtenidos de trampas pitfall y muestras de suelo, citándose un total de 11 especies. Las comunidades de especies de bosques de La Gomera y El Hierro por una parte, y las de La Palma por otra, fueron muy diferentes a pesar de la similitud de la estructura forestal, la vegetación arbórea y las condiciones climáticas en las tres islas. La especie nativa *Porcellio meridionalis* es dominante en La Gomera y El Hierro, y alcanza su mayor abundancia en localidades frescas y húmedas por encima de 1200 m s.n.m. En todas las localidades forestales de La Palma fue siempre dominante *Armadillidium vulgare*, a menudo acompañada por pequeños Trichoniscidae endogeos. Cinco de las especies mencionadas han sido introducidas en las islas por el hombre en fechas históricas. Esas especies invasoras dominan cuantitativamente en muchos sitios del estudio, con una media en la proporción de especímenes invasivos:nativos de 3,1:1 en trampas pitfall, y de 1,1:1 en muestras de suelo. Las condiciones climáticas parecen afectar fuertemente el éxito de la invasión. Las especies invasoras más frecuentes, *A. vulgare* y *Eluma caelatum*, presentan las mayores abundancias en las parcelas forestales más cálidas a menores altitudes pero no son capaces de dominar los sitios más frescos con baja insolación potencial.

Palabras clave: islas Canarias, Isópodos, Oniscidea, laurisilva, especies invasivas.

ABSTRACT: Isopoda were examined in different laurel forests of the Western Canary Islands La Gomera, El Hierro, and La Palma using data from pitfall traps and soil samples. Eleven species were recorded. The species communities from forests of La Gomera and El Hierro on one side and La Palma on the other side

are extremely different in spite of the similar forest structure, tree vegetation and climatic conditions on the three islands. La Gomera and El Hierro are dominated by the native *Porcellio meridionalis* which reaches greatest abundance in cool and moist localities above 1200m a.s.l. All forest sites on La Palma are dominated by *Armadillidium vulgare*, often accompanied by small endogean Trichoniscidae. Five recorded species have been introduced to the islands by man in historical time. These invasives dominate quantitatively in many study sites, the average ratio of invasive:native specimens was 3.1:1 in pitfall traps and 1.1:1 in soil samples. Climatic parameters seem to strongly affect the invasion success. The most frequent invading species, *A. vulgare* and *Eluma caelatum*, occur in highest abundances in warmer forest plots at lower altitudes but are not able to dominate the cooler sites with low potential insolation. Key words: Canary Islands, Isopoda, Oniscidea, laurel forest, invasive species.

INTRODUCTION

In spite of their small land area, the Canary Islands harbour a high biodiversity, with 524 recorded endemic species of vascular plants and 2995 endemic animal species (Martín *et al.*, 2005). One reason of this extraordinary diversity is the occurrence of numerous different biotope types along the vertical gradients on the mountainous western islands. The laurel forest is one habitat type with particularly high species richness. Laurel forests occur as cloud forests on the north parts of the western five Canary Islands (as well as on the Azores and Madeira) at elevations between 600 and 1400m. Influenced by trade winds we find comparably cool and moist conditions in these forests. Four endemic species of the family Lauraceae, together with 16 other trees and shrubs (e.g. *Myrica faya*, *Erica arborea*, and *Viburnum rigidum*) comprise the dominant plants in laurel forests.

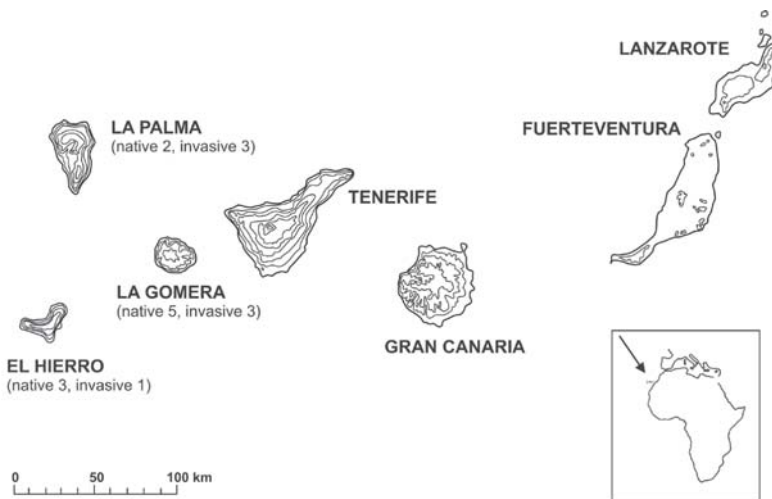


Fig. 1. Map of the Canary archipelago with number of recorded isopod species in laurel forests.

Vegetation, soil structure and, depending on elevation and exposition, also climatic conditions are very similar between different islands. But there are pronounced differences among the invertebrate soil fauna of different islands.

Terrestrial isopods belong to the little known soil macro-invertebrates of the Canarian archipelago. Rodríguez *et al.* (2004) list 55 terrestrial species on the islands, 29 of which are endemic. The majority of these endemic species (19) are reported only from a single island. Despite a large number of faunistic publications and species descriptions (e.g. Arcangeli 1958; Rodríguez & Vicente 1992a-c; Vandel 1954), ecological data of Canarian isopods are widely lacking. It is the aim of this paper to present ecological data of the laurel forest isopod community. Such a study is timely in view of the large number of introduced isopod species in these forests, and their potential impact on nutrient turnover or the native endemic fauna.

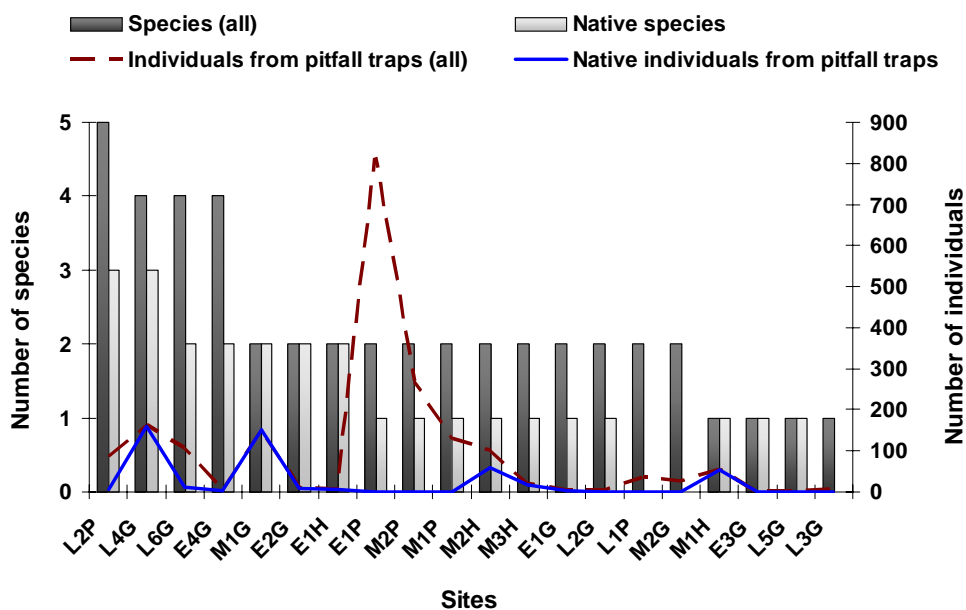


Fig. 2. Numbers of isopod species and pitfall trapped individuals in the examined laurel forest sites. The sites are listed from highest to lowest species numbers.

STUDY AREA, METHODS AND MATERIAL

STUDY SITES

The examination presented here is confined to La Palma, El Hierro, and La Gomera (Fig. 1). We selected 12 study sites on La Gomera, 5 on La Palma and 4 on El Hierro corresponding with the actual forest area of the different islands. All sites were located in the “Laurel forest” vegetational zone (Del-Arco *et al.*, 1999) characterized by potentially similar vegetation, soil conditions and comparable climatic conditions. The sites selected differ in age, human impact, elevation (metres above sea level; m a.s.l.), and aspect. Detailed

characteristics of sites are given in Table I, but the following major categories reflecting the degree of human influence on the vegetation can be summarized:

L: Nearly natural forest sites with old trees dominated by *Laurus* and *Persea*. Such natural forests have disappeared completely on Gran Canaria, and on El Hierro they are restricted to a very small area.

M: Secondary forests, where parts of the laurel trees were removed (Del-Arco et al. 1999; Hohenester & Welss 1993; Pérez de Paz et al., 1990; “fayal-brezaI” in Canarian terminology), often dominated by *Myrica*. *Myrica*- and *Erica* dominated forest plots might generally be regarded as a successional stage following removal of the natural laurel forest. However, native late successional *Myrica-Erica* stands exist on La Gomera in the upper, cooler and drier region of the laurel zone on the mountain ridges. These native *Myrica-Erica* forest plots are very rare, the only examined study site is M1G.

E: Sites dominated by *Erica* and partly covered with *Ilex* describe young tertiary forests with pioneer vegetation. The examined sites are 15-40 years old.

Island	La Gomera												El Hierro				La Palma				
	E1G	E2G	E3G	E4G	L1G	L2G	L3G	L4G	L5G	L6G	M1G	M2G	M1H	M2H	M3H	E1H	E1P	L1P	L2P	M1P	M2P
Tree layer total [%]	60	90	75	60	90	75	76	80	85	90	80	50	60	85	85	50	80	80	95	85	85
<i>Laurus novocanariensis</i>	18	0	5	0	70	35	65	77	70	46	0	8	0	0	0	0	20	40	95	60	50
<i>Ocotea foetens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0
<i>Persea indica</i>	0	0	0	0	0	34	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilex canariensis</i>	0	0	10	5	5	0	3	1	0	4	0	10	0	0	0	0	12	0	0	0	0
<i>Erica arborea</i>	36	80	55	40	0	0	0	1	0	12	50	12	6	17	8.5	40	24	0	0	0	17
<i>Myrica faya</i>	6	10	5	10	5	0	3	1	0	3	30	12	54	68	76.5	10	24	0	0	17	18
<i>Viburnum rigidum</i>	0	0	0	5	10	6	0	0	7	25	0	8	0	0	0	0	0	0	0	0	0
<i>Rhamnus glandulosa</i>	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pinus canariensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0
Herbaceous layer total [%]	50	80	2	5	35	50	50	10	5	5	75	80	90	85	15	30	10	10	10	5	30
Litter layer [cm]	0.5	0	1	1	8	8	8	8	1.5	2	1	2	3	1.5	7.5	0	3	1	10	3	3
Location (m.a.s.l.)	1000	1200	1000	800	800	950	950	1300	1000	1000	1350	800	1300	1200	860	860	1000	600	700	1200	1200
Age	40	50	16	30	100	100	100	100	100	100	100	8	100	30	15	15	30	100	100	60	60
PDSI [cal/cm ² /day]	510	690	648	572	476	607	550	417	682	702	369	500	652	607	514	514	637	587	551	551	587

Tab. I. Vegetation and ecological data of examined study sites. PDSI: potential direct solar insolation.

L, M, and E represent the first letters of site code in Table I.

G, H and P indicate the specific islands (La Gomera, El Hierro or La Palma respectively).

DATA SAMPLING

Isopods were collected using pitfall traps and soil samples. Pitfall traps were used to sample the mainly surface active specimens. Five traps (plastic cups, 65 mm diameter, containing a 5% acetic acid/salt mixture) were placed in one line about 3-4 m distant from each other. The traps were run for three weeks each in March and in August and were checked weekly. The sampling took place on La Gomera (10 sites) and La Palma in 2002 as well as on La Gomera (2 further sites) and El Hierro in 2003. Leaf litter accumulated in few cases during stormy weather conditions and made it impossible to use some traps. Therefore, the pitfall samples of all sites were scaled to “100 trap days”.

The mainly endogenous fauna was examined with soil samples. For this purpose, eight soil samples (25x25x15 cm) were taken per site (five in March, three in August, same period as pitfall traps). The soil samples were brought to the laboratory and carefully searched for invertebrates ≥4mm using shovel, tweezers and a stereo microscope. All specimens were transferred to 70% EOH, counted and identified.

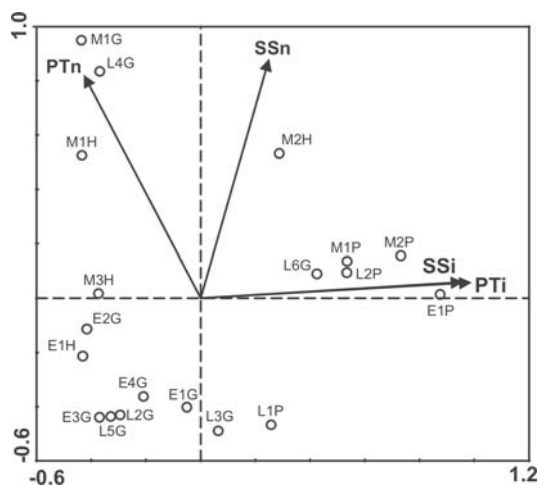


Fig. 3. Principal component analysis (log-ratio PCA) of native and invasive isopod species in laurel forest of the three Western Canary Islands. Circles indicate the examined sites. i – invasive species, n – native species, PT – pitfall traps, SS – soil samples.

DATA ANALYSIS

Pearson correlation analyses were used to examine the relationship between incidence and abundance of recorded isopod species and several environmental factors: coverage of tree species (*Erica arborea*, *Myrica faya*, *Laurus novocanariensis*, tree cover as a whole), coverage of herb stratum, leaf litter, age of forest site, altitude, and potential insolation.

A log-ratio PCA (Ter Braak & Šmilauer, 2002) was applied to visualize the distribution pattern of sampled native and invasive isopods. For this purpose we separately summarized the abundances of native and invasive species per study site. Subsequently the data were log-transformed and centered by the species groups.

The Discussion chapter refers to the calculation of generalised linear models (GLMs, Crawley, 2002). The proportion of invasives [invasives/(invasives + natives)] was modelled for each sample method using abundances as well as species numbers of isopods and the aforementioned environmental parameters.

RESULTS

SPECIES NUMBERS AND COMMUNITIES

Eleven species of terrestrial isopods were recorded in the laurel forests of the western three islands (Tab. II). The results from pitfall traps differ distinctly from those of soil samples. Surface-active species like the pillbugs (Armadillidiidae) are over-represented but ground dwelling species like Trichoniscidae are under-represented in the pitfall traps.

Four species were sampled exclusively from pitfall traps: *Agabiformis lentus* Budde-Lund, *Porcellio* sp.n., *Soteriscus stricticauda* (Dollfus), and *Ctenorillo ausseli* (Dollfus).

Haplophthalmus danicus Budde-Lund and *Trichoniscus pygmaeus* Sars were recorded in soil samples but not in pitfall traps.

No significant correlation was seen between the abundance of any isopod species and any of the examined environmental factors. This indicates that neither the laurel forest type nor the anthropogenic influence (reflecting the age of the forest site and the proportion of secondary trees) significantly affect the species composition of isopods.

However we found clear differences between the forest fauna of the different islands. Forests of El Hierro and La Gomera are dominated by *Porcellio meridionalis* Vandel (Tab. II). *P. meridionalis* was recovered in all but 4 of the 16 sites sampled at El Hierro and La Gomera; these 4 sites were characterized by the highest coverage of *Ilex canariensis* (3-10%). Because *P. meridionalis* is lacking or extremely rare on all sites with more than 2 % coverage of *Ilex*, this tree may render habitats which are not suitable for *P. meridionalis*. *Ilex canariensis* as pioneer tree species is often connected with open forest sites and heat benefiting conditions. The largest abundances of *P. meridionalis* were reported at sites located above 1200m a.s.l. under cool and moist conditions. The mean annual potential radiation in these sites is 369-417 cal/cm²/day (Tab. I). The average of potential radiation of all sites was much higher on La Gomera (566 cal/cm²/day).

Armadillidium vulgare (Latreille) dominated the study sites on La Palma. It occurred on La Palma at all sites in extreme abundances, whereas it was collected only from 3 of the 16 sites

Island	La Gomera													El Hierro				La Palma				
Site	E1G	E2G	E3G	E4G	L1G	L2G	L3G	L4G	L5G	L6G	M1G	M2G	M1H	M2H	M3H	E1H	E1P	L1P	L2P	M1P	M2P	
Pitfall traps																						
<i>Agabiformis lentus</i>	I	0	0	0	0	0	0	0	0,9	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Armadillidium vulgare</i>	I	0	0	0	1	0	0	0	0	0	20	0	19,7	0	0	0	812,2	32	50,1	127,8	267,2	
<i>Ctenoscia minima</i>	N	0	0	0,8	0	0	0	0	1,8	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eluma caelatum</i>	I	2,3	0	0	2,9	0	0,8	6,3	0	0	70,8	0	6,06	0	41,58	0,77	0	0	2,9	35,5	0	0
<i>Porcellio meridionalis</i>	N	1,5	0	0	1	0	0,8	0	157,4	0	4,2	144,3	0	54,27	60,06	17,71	6,16	0	0	0	0	0
<i>Porcellio septentrionalis</i>	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6,4	0	0
<i>Porcellio sp. n.</i>	N	0	1,0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Soteriscus stricticauda</i>	N	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ctenorillo ausseii</i>	N	0	7,6	0	0	0	0	0	0,9	0	6,7	7,4	0	0	0	0	0,77	0	0	0	0	0
Soil samples																						
<i>Armadillidium vulgare</i>	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16,1	0,3	2,25	1,75	7,12	
<i>Ctenoscia minima</i>	N	0	0	0	0	0	0	0	0,375	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eluma caelatum</i>	I	1,2	0	0	0	0	0	0,75	0	0	5,75	0	1,7	0	4,125	0	0	1,1	4,1	0	0	0
<i>Haplophthalmus danicus</i>	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10,6	0	0
<i>Porcellio meridionalis</i>	N	0	0,125	0	0	0	0	0	10	0,2	0,25	20,875	0	3,125	1,25	0	0	0	0	0	0	0
<i>Porcellio septentrionalis</i>	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,38	0	0
<i>Trichoniscus pygmaeus</i>	N	0	0	0	0	0	0	0	0	0	0	0	0	0,25	0,125	0	2,1	0	0,12	6,88	6,75	

Tab. II. List of recorded Isopoda in laurel forests of the western Canary Islands. Results of pitfall traps were scaled to 100 trap days, those of soil samples are listed in average numbers per sample. I-invasive, N-native.

sampled on the other two islands (Tab. II). Several species of *Porcellio* were described from La Palma as well, but only *P. septentrionalis* Vandel occurred at our study sites in low abundances. A *Porcellio* species with comparable abundance to that of *P. meridionalis* on La Gomera and El Hierro is lacking in the examined forest plots of La Palma. Warm localities in lower forest parts on La Palma could support the invasion of *A. vulgare*. The site with the largest abundance of *A. vulgare* has a yearly potential radiation of 637 cal/cm²/day (average of all sites on La Palma is 582 cal/cm²/day). Laurel forests of La Palma are furthermore characterized by a comparable high portion of subterranean trichoniscids. There were recorded up to 72 *Haplophthalmus danicus* and 26 *Trichoniscus pygmaeus* in a single soil sample. These

trichoniscids were only active in winter and spring and disappeared during summer presumably moving deeper within the B soil horizon.

ECOLOGICAL RELATIONS BETWEEN NATIVE AND INVASIVE ISOPOD SPECIES

The majority of species recorded in the laurel forests are endemic to the Canary Islands. In contrast, invasive species dominate quantitatively in many study sites (Tab. II). The average relation of invasive:native specimens was 3.1:1 in pitfall traps and 1.1:1 in soil samples. The quantitative dominance of introduced species in pitfall traps shows Fig. 2. The sites with the largest individual numbers of isopods were those without native isopods, while the sites yielding the largest species numbers had comparatively fewer individuals.

DISCUSSION

Regarding species' abundances, the isopod fauna in Canarian laurel forests is dominated by introduced species. *Armadillidium vulgare*, *Eluma caelatum* (Miers), *Agabiformis lentus*, and probably all Canarian *Haplophthalmus* species have their origin in Europe or the mainland Mediterranean region and were introduced to the islands by man in historical times (Vandel 1954 and own studies). Some of these representatives are distributed over large parts of the world today. All introduced isopods are invasive species in the sense of Williamson (1996).

The quantitative dominance of introduced isopods in the surface active fauna raises several questions: (i) How do they interact with native species? (ii) Does competition occur between native and invasive species? (iii) Which factors do patterns of invasion control.

Pimm (1991), Tilman (1999) and other ecologists supported the diversity invasibility hypothesis (DIH, founded by Elton, 1958) basing on invasive plant species. This hypothesis describes the relation between an increasing number of invasives in ecosystems with a decreasing number of native species. A similar context is known as diversity-resistance-hypothesis (Kennedy *et al.*, 2002) describing a strong resistance against invasive species in ecosystems with high biodiversity. Both aspects of the hypothesis were not investigated using terrestrial invertebrate animals in the past. Our study showed that the diversity of native isopod species is not significantly (negative) correlated with the diversity of invasives in Canarian laurel forests. Therefore our data set does not support the invasion theory which is based on plant community studies. The invasion success of invasive isopods is rather negatively correlated with altitude but positively related to potential insolation which reflects climatic conditions (Fig. 4). This means that invasive isopods benefit from the warm climate in lower altitudes and disappear in the cold and moist upper regions of the forests.

The questions of interaction and competition between species cannot be answered with our data set sufficiently. However, we analysed the pillbugs (*A. vulgare*, *E. caelatum*) as the most common invasive species to approach these questions. Both pillbug species occur in heat-benefiting forest plots in highest abundances but are not able to invade the cooler sites with low potential radiation. The latter are north-slopes or sites higher than 1000 m a.s.l. Additionally, *A. vulgare* seems to benefit by ambient factors: it is monodominant in settlements, gardens and meadows used by agriculture (Arndt, unpubl.).

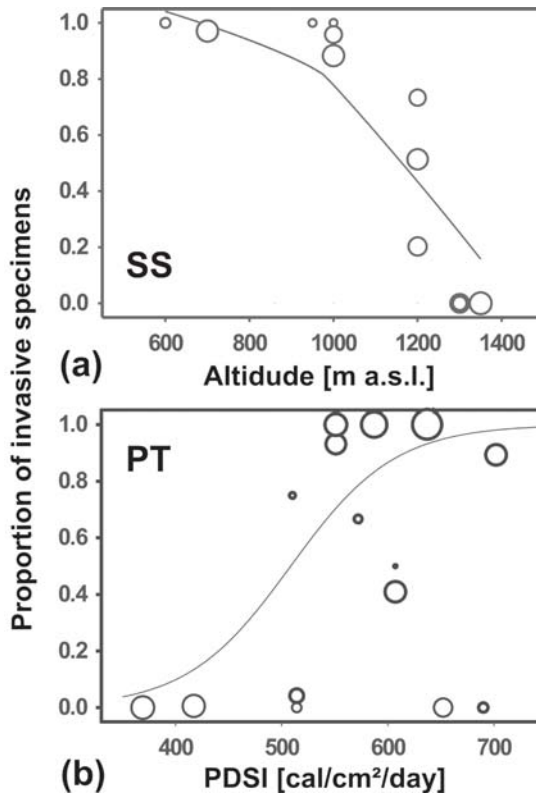


Fig. 4. Proportion of invasive isopod specimens in Canarian laurel forests related to environmental parameters, calculated using generalised linear models. Only significant relations are figured. PDSI - potential direct solar insolation; PT - pitfall trap; SS - soil samples. The invasion success is significantly correlated to altitude (negatively) and potential radiation (positively) as climatic parameters, but not to tree species, litter layer or disturbance parameters.

A. vulgare is surely able to penetrate the forests from these sites. Competition between species of *Porcellio* and *A. vulgare* as implicated by Dangerfield (1989) and Hassall & Dangerfield (1989) cannot be ruled out. Laboratory and field data of these authors indicate a decrease of the *A. vulgare* population in co-existence with *Porcellio scaber* Latreille. The supposed reason of this competitive decrease is a “disturbance factor”. *A. vulgare* and *P. meridionalis* are largely exclusive on La Gomera and El Hierro. They co-occur only at 2 of 16 sites. Though climatic factors may be one reason for that, an influence of competition cannot be excluded.

This examination concerned only isopods of one forest type on the islands. The identification of a new species and the not expected high proportion of invasive species illustrate the need of further studies to complete our knowledge of Canarian isopods. As a next step, a comparison between the isopod fauna in forests on Tenerife and the relict

laurel forests on Gran Canaria with that of the western islands is needed. Finally the drier habitat types and settlements should be examined in detail.

ACKNOWLEDGEMENTS

We want to thank Ángel Fernández and co-workers (Garajonay National Park, La Gomera), José-María Fernández Palacios (University of La Laguna, Tenerife), and Antonio Machado (University of La Laguna, Tenerife) for the support of our field work. Birte Wisser, Michael Klemm, Pierre Angelo Cocco, and Stephan Fiedler (Anhalt University, Bernburg, Germany) carried out most of the field work spending much of their time in the project. J. Perner (University of Jena) was an irreplaceable help in advising us concerning statistical methods. Finally we thank Jonathan C. Wright (Claremont, U.S.A.) for proof reading and valuable remarks. G. Delgado Castro (Museum of Natural Sciences, S/C de Tenerife) prepared the Spanish resumen which we kindly appreciate.

REFERENCES

- ARCANGELI, A. (1958). La Fauna Isopodologica Terrestre degli Arcipelaghi di Madera e delle Canarie: la sua importanza per la sistematica e la biogeografia. *Memórias e estudos do museu zoológico da universidade de coimbra* 255: 108pp.
- CRAWLEY, M. J. (2002). *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. John Wiley and Sons, Chichester.
- DANGERFIELD, J. M. (1989). Competition and the effects of density on terrestrial isopods. *Monitore zoologico italiano (N.S.) Monogr.* 4: 411-423.
- DEL-ARCO, M., J.-R. ACEBES, P.-L. PÉREZ-DE-PAZ & M. C. MARRERO (1999). Bioclimatology and climatophilous vegetation of Hierro (part 2) and La Palma (Canary Islands). *Phytocoenologia* 29: 253-290.
- ELTON, C. S. (1958). *The ecology of invasion by animals and plants*. Chapman & Hall, London.
- HASSALL, M. & J. M. DANGERFIELD (1989). Inter-specific competition and the relative abundance of grassland isopods. *Monitore zoologico italiano (N.S.) Monogr.* 4: 379-397.
- HOHENESTER, A. & W. WELSS (1993). *Exkursionsflora für die Kanarischen Inseln*. Ulmer, Stuttgart 374 pp.
- KENNEDY, T. A., S. NAEEM, K. M. HOWE, J. M. H. KNOPS, D. TILMAN & P. REICH (2002). Biodiversity as a barrier to ecological invasion. *Nature* 417: 636-638.
- MARTIN, J. L., M. MARRERO, N. ZURITA, M. ARECHA VALETA & I. IZQUIERDO (2005). Biodiversidad en gráficas. Especies Silvestres de las Islas Canarias. Consejería de Medio Ambiente y Ordenación Territorial. Gobierno de Canarias. 56 pp.
- PÉREZ DE PAZ, P. L., M. DEL-ARCO, J. R. ACEBES, & W. WILDPRET (1990). La vegetación cormofítica (vascular) del Parque Nacional de Garajonay, pp. 137-172. In: Pérez

- de Paz, P. L. (ed.) *Parque Nacional de Garajonay*. Patrimonio Mundial. ICONA y Excmo. Cabildo insular de La Gomera.
- PIMM, S. L. (1991). *The balance of nature?* University of Chicago Press, Chicago.
- RODRIGUEZ, R., P. OROMI & N. ZURITA (2004). Isopoda, Decapoda. In: IZQUIERDO, I., J. L. MARTIN, N. ZURITA & M. ARECHAVALETA (eds.). *Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres)*. Consejería de Medio Ambiente y Ordenación Territorial. Gobierno de Canarias, p. 175-176.
- RODRIGUEZ, R. & M. C. VICENTE (1992a). Las especies de *Porcellio* Latreille, 1804 del grupo *laevis* en las Islas Canarias, con la descripción de *Porcellio ancaramum* n. sp. (Oniscidea, Porcellionidae). *Boletín de la asociación española de entomología*, 16: 227-241.
- RODRÍGUEZ, R. & M. C. VICENTE (1992b). *Soteriscus trilineatus* n. sp. de Isópodo terrestre de las Islas Canarias (Oniscidea, Porcellionidae). *Zoologica Baetica, Granada* 3: 191-198.
- RODRÍGUEZ, R. & M. C. VICENTE (1992c). *Porcellio eserensis* sp. n. of terrestrial Isopods from Canary Islands (Isopoda, Oniscidea, Porcellonidae). *Bocagiana*, 162: 1-7.
- TER BRAAK, C. J. F. & P. ŠMILAUER (2002). CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY.
- TILMAN, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80: 1455-1474.
- VANDEL, A. (1954). Étude des isopods terrestres recueillis aux îles Canaries. *Memoires du Museum National d'histoire Naturelle, Série A, VIII*: 1-60.
- WILLIAMSON, M. (1996). *Biological invasions*. Chapman & Hall, London etc., 256pp.