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SPECIES/AREA AND OTHER RELATIONSHIPS IN LAND SNAIL (MOLLUSCA: GASTROPODA TERRESTRIA) FAUNAS OF SOME ADRIATIC ISLANDS

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Data from a number of surveys of land snails on islands off the Adriatic coast of Croatia are used to investigate the nature of the island species-area relationships (ISARs) both among larger islands and, in greater detail, among 83 islets in the Kornati archipelago. These islands and islets are all continental, and separated from the mainland no more than 10,000 years ago. In both cases there are significant positive ISARs, but in the case of the islets the slope of the log/log regression is shallow ($z = 0.131$) relative to most reported ISARs from elsewhere. Island area and altitude are very strongly correlated, and it is impossible to distinguish between an effect due to area alone and one related to a greater range of habitats on higher islets. Despite the very small size of some islets, there is no evidence for any Small Island Effect. Increasing isolation does not result in impoverishment. Snail species differ in the extent to which they are more likely to occur on large islands; while many show a strong association with island area, others, especially some not restricted to rocks, do not. The faunas are not strongly nested and some species found on small islets are not found on some larger ones, or on the much larger Kornat Island itself. Single site faunas on small islets are not much poorer than those from single sites on larger islands. We interpret the pattern as being mainly the product of long-term survival through the period of island formation, but we cannot rule out the possibility of some passive transport by humans.

Key words: land snails, Adriatic, islands, island species-area relationship (ISAR), Small Island Effect (SIE)

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Da bi se proučili odnosi vrsta i površine većih, a naročito manjih otoka (ISAR – Island Species-Area Relationship), u radu su korišteni podaci iz istraživanja kopnene malakofaune nekoliko većih otoka i 83 otočića Kornatskog arhipelaga, svih smještenih u hrvatskom dijelu Jadrana. Svi ti otoci i otočići su kontinentalnog porijekla odvojeni od matičnog kopna oko 10 000 godina. Veliki otoci, a isto tako i otočići imaju značajni pozitivni ISAR. U odnosu na većinu objavljivanih ISAR-a, iz različitih geografskih područja, naši istraživani otočići ističu se malim nagibom pravca linearne regresije u logaritamskom obliku ($z = 0{,}131$). Površina i nadmorska visina otočića su u jakoj pozitivnoj korelaciji. Zbog toga nije moguće odvojiti učinak same površine od učinka većeg raspona staništa koji postoji na višim otočićima. Usprkos veoma maloj površini nekih otočića, nema dokaza za postojanje učinka malih otoka (Small Island Effect). Povećanje izolacije nije dovelo do osiromašenja malakofaune. Postoje razlike u sklonosti pojavljivanja vrsta puževa na velikim otocima; dok mnoge pokazuju vezanost za veličinu otoka, druge, pogotovo one koje nisu vezane za stijene, neovisne su o njoj. Faune nisu izrazito nadopunjavajuće, pa neke vrste nađene na malim otočićima nisu nađene na većim otočićima, pa čak i na najvećem otoku u arhipelagu, otoku Kornatu. Faune pojedinih lokaliteta na malim otočićima nisu znatnije siromašne od faune lokaliteta većih otoka. Dobiveni rezultati prvenstveno su posljedica dugog opstanka puževa na otocima, ali ne možemo isključiti i poneku mogućnost pasivnog transporta putem čovjeka.

Ključne riječi: kopneni puževi, Jadran, otoci, odnos vrsta/površina na otocima (ISAR), učinak malih otoka (SIE)

INTRODUCTION

The increase in the number of species as the area examined increases, the species/area relationship (SAR) has been claimed as one of the few universal relationships seen in biogeography and ecology (Lomolino, 2000). Such SARs vary with scale and circumstances, and their precise form also depends on properties of the taxa considered (Rosenzweig, 1995). As attention has moved from description to interpretation of such relationships, the particular case of islands (ISARs) has become a focus for many studies, starting with the seminal model of Macarthur & Wilson (1967). That model focused on the processes of extinction, colonisation and persistence, relating them to island size and isolation. While "wrong in interesting ways" (Whittaker, 2001), it stimulated many other studies designed to elucidate the mechanisms determining the richness of island fauna and flora.

Many of these later studies discussed influences applicable to all kinds of islands, such as the effect of habitat diversity (Triantis *et al*., 2003), altitude (Solem, 1973), the existence (or not) of a Small Island Effect (Lomolino & Weiser, 2001; Triantis *et al*., 2006) and island history in terms of age and changing size (Whittaker & Fernández-Palacios, 2007). The differing powers of dispersal and minimum area requirements of different taxa have also been considered (Lomolino, 2000; Whittaker & Fernández –Palacios, 2007).

Most attention in these studies, however, has been given to oceanic islands and archipelagos (Whittaker *et al*., 2008), and perhaps more generally to islands in which independent evolutionary processes generate endemic species. Less attention has been paid to those continental islands that were a part of a mainland until geologically recent times, where isolation is a consequence of rising sea levels in the Holocene. Here, while immigration is still a factor, the decrease in size and connectedness of islands over time may result in an extinction debt (Rosenzweig 1995; Ewers & Didham 2005; Triantis *et al*. 2010; Halley *et al*. 2014), a lag in the achievement of an equilibrium resulting from both stochastic events and the loss of habitats required by particular species.

The Adriatic coast of Croatia holds more than one thousand islands and islets (DRŽAVNI ZAVOD ZA STATISTIKU RH, 2009), ranging in size from a few m^2 up to islands such as Cres (406 km^2) or Brač (395 km^2). These are continental islands isolated from the Croatian mainland by rising sea levels in the late Pleistocene and early Holocene, and it is unlikely that any island has been isolated for more than about 10,000 years. In this study we report on the land snail faunas of some of the larger islands and on 83 smaller islets in the Kornati archipelago, ranging in size from 874 m^2 to 2.8 km^2. Although there are a few nominally endemic species or subspecies, the snail faunas of these islands are largely subsets of that found on the mainland. We examine the ISARs both among the larger islands and in particular among the Kornati islets themselves and in relation to their larger neighbour Kornat (32.5 km^2). We use these to examine the roles of area, altitude and isolation on the land snail faunas, the existence or not of a Small Island Effect and the potentially differing responses of species related to their traits.

MATERIALS AND METHODS

Area and material

Data used in this study are restricted to those obtained in our own published studies where the same methods of collecting and laboratory techniques were used (Štamol 1986; Štamol & Velkovrh, 1995; Štamol & Poje, 1998; Štamol, 2004; Štamol & Kletečki, 2005; Štamol *et al.*, 2012). The data refer to the islands of Cres, Susak, Dugi otok, Kornat and Brač, and the islets of the Kornati archipelago (Fig. 1). Most of these Adriatic islands date from some 10,000 years ago when the sea level rose by 100 meters, the valleys were flooded and only higher parts of a once continuous land mass remained above water. The underlying rock of these islands is mostly limestone, and to a smaller extent dolomites of the Cretaceous period. The climate is typically Mediterranean, with long, hot and dry summers, and mild and rainy winters. In the north and at higher altitudes in the south there is a stronger influence of continental climate, and besides the eumediterranean there also exists the submediterranean vegetation zone at higher altitudes. The climax vegetation of the eumediterranean zone is holm oak forest (ass. *Orno-Quercetum ilicis*); this has mostly been destroyed and is now represented by degraded forms – macchia, garrigue, and grassland vegetation. Forest vegetation is virtually absent from Kornat and its associated islets. Among the larger islands surveyed Cres has the northernmost position and belongs to the so-called Kvarner area, while Brač in central Dalmatia is the furthest south. Within the Kornati archipelago we investigated 97 islets and rocks (further: islets) of which 88 are situated in the Kornati National Park, and 9 within the boundaries of Telašćica Nature Park. While varying in altitude, all islets are predominantly rocky; the higher ones hold more substantial vertical cliffs. Not all islets held snails (see below). More details about natural characteristics, positions of researched localities and faunistic results were published earlier (Štamol, 1986; Štamol & Velkovrh, 1995; Štamol & Poje, 1998; Štamol, 2004; Štamol & Kletečki, 2005; Štamol *et al.*, 2012). The names of islets are taken from Croatian topographical maps at the scale 1:25,000. The species list for islets of the Kornati archipelago is given in the Appendix.

Sampling

Samples were made within restricted areas by a team of 2–3 people, always including the first author. A visual search was supplemented by the collection of soil and litter for later examination in the laboratory. Single searches of this kind are inadequate for slugs (Cameron & Pokryszko, 2005), and slugs are excluded from our analyses. The number of sites sampled varied with the size of the island; small islets were usually represented by a single sample. Where more than one sample was made, the sites were arranged to maximise geographical spread and the range of visible habitats. We note that although variation in the number of samples among islands may affect the parameters of a derived ISAR, such proportional sampling is recommended by Schoereder *et al.* (2004), and its effects can be factored out to examine variation in site diversity.

Specimens were identified to species wherever possible. In a very few cases in the Kornati islets, species were represented by juvenile shells that were clearly distinct from others in the sample, but not certainly identifiable to species. In such cases the aggregate total of species for the site included such shells, but in considering the fauna of the archipelago as a whole only identified species were considered. It is almost certain that these unidentified shells belong to species identified with certainty on other islets.

Data analysis

Relationships between species richness, area, altitude and isolation were analysed using the Power Function Model (PFM), which appears to be the most reliable among the many possible methods (Triantis *et al.*, 2012). It is expressed as logarithmic equations in the form Log y = z log x + log c, where y = species richness, z = the slope of the regression, x = the independent variable. The intercept, c, is scale dependent; it is not considered further. For the larger islands a simple SAR based on planar area (km^2) was used. For Kornati islets, regressions of species richness on area (ha), altitude and isolation were carried out. Equations and their coefficients of determination (R^2) are given either within the relevant figures or in tabular form. The effect of sampling intensity among the islets was investigated first by examining the relationship between the residuals of the ISAR and the number of samples, and secondly by examining the ISAR among islets subject to the same sampling intensity.

For Kornati islets the ISAR analysis was done initially both using planar areas taken from polygons defined in the central register of regional units available from Croatian State Geodetic Administration (http://geoportal.dgu.hr/) and using total surface area allowing for topography. The latter was estimated using ArcGIS 10 (ESRI, 2011) with the "Interpolate

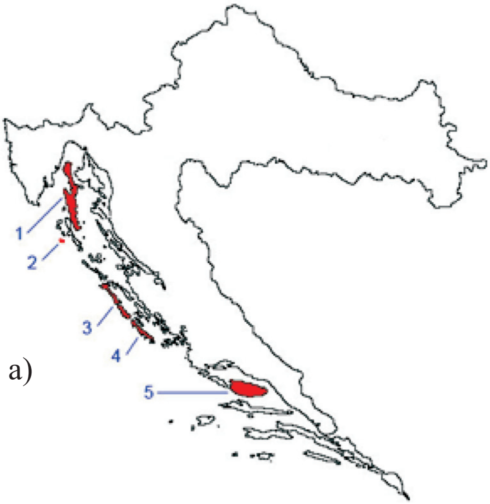

Fig. 1. a) Map of Croatia showing the location of islands used in this study (1. Cres; 2. Susak; 3. Dugi otok; 4. Kornat; 5. Brač). **b)** The inset shows Kornat and the Kornati archipelago in more detail.

Tab. 1. Details of the large islands studied. I_w, Whittaker's Index; I_{max}, Whittaker's Index using richest site (see text).

Island	Area (km²)	Max height above sea level m	No. of localities	No. of species	Mean spp /site	Max spp/ site	I_w	I_{max}
Susak	3.75	98	8	23	10.9	18	2.1	1.3
Kornat	32.51	237	68	31	8.7	17	3.6	1.8
Dugi otok	114.44	338	102	44	9.8	20	4.5	2.2
Brač	394.57	780	25	43	11	20	3.9	2.1
Cres	405.78	650	70	60	8.5	25	7.1	2.4

polygon to Multipatch" tool. To create the digital elevation model (DEM) and three-dimensional triangulated irregular network (TIN) from which the surface area was calculated, elevation points were digitized from 1:5,000 topographic maps. The total surface area ISAR gave a marginally better fit to the data (higher R^2), and has been used in subsequent analyses and discussion. Within the Kornati archipelago, isolation or distance from a possible source for each islet was measured in two ways: i) distance from Kornat island, the largest land mass in the archipelago, and ii) distance to the closest larger islet, or Kornat itself if closest, because the larger islet is a more probable source than the smaller.

Following Cameron & Pokryszko (2005), for the larger islands heterogeneity in fauna among samples was estimated using Whittaker's Index (I_W) and its variant (I_{max}), where $I_W = S_A / S_L$, and $I_{max} = S_A / S_{max}$ where S_A is the recorded species richness for the island, S_L is the mean number of species per site and S_{max} is the richness of the richest site.

RESULTS

1. The larger islands

Tab. 1 lists the islands sampled, their planar areas and their recorded land snail faunas. The ISAR equation, $\log S = 0.176 \log A + 1.254$, though based on only five islands has a high coefficient of determination of 0.884 and is formally significant ($P < 0.05$). While the mean richness per site and the number of species in the richest site differ only slightly among islands, the values of both variants of Whittaker's Index indicate considerable heterogeneity among sites in the larger islands.

2. The Kornati islets

(a) Associations with species richness

Tab. 2 gives details of all the 83 Kornati islets on which snails were found. A further 14 (mostly very small or very exposed) islets proved unsuitable for snails. Fig. 2 shows the ISAR based on total surface area. The equivalent regression of $\log_{10}$ species on $\log_{10}$ altitude gave a very similar relationship, but with a marginally higher coefficient of determination (0.510). Altitude and area are very strongly correlated ($R^2 = 0.845$, $P \ll 0.001$), and the residuals of the relationship with area do not relate to altitude ($R^2 = 0.019$). The relationship with area has been used in most subsequent analyses so that slopes can be compared with other studies.

Tab. 2. Details of islets in the Kornati archipelago on which snails were collected. Distances to the nearest refer to the nearest larger islet, or, where this is closer, to Kornat.

Islet	Planar area (ha)	Total area (ha)	Altitude (m)	Distance from nearest (m)	Distance from Kornat (m)	Number of sites	Number of species
Aba donja	38.85	40.00	54.6	1,400	1,400	3	15
Abica	3.26	3.48	28	1,400	5,000	1	14
Arapovac	1.05	1.07	10	1,200	2,300	2	12
Babina guzica	1.26	1.31	17.3	4,600	16,000	1	9
Balun	5.27	5.44	29	600	8,400	3	10
Bisaga	9.32	9.48	21	2,400	2,400	3	13
Bisaga II	0.61	0.66	9	500	2,300	1	10
Blitvica	0.52	0.54	8	1,000	3,300	1	11
Borovnik	28.08	29.04	55.8	700	6,100	2	9
Buč mali	2.84	3.05	25	800	1,400	1	11
Buč veli	10.56	11.17	42	200	200	2	11
Desetinjak južni	0.27	0.27	2	200	12,200	1	3
Dragunara	1.79	1.89	18	900	2,400	1	14
Garmenjak mali	5.08	5.24	28	600	11,000	3	13
Garmenjak veli	13.28	13.81	53	2,300	12,500	3	12
Golić	1.02	1.04	5.9	600	2,800	1	7
Gominjak	25.76	26.78	62.4	1,100	12,400	3	13
Gornja Aba	22.88	23.94	75	1,700	4,500	3	14
Gustac, Lavsa	28.53	29.96	78	900	7,000	2	6
Gustac, Piškera	28.47	29.35	43	1,100	1,100	2	13
Hrid Kaselica	0.24	0.27	9	1,100	10,000	1	7
Hrid Katinica	0.09	0.09	2	1,100	1,600	1	6
Jančar	6.36	6.47	18	500	9,400	1	8
Kameni puh	0.75	0.76	8	1,800	30,000	1	9
Kameni Žakan	33.15	33.66	30	2,600	7,700	4	10
Kasela	34.72	36.19	61	4,000	7,500	2	15
Katina	114.21	119.81	116.5	500	500	5	17
Klobučar	10.84	12.40	83	300	10,400	3	5
Koritnjak	11.71	12.28	46	1,000	1,000	4	11
Krpeljina	1.37	1.55	17	1,300	1,300	1	8
Kurba vela	174.32	185.17	116.9	10,500	10,500	18	15
Lavsa	177.50	184.23	111.2	500	4,600	6	20
Levrnaka	184.23	191.91	117.2	600	600	9	17
Lucmarinjak	10.21	10.72	43.3	3,500	26,000	1	10
Lunga	62.08	65.20	80	5,500	7,300	5	12
Mala Aba	0.08	0.09	4	400	4,700	1	5
Mali Babuljaš	0.37	0.37	7	1,100	4,100	1	6
Mana	41.17	43.93	77	5,400	6,400	5	14
Maslinjak	6.53	6.86	39	2,000	2,000	3	14
Mrtovac	5.98	6.56	31.7	1,000	8,000	2	12
Mrtovnjak	9.87	10.27	41.6	8,600	26,200	3	11

Tab. 2. Continued.

Islet	Planar area (ha)	Total area (ha)	Altitude (m)	Distance from nearest (m)	Distance from Kornat (m)	Number of sites	Number of species
Obručan mali	0.61	0.88	24	800	7,800	3	12
Obručan veli	10.15	11.16	67	200	6,300	3	13
Oključ	36.02	38.21	68	2,500	15,500	4	12
Otok Puh	1.35	1.41	14	3,800	27,900	1	11
Panitula mala	3.21	3.69	28	1,100	10,000	3	8
Panitula vela	15.67	16.40	32	300	1,100	2	8
Piškera	267.72	280.42	126.2	4,700	4,700	9	14
Plešćina	4.03	4.21	26	1,100	5,300	3	11
Prduša mala	2.72	2.82	23	900	10,700	1	11
Prduša vela	4.81	4.95	23	1,700	8,600	3	12
Prišnjak mali	0.65	0.69	11	1,000	8,500	1	9
Prišnjak veli	9.20	9.64	34.7	1,800	7,700	3	11
Puh gornji	0.80	0.82	8	900	29,200	1	5
Purara	2.91	3.15	30.4	7,200	17,500	1	10
Rašip mali	15.87	16.93	56.3	2,700	5,600	3	13
Rašip veli	25.91	28.20	62	1,500	5,800	3	11
Rašipić	1.12	1.13	9	800	7,500	2	7
Ravna Sika	3.98	4.22	28	1,300	1,300	2	11
Ravni Žakan	31.07	31.47	36.4	500	5,200	4	13
Samograd	4.51	4.94	33.4	9,900	36,600	2	14
Sestrica mala	2.97	3.21	30	600	7,100	2	12
Sestrica vela	9.50	10.31	55.4	4,100	7,700	4	18
Šilo malo	2.14	2.17	8	400	1,200	3	6
Šilo velo	68.39	70.19	62	1,200	1,200	3	13
Skrižanj mali	1.44	1.46	9	200	23,900	1	6
Skrižanj veli	7.64	7.77	18	3,300	24,600	3	9
Škulj	88.67	94.99	145.04	2,400	3,700	9	14
Smokvenjak	8.09	8.40	41	500	500	3	11
Smokvica mala	1.13	1.14	6	1,000	9,500	1	4
Smokvica vela	106.28	109.79	94	2,800	2,800	6	18
Strižnjak	2.68	2.71	14	700	700	2	8
Sušica	6.02	6.30	17	200	2,100	3	12
Svršata mala	1.54	1.60	18	1,600	3,700	1	10
Svršata vela	27.16	27.72	32	700	700	2	12
Tovarnjak	2.50	2.53	10.9	1,800	1,800	3	9
Veli Babuljaš	0.55	0.57	9	1,600	5,500	1	7
Veseljuh	1.44	1.44	4	500	4,400	1	8
Vodeni puh	1.01	1.07	18.2	4,200	31,400	1	8
Vodenjak	8.17	8.66	41	1,300	12,100	4	13
Vrtlić	1.25	1.27	8	3,000	33,000	1	7
Žakanac	0.85	0.86	8	700	9,500	1	7
Zornik	0.69	0.70	6	700	1,400	1	11

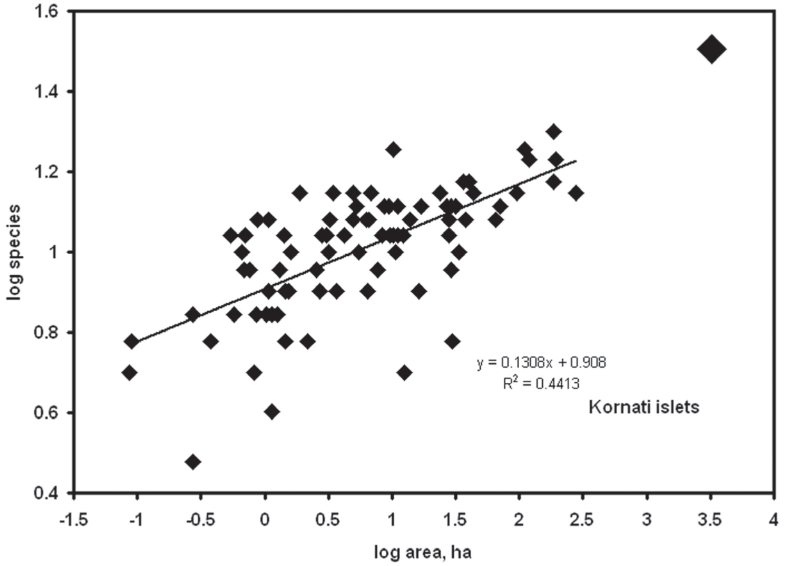

Fig. 2. The logarithmic ISAR for snail species on islets in the Kornati archipelago. The large symbol at top right represents the values for Kornat itself (not included in the regression analysis).

Tab. 3. Logarithmic regressions of richness on area and on number of samples per islet. The form of the ISAR is determined mainly by islets on which only one sample has been made.

Regression	n	z	c	R^2	R	P
Richness on no. of samples	83	0.310	0.905	0.347	0.589	<<0.001
Residuals of ISAR on no. of samples	83	0.025	–0.008	0.004	0.063	ns
Richness on area, all (ISAR)	83	0.131	0.908	0.441	0.664	<<0.001
Richness on area, singles	30	0.176	0.898	0.285	0.534	<0.01
Richness on area, 2 sites	14	0.019	0.999	0.007	0.084	ns
Richness on area, 3 sites	24	0.099	0.947	0.136	0.369	ns
Richness on area, 4+ sites	15	0.078	1.017	0.193	0.439	ns

The number of species recorded on each islet also relates to the number of sites investigated on each (Tab. 3). These in turn were strongly associated (by design) with the size of the island. The residuals of the ISAR, however, show no association with number of samples ($R^2 = 0.004$). Furthermore, when islets represented by a single sample (N = 30) are considered on their own, there remains a significant relationship between species richness and area (Tab. 3), with a (non-significantly) steeper slope than that for the whole array. Tab. 3 also shows that when islets with other specified numbers of samples are considered, the slopes obtained are varied, and show no significant relationships. The ISAR is not dependent on sampling intensity, and is strongly influenced by the smallest islands.

Tab. 4. The mean areas (logarithmic) of islets with or without the listed species that occur on at least eight islets and the significance of the differences recorded. Probabilities given in bold font are those remaining significant after a sequential Bonferroni correction (cut off point, P = 0.0029). Values of P are also given for uncorrected values approaching significance. Authorities for species names are given in the appendix.

Species	**present**	**absent**	**Mean area (log) present**	**Mean Area (log) absent**	**p (t test)**
Rupestrella rhodia	40	43	1.289	0.25	**<0.0000**
Cochlostoma scalarinum	74	9	0.86	–0.1447	**0.0003**
Poiretia cornea	52	31	1.037	0.271	**<0.0000**
Hypnophila pupaeformis	67	16	0.895	0.144	**0.0004**
Granopupa granum	17	66	1.331	0.601	**0.0004**
Rupestrella philippii	10	73	1.334	0.671	0.0115
Delima bilabiata	75	8	0.813	0.162	0.025
Monacha cantiana	25	58	1.194	0.56	**0.0005**
Granaria illyrica	70	13	0.844	0.246	0.011
Vitrea botterii	30	53	1.125	0.539	**0.0008**
Monacha parumcincta	56	27	0.923	0.394	0.0035
Delima albocincta	22	61	1.117	0.619	0.0099
Truncatellina callicratis	38	45	0.984	0.553	0.0119
Lauria cylindracea	11	72	1.05	0.705	ns
Vitrea subrimata	55	28	0.867	0.522	ns=0.058
Cecilioides acicula	8	75	1.061	0.717	ns
Helix cincta	8	75	1.05	0.719	ns
Chondrula quinquedentata	11	72	1.004	0.712	ns
Oxychilus sp.	9	74	0.942	0.727	ns
Cernuella virgata	8	75	0.818	0.743	ns
Chilostoma setosa	9	74	0.777	0.747	ns
Pomatias elegans	75	8	0.737	0.876	ns
Eobania vermiculata	60	23	0.664	0.977	ns=0.105
Rumina decollata	17	66	0.444	0.829	ns=0.07

In terms of isolation, distance from Kornat itself appears to have no effect, but distance to the nearest larger islet does (log species = 0.129 log distance (m) + 0.609, $R^2 = 0.113$, $P < 0.01$). Rather surprisingly, therefore, isolation promotes richness, but the explanatory power of the relationship is low and it explains less than 6 % of deviations from the standard ISAR.

(b) Differences among species

The distribution of snail species among islets is given in the Appendix. The extent to which a species is more likely to occur on a large rather than a small islet has been tested by considering the difference in the logarithmic mean size of islands occupied or unoccupied by each species with at least eight recorded occurrences or absences (the most frequent species is missing from eight islets). Island sizes (as logarithms) have a near-normal distribution, and the significance of differences has been assessed with t-tests, adjusted for multiple comparisons with a sequential Bonferroni correction (HOLM 1979) (Tab. 4). While most species available for testing do show a trend for occurring more often on larger islets, the pattern is not universal and a few species show a trend (albeit not significant) to occur more often on smaller islets; at the very least, their distribution appears to be independent of islet size. Species showing very strong associations with islet size vary in their ecology. *Rupestrella rhodia*, *Granopupa granum*, *Granaria illyrica* and *Cochlostoma scalarinum* can be regarded as typical species of rocky environments, but species such as *Poiretia cornea*, *Hypnophila pupaeformis* and *Monacha cantiana* are by no means restricted to such environments. Conversely, however, species showing the weakest (or no) association with islet size are those that have no special requirement for rocks, although they certainly do not avoid them.

(c) Species richness and faunal similarities

When the ISAR regression derived from the islets is extrapolated, it underestimates the number of species to be found on the larger islands (Tab. 5); with the exception of Brač, the proportional error appears to increase with island size. On average, the richness of faunas recorded on islets sampled at only one site (mean, 8.4 species) is only marginally poorer than the mean richness recorded per site on the larger islands, but the richest sites on the latter are richer than any single site recorded on the one-sample islets (two records of 14 species). Given the high values of Whittaker's Index on the larger islands, it seems that their greater than predicted richness is a product of differences among the many sites sampled on each.

In terms of species composition, comparisons are restricted to Kornat, as the other large islands hold geographically restricted species not found in Kornat or the islets. Four species found on Kornat were not found on any islet, while seven were found among the islets but not on Kornat itself (Tab. 6). There is no clear pattern; most of the species found only on the islets are infrequent and only *R. decollata* is widespread. Of those found only on Kornat, the absence of *P. rupestris* from the islets is perhaps due to its association with higher altitudes in the region. While accidents of sampling might account for some of these differences, it is worth noting that Kornat itself was intensively surveyed (68 samples) with an effort to encompass the full range of biotopes observed.

The pattern on the islets is created by a few very widespread species and a large number of species restricted to a few islets only. While no species was found on all islets, 9 out of the 39 recorded overall (23 %) were found on more than half the islets, while 14 (36 %) (excluding those not assigned to species) were found on less than 10 % of the islets. These infrequent species show only a very weak association with islet size (mean log area for those holding any such species, 0.915; for those with none, 0.625, P = 0.106, t-test).The richest islet (Lavsa), held 20 species, ca. 58 % of those found on the islets as a whole, including two anthropochorous species, *Cornu aspersum* and *Charpentieria gibbula*. Among the remaining 82 islets 27 (33 %) had only species also found on Lavsa, but up to 30 % of species on remaining islets were absent from Lavsa. Of the 14 species not found on Lavsa, none was recorded from more than eleven islets. While no formal test of nestedness has been carried out, it is evident that the pattern is not simply one of species dropping out as island size or faunal richness decreases.

Tab. 5. Species richness on the larger islands, and the estimates generated by applying the islets ISAR. The values for mean species per site should be compared with the mean of 8.4 species on islets with only one sample.

island	Area (km^2)	No. of species	Estimate from Kornati	Mean spp /site	Max spp /site
Susak	3.75	23	17.5	10.9	18
Kornat	32.51	31	23	8.7	17
Dugi otok	114.44	44	27	9.8	20
Brač	394.57	43	32	11	20
Cres	405.78	60	32	8.5	25

Tab. 6. Species found on islets, but not on Kornat, with the number of islets on which they were found, and species found on Kornat, but not on the islets.

Species found in islets but not Kornat	No. of islets on which found	Species found only on Kornat
Cernuella cisaplina	1	*Lauria sempronii*
Rumina decollata	17	*Pyramidula rupestris*
Delima vidovichii	1	*Acanthinula aculeata*
Agathylla lamellosa	1	*Helix secernenda*
Cecilioides veneta	2	
Chondrula tridens	5	
Chondrula quinquedentata	11	

DISCUSSION

The effect of habitat change and human activity

The islands involved in this study have been created by rising sea levels. Their snail faunas may thus be derived both from persistence and by later immigration across the relatively short distances involved. There may also have been extinctions. While these might be a product of stochastic events or natural changes in habitats over the Holocene, all islands have been heavily influenced by human activity and natural forest environments largely destroyed. Most islets, even though uninhabited, have been used for grazing. This process is thought to have started during the Neolithic period before 4000–7000 years BC and it has continued into modern times (Štamol *et al.*, 2012). That has made the survival of true forest snail species impossible in most parts of the archipelago. A lack of fossils prevents us documenting the effects of these changes, but on the northern island of Susak comparison of the present fauna with late Pleistocene fossils show a nearly complete faunal turnover: of 23 species found in each period, only one is held in common (Štamol & Poje, 1998). Here, however, we may suspect that the climate and habitats available at the time were not representative of conditions slightly later and further south.

While there are only two species recorded in our study of the Kornati that are clearly anthropochorous, *Cornu aspersum* and *Charpentieria gibbula*, we cannot exclude the possibility that others have also been moved to and between islands. The single record of *Cernuella cisalpina* may reflect such an event. *Rumina decollata*, though known in many areas as an invasive species well-known for its rapid spread, undoubtedly aided by humans (De Francesco & Lagiglia, 2007), has a Mediterranean origin, and it is possible that investigated area belongs to its natural distribution area. The more significant question concerns the faunas of open and rocky environments that are typical of those found at most sites and on most islands. We do not have direct evidence to distinguish between survival in what was previously a more forested environment and colonisations following the removal of forest cover; this issue is discussed further below.

The island species/area relationship, habitat and isolation

Our results show significant ISARs both among larger islands and among islets within the Kornati archipelago. In both cases, the slopes of these relationships are shallow. While that for the larger islands, based on only five islands, should be regarded with caution, and cannot be claimed as an exceptional result, the slope for the islets (0.131) is lower than the "canonical" range of 0.25 to 0.45 given by Rosenzweig (1995). While the observed range of ISARs goes beyond this range (Whittaker & Fernández –Palacios, 2007), the slope is more characteristic of those seen in (differently constructed) studies of the effect of area on species richness within a biogeographically uniform continental region (Rosenzweig, 1995; Cameron, 2002). The smallest islets are less impoverished relative to the largest than would be expected. On the other hand the ISAR based on the islets of Kornati underestimates the richness of larger islands. Our interpretation, based on the high values of Whittaker's Index found in the larger islands is that these have retained a wider range of habitats despite massive human interference. The survival of *Acanthinula aculeata* on Kornat but not on the islets could be an example.

Habitats on the islets were all open, and mostly rocky, with limestone as the predominant bedrock. Although the range of habitats appeared to be narrow, higher islands had more substantial fissured cliffs that might offer an additional range of microhabitats. The very close association between islet height and area prevents us distinguishing between the effects of area *per se* (relating to minimum area needed to support a viable population) and the effect of area and altitude on the range of microhabitats available (Whittaker & Fernández –Palacios, 2007). It has been noted elsewhere (Cameron *et al.*, 2000) that land snails can sustain viable populations in very small areas of suitable habitat and other evidence (see below) supports the hypothesis that the ISAR in this case is driven by the availability and range of rocky habitats.

Isolation has no negative effect on species richness among the islets; there is even a very slight tendency for the most isolated islets to be richer. This runs counter to the expectations of the original MacArthur & Wilson (1967) model, and indicates that the richness of the snail faunas is not determined by a simple balance of immigration and extinction.

The Small Island Effect

The Small Island Effect (SIE) occurs when, below a threshold of island size, the relationship with area disappears or becomes much weaker (Lomolino & Weiser, 2001; Triantis *et al.*, 2006). While both the SIE itself, and the methods for detecting it remain subjects of debate (Triantis *et al*. 2006; Triantis & Sfenthourakis, 2012), the evidence here indicates that there is no such effect. Amongst the islets, there is a clear ISAR even among small islets represented by single site samples; if anything, the strength of the relationship is stronger and the slope steeper than among larger islets. This result stands in opposition to that obtained by Botsaris, reported in Triantis *et al*. (2006) for land snails on 76 islets in the Saronikos Gulf (Greece). There, a break point at which the normal ISAR ceased to operate was estimated at islet areas of less than 2.5 ha or 0.13 ha depending on the method used. While only three Kornati islets sampled have areas less than the latter figure, 28 are smaller than the former, and they show a relatively steep ISAR slope ($z = 0.172$) and the regression is significant ($P < 0.05$). Another study in the north Aegean, with fewer islands (12), also found no evidence of an SIE using the first method; the smallest islet being 0.2 ha in size (Triantis *et al*., 2006). Given that the mean number of snail species in single sites on these small Kornati islets is not much different from the mean found for sites found on much larger islands, it appears that the connection between species richness, area and the presence of rocky habitats is maintained among islets considerably smaller than 1 ha. Where there is the habitat, there also are the snails appropriate to it.

The differential response of species

SARs in general and ISARs in particular can only be analysed if there is a large enough number of species to consider and analyse. Since species have particular properties in terms of reproduction, habitat, minimum area requirements and powers of dispersal (Lomolino, 2000a) any SAR or ISAR is using a mean or consensus analysis of individual responses. The choice of taxa can therefore affect the outcome of the analysis. It is easy to see, for example, that birds and mammals have different powers of dispersal over sea, and that a simple combination of all species in both groups might obscure relationships specific to each (Whittaker & Fernández-Palacios, 2007). Even within a group possessing overall similarities in gross morphology, such differences may affect the pattern of occupation among islands. This was noted a long time ago in the case of birds, where Diamond (1975) distinguished between sedentary, tramp and supertramp species in terms of their powers of dispersal. While the powers of active dispersal in snails are proverbially small, their colonisation can depend on the chances of passive dispersal, which are generally greater for small than for large species except where human agency is involved (Cameron, 2013).

Our results show that different species respond differently to the size of islets in the Kornati archipelago. The occurrence of most but not all of the relatively frequent species is positively associated with islet area. It is the distribution of this majority that gives rise to the ISAR when all species are considered together. At this stage, we cannot draw firm conclusions about the features of species that cause them to show different degrees of dependence on islet size, other than noting that those least dependent on islet size are mostly rather large species with broad geographical distributions and habitat ranges.

Survival, colonisation and the role of extinction

The differences among species or between groups of species categorised by habitat or by size draw attention to the mechanisms involved in determining the richness and composition of snail faunas in the Kornati archipelago. Many of the species are typical of the open rocky habitats available. While some rock-dwelling snails have been carried long distances by humans, usually in connection with trade in marble or other stone (Uit de Weerd *et al.*, 2005; Ridout Sharpe, 2007; Giokas *et al.*, 2010) most live in places where human activity is limited to pastoral agriculture. In the Kornati archipelago buildings use local materials and the rock-dwelling species recorded are within what is believed to be their natural ranges. Studies elsewhere show that species typical of these exposed rocky habitats are generally very sedentary, moving only a few metres in a normal lifespan (e.g. Giokas & Mylonas, 2004). The occurrence of many restricted and endemic rock-dwelling species in the Mediterranean region (Nordsieck, 1969, 1970, 1970a; Gittenberger, 1991; Welter-Schultes, 2012) also indicates rather poor powers of long-term dispersal. Populations of snails can maintain themselves in very small patches of suitable habitat. We can note also that there are few cases in the Adriatic islands where Clausiliidae species have been described as species or subspecies distinct from continental forms (e.g. *Delima hiltrudis* H. Nordsieck, 1969, *Medora dalmatina leucopleura* (Brusina, 1866), *Medora hiltrudae* H. Nordsieck, 1970). Rock-dwellers may be found both in the open and in the shade of tree canopies provided appropriate rocks are available (Cameron *et al.*, in press). The evidence, while far from conclusive, suggests that much of this fauna is a survival throughout the process of isolation by rising sea levels. The lack of any negative effect of isolation on richness is in conformity to this hypothesis.

The status of some other species is less certain. The relatively even spread of some large species across islets could indicate that habitats suitable for them have persisted even on very small low islands. Equally, though, they are species most likely to be spread accidentally or deliberately by man. Apart from their use as food (Lubell, 2004), there is evidence that they may be carried on domestic animals (Aubrey *et al.*, 2006), and can certainly be carried in plant material used to feed humans or their livestock. It is likewise hard to classify the small species not specifically associated with rocks; very small ones can certainly be transported by wind over considerable distances (Rees, 1965; Vagvolgyi, 1975).

If, however, the islet faunas are composed, at least in part, by survivors from a period when the islands were part of a mainland, they might not be in a state of equilibrium, but be slowly "relaxing" to a lower number as stochastic events and the lag between habitat loss and extinction is closed, the extinction debt (Rosenzweig, 1995). While the shallow slope of the ISAR on the islets might support this interpretation (implying that smaller islets are supersaturated with species), we have no evidence from fossils or earlier surveys to detect changes in time. While the concept of equilibrium is difficult to test (Whittaker & Fernández –Palacios, 2007), and may be trivial when turnover is restricted to a minority of transient species (Williamson, 1989), we suggest that a substantial element of the snail fauna recorded on the islets consists of a suite of species surviving over the long term wherever their habitat is still present.

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Appendix. Land snails species list for islets of the Kornati archipelago.

	Agathylla lamellosa (J. A. Wagner, 1829)	*Cecilioides acicula* (O. F. Müller, 1774)	*Cecilioides veneta* (Strobel, 1855)	*Cecilioides* sp.	*Cernuella cisalpina* (Rossmässler, 1837)	*Cernuella virgata* (Da Costa, 1778)	*Charpentieria gibbula gibbula* (Rossmässler, 1836)	*Chilostoma setosa setosa* (A. Férussac, 1832)	*Chondrina spelta ventilatoris* (Westerlund, 1875)	*Chondrula quinquedentata quinquedentata* (Rossmässler, 1837)	*Chondrula tridens eximia* (Rossmässler, 1835)	*Chondrula* sp.	*Cochlostoma scalarinum scalarinum* (A. & B. J. Villa, 1841)	*Cornu aspersum aspersum* (O. F. Müller, 1774)	*Delima albocincta albocincta* (L. Pfeiffer, 1841)	*Delima bilabiata alschingeri* (Charpentier, 1852)	*Delima vidovichii robusta* (Küster, 1847)	*Delima* sp.	*Eobania vermiculata vermiculata* (O. F. Müller, 1774)	*Euconulus fulvus* (O. F. Müller, 1774)	*Granaria illyrica illyrica* (Rossmässler, 1835)	*Granopupa granum* (Draparnaud, 1801)	*Helix cincta cincta* O. F. Müller, 1774	*Helix* sensu lato sp.	*Hypnophila pupaeformis* (Cantraine, 1836)	*Lauria cylindracaea* (Da Costa, 1778)	*Lauria* sp.	*Monacha cartusiana* (O. F. Müller, 1774)	*Monacha parumcincta* (Menke, 1828)	*Monacha* sp.	*Oxychilus* sp.	*Poiretia cornea* (Brumati, 1838)	*Pomatias elegans* (O. F. Müller, 1774)	*Pseudochondrula seductilis seductilis* (Rossmässler, 1837)	*Punctum pygmaeum* (Draparnaud, 1801)	*Rumina decollata* (Linnaeus, 1758)	*Rupestrella philippii* (Cantraine, 1841)	*Rupestrella rhodia* (Roth, 1839)	*Rupestrella* sp.	*Truncatellina callicratis* (Scacchi, 1833)	*Vitrea botterii* (L. Pfeiffer, 1853)	*Vitrea subrimata* (Reinhardt, 1871)	*Vitrea* sp.		number of species
Aba donja	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	1	0		15
Abica	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	0		14
Arapovac	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	1	1	0		12
Babina guzica	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0		9
Balun	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0		10
Bisaga	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	1	0		13
Bisaga II	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	1		10
Blitvica	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0		11
Borovnik	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0		9
Buč mali	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	1	0		11
Buč veli	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	1	0		11
Desetinjak južni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0		3
Dragunara	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0		14
Garmenjak mali	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	0	1	0	1	0	1	0		13
Garmenjak veli	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	0	1	0	0	0	1	0		12
Golić	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0		7

Gominjak	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0		13
Gornja Aba	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	1	0	1	0		14
Gustac, Lavsa	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0		6
Gustac, Piškera	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	0		13
Hrid Kaselica	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0		7
Hrid Katinica	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0		6
Jančar	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0		8
Kameni puh	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0		9
Kameni Žakan	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0		10
Kasela	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0		15
Katina	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	1	0		17
Klobučar	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		5
Koritnjak	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0		11
Krpeljina	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0		8
Kurba vela	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0		15
Lavsa	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	1	0	1	1	0	1	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0		20
Levrnaka	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	0		17
Lucmarinjak	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0		10
Lunga	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0		12
Mala Aba	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		5
Mali Babuljaš	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0		6
Mana	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0		14
Maslinjak	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0		14
Mrtovac	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0		12
Mrtovnjak	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0		11
Obručan mali	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0		12
Obručan veli	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0		13
Oključ	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0		12
Otok Puh	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0		11
Panitula mala	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0		8
Panitula vela	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0		8
Piškera	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0	1	1	1	0		14
Plešćina	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	1	0	0		11
Prduša mala	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0		11

Prduša vela	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	1	0		12
Prišnjak mali	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0		9
Prišnjak veli	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	1	0		11
Puh gornji	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0		5
Purara	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0		10
Rašip mali	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0		13
Rašip veli	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0		11
Rašipić	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0		7
Ravna Sika	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	1	0		11
Ravni Žakan	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0		13
Samograd	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0		14
Sestrica mala	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0		12
Sestrica vela	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	1	0	1	0	1	1	0	0	1	0	0	1	1	0	1	0	1	1	0	1	0	1	0		18
Skrižanj mali	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0		6
Skrižanj veli	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0		9
Smokvenjak	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0		11
Smokvica mala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0		4
Smokvica vela	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	0		18
Strižnjak	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0		8
Sušica	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0		12
Svršata mala	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1	0		10
Svršata vela	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0		12
Šilo malo	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0		6
Šilo velo	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0	1	1	0		13
Škulj	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	1	1	0		14
Tovarnjak	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0		9
Veli Babuljaš	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0		7
Veseljuh	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0		8
Vodeni puh	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0		8
Vodenjak	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	1	0		13
Vrtlić	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0		7
Zornik	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0		11
Žakanac	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0		7