



## ENDEMIC LAND MOLLUSCS IN GEORGIA (CAUCASUS): HOW WELL ARE THEY PROTECTED BY EXISTING RESERVES AND NATIONAL PARKS?

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### ABSTRACT

The globally significant Caucasus hotspot of biological diversity holds a rich and largely endemic fauna of land molluscs. Georgia holds the majority of these regional endemics. Land molluscs are particularly sensitive indicators of habitat quality and faunal diversity. In this study, we examine the extent to which the existing network of protected areas (PAs) within Georgia captures the hotspots of endemic molluscan diversity. We collected and mapped the records of Georgian and Caucasian endemic species onto a 20 × 20 km<sup>2</sup> UTM grid to identify the most important endemic areas in Georgia. We related these to the existing network of PAs. Less than half of the richest grid cells included significant PAs. Although those endemics with the smallest known ranges were better protected than the remainder, the incomplete state of knowledge means that our estimates of existing protection are surely optimistic. To date, the designation of PAs in Georgia has not used distributional data for invertebrates, although elsewhere they have been shown to be an effective aid to planning and management for conservation. Further surveys of molluscs and their monitoring in existing PAs can and should inform a systematic conservation strategy in Georgia.

### INTRODUCTION

The Caucasus ecoregion is one of the 34 hotspots of biological diversity recognized as being of global importance (Zazanashvili *et al.*, 2004). It is one of the most significant West-Palaearctic refugia in which forest fauna and flora survived through the climatic oscillations of the Pleistocene and has a high proportion of endemic taxa. Designation of protected status in the region has been based largely on the distribution of vegetation and of charismatic vertebrates, and has been an *ad hoc* selection not based on detailed distribution data. Such designation may not protect all, or even most, of the endemic invertebrate fauna (Pressey, 1994; Kerr, 1997; Bakarr & Lockwood, 2006), although such faunas provide better proxies for identifying hotspots of endemic diversity (Moritz *et al.*, 2001). A major problem in using invertebrate groups in conservation planning has been the lack of adequate distributional data.

Where such data are available, land molluscs have proved useful in identifying hotspots of endemic invertebrate diversity (Moritz *et al.*, 2001). In well-worked countries such as Hungary it has been possible to determine the extent to which protected areas (PAs) safeguard this fauna (Sólymos, 2007). The Caucasus

region in general, and Georgia in particular, has an exceptionally rich land mollusc fauna with high levels of endemism (Schütt, 2005; Sysoev & Schileyko, 2009). Many species appear to have very restricted distributions within the region. While distributional data are far less complete than those for Hungary, they can be used to assess the effectiveness of the existing set of PAs in safeguarding such species.

This study used the collated data from all reliable sources, old and new, to map the distribution of endemic mollusc species within Georgia, and to detect the hotspots of greatest endemic diversity. It considers both species endemic to Georgia itself and others endemic to the whole Caucasus region. While there is no doubt that knowledge of these distributions is incomplete and biased, it is important to establish the extent to which existing PAs safeguard the fauna as now known. For Georgian endemics (GEs), only national policies can provide protection, and even for Caucasian endemics (CEs) the central position of Georgia means that protection within that country is vital. The known distributions of these endemic species are thus related to the location of PAs in Georgia to provide a provisional assessment of the extent to which such areas safeguard the fauna, and to identify areas in which further protection is needed.

## MATERIAL AND METHODS

125 *Material*

Studies on the Caucasian land-mollusc fauna started early in the 19th century (Dubois de Montpereux, 1839, 1840) and have continued thereafter, sustained by visiting Soviet scientists. They diminished in the late 20th century and have only recently resumed. A new stage in malacological research in Georgia was started by the first author in collaboration with foreign malacologists (Mumladze, Tarkhnishvili & Pokryszko, 2008; Pokryszko *et al.*, 2011; Mumladze, Tarkhnishvili & Murtskhvaladze, 2013; Mumladze, 2013; B. Hausdorf *et al.*, in press). The most up-to-date catalogue of the land molluscs of Georgia is that by Sysoev & Schileyko (2009). Except in the cases of species known only from their type localities, however, they usually gave only very general descriptions of ranges. Far more detail was given by Lezhava (1973), whose work was based on collections deposited in various museums [Tbilisi National Museum (Georgia), Zoological Museum of Ilia State University (Georgia), St Petersburg Zoological Institute (Russia) and the Zoological Institute of Yerevan (Armenia)]. However, many species listed by him have subsequently been eliminated by synonymy, while others have been newly described or found in further localities. These data have therefore been supplemented by personal collection by L.M. and by information from Riedel (1966), Hausdorf (2000, 2001, 2003), Egorov & Greke (2005), Sysoev & Schileyko (2005), Schütt (2005), Neubert & Bank (2006) and Pokryszko *et al.* (2011). Many of these studies also draw upon earlier museum records. Nomenclature used here generally follows that of Sysoev & Schileyko (2009), with some exceptions (Riedel, 1966; Neubert & Bank, 2006). Authorities for the species included are given in the Supplementary Material.

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*Methods*

Records of CE and GE mollusc species (see Table 1 for abbreviations used in the text), with locations, were entered in a database. All the following analyses were performed separately for the GE and CE species groups. Using ArcGIS v. 9.3 (ESRI, Inc., Redlands, CA, USA), a 20 × 20 km net based on UTM grid cells was superimposed on a map of Georgia and for each grid cell endemic species presence data were attached. The choice of UTM grid cell size was made to enable the maximum use of bibliographic data with minimal bias. Occurrence records (often place names) generally fell within a maximum 20 km<sup>2</sup> spatial error range. Marginal cells with more than 50% situated outside Georgia were excluded from the analysis, which thus used 244 cells in total. Since distribution data are incomplete, we tested for the influence of site accessibility on records by examining linear correlations between both raw and weighted richness (WR) (see below) and the distance from large towns.

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**Table 1.** Abbreviations used in the text.

| Abbreviation | Definition                           |
|--------------|--------------------------------------|
| GE           | Georgian endemic species group       |
| CE           | Caucasian endemic species group      |
| RR           | Raw richness (raw endemicity)        |
| WR           | Weighted richness                    |
| PSS          | Protection status of species         |
| gPSS         | General protection status of species |
| RS           | Range size                           |
| PA           | Protected area                       |

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Based on the endemic species distributional data associated with this 20 × 20 km UTM grid, we calculated raw richness (RR) of the endemic species as a sum of all the species for a given cell. We also calculated WR – an alternative measure of endemism (Williams & Humphries, 1994; Crisp *et al.*, 2001; Linder, 2001). To calculate WR, each species was first down-weighted by its range size (RS), represented by the total number of cells ( $I$ ) of its occurrence within Georgia. For each cell in which the species occurs, its contribution to WR was the reciprocal of the RS,  $1/I$ , which can be very close to zero (depending on the size of the species range and study area) up to 1 (when the species occurs in only one cell). Thus, for each cell WR was the sum of such scores:  $WR = \sum(1/I_i)$ , where  $i$  is the species number recorded in the focal cell. For CEs, this WR weighting reflects only the Georgian range. While this overestimates the weighting that such species merit in a regional assessment, it reflects their status within Georgia itself, a useful indicator for national conservation planning.

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While WR is a frequently-used index for assessing the conservation value of designated areas (e.g. Slatyer, Rosauer, & Lemckert, 2007), it is not fully independent of overall richness (RR). To determine whether it represents a pattern other than that expected from a random process, we conducted a randomization test. The presence-absence matrix was randomly rearranged 100 times (using PopTools v. 3.2; Hood, 2011) in such a way that the column totals remained constant. In other words, we randomized species occurrence among the grid cells but did not change RS expressed as a number of cells of occurrence (this procedure will thus help to delimit an influence of small-ranged species on overall WR pattern). Then the difference in actual correlation coefficients (Pearson's  $R$ ) were tested for significance.

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We used two approaches to assess the protection status of endemic species (PSS). First, we determined what proportion of the richest 5% of cells (12 out of 244 UTM squares) had at least 10% of their area subject to protection. These are deemed to be protected. The 5% selection is an arbitrary, but frequently used, threshold (Prendergast *et al.*, 1993; La Ferla *et al.*, 2002; López-Pujol *et al.*, 2011). Second, in order to derive a single threshold-independent measure of general PSS (gPSS), we determined (for each species) a percentage of occupied grid cells included in the PAs (where grid cell value is either 0 or 1 and at least 10% is covered by the PAs) and then calculated an average of these values. Analyses were performed using the software packages ArcGIS v. 9.3 and SPSS v. 16.0 (SPSS Inc., Chicago, IL, USA).

Of the Caucasian ecoregion, 12.7% is currently protected (Caucasus Ecoregion: <http://wwf.panda.org/>; data retrieved 01.02.2012). Georgia is situated in the centre of this region, constituting only 12% of its area, but including most of its climatic zones and vegetation types, especially in the variety of forests. Currently, only 7.3% of Georgia is subject to legal protection. The distribution of such areas is shown in Figure 1, with the 20 × 20 km grid superimposed.

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## RESULTS

A total of 255 species of land snails and slugs is currently recorded from Georgia (Sysoev & Schileyko, 2009). Of these species, 165 (64%) are endemic to the Caucasus region (Supplementary Material). Of the endemic species, six (Supplementary Material) were excluded from the analysis as we were unable to locate records in Georgia with the required degree of accuracy. Of the 159 remaining, 55 are endemic to Georgia (GE), while 104 are also found elsewhere in the Caucasus (CE).

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While there is no means of assessing the intensity of collecting effort across the country, it is clear from published accounts that areas now designated as national parks have been searched most thoroughly. More generally, there is a slight but significant

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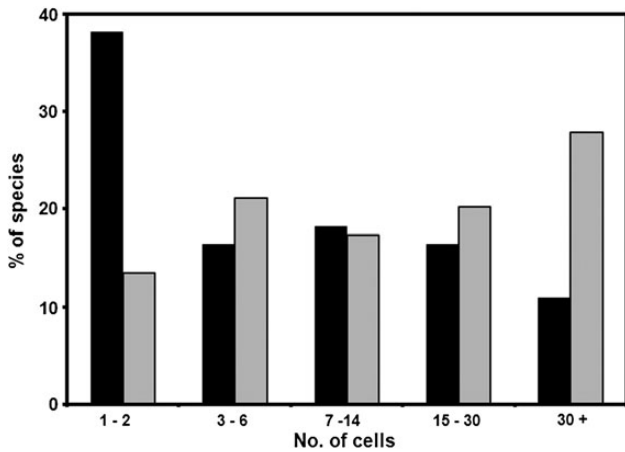


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**Figure 1.** General map of Georgia, showing the main districts of Georgia (A, Abkhazia; B, Svanetia; C, Mingrelia; D, Guria; E, Ajaria; F, Racha; G, Imereti; H, Javakheti; I, Shida Kartli; J, Qvemo Kartli; K, Tianeti; L, Tbilisi; M, Kakheti), PAs (1, Ritsa; 2, Pskhu; 3, Gumista; 4, Miusera; 5, Kolkheti; 6, Kintrishi; 7, Mtirala; 8, Machakhela; 9, Sataplia; 10, Ajameti; 11, Borjom-kharagauli; 12, Ktsia-Tabatskuri; 13, Javakheti; 14, Algeti; 15, Liakivi; 16, Kazbegi; 17, Tusheti; 18, Babaneuri; 19, Mariamjvari; 20, Iori-Chachuna; 21, Vashlovani; 22, Lagodekhi) and the grid of 20 by 20-km cells.

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**Figure 2.** Frequency distribution of RS s of endemic species. Black bars are GEs and grey bars CEs. Frequencies (ordinate) are reported as percentage of species numbers.

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negative association between the overall endemic richness of a cell and its mean distance from a large centre of population ( $r^2 = -0.22$ ,  $P < 0.001$ ), the easiest surrogate available for accessibility.

Figure 2 shows the frequency distributions of GE and CE species by number of cells occupied within Georgia. It is evident that GE species are generally more restricted within Georgia than those also known from elsewhere in the region (CE species). Not all restricted ranges are represented by adjacent cells, which can be a result of either sampling bias or sporadic distribution of the species. There are significant positive correlations between RR and WR scores for both GE and CE species (see Figure 3A, B for respective statistics). These are stronger ( $P < 0.001$ ) than those predicted by randomization ( $r_{rand}^2 = 0.25$ ,  $SD = 0.05$  for CE and  $r_{rand}^2 = 0.26$ ,  $SD = 0.05$  for GE), indicating that species distributions are clustered and that the cells with a high WR score include more restricted species than expected by chance. WR scores thus convey information not encompassed by RR scores alone. For RR scores for GE species, only three out of the 12 highest-scoring cells have at least 10% of their area under protection – a PSS score of 25%. For WR scores, the situation is improved, with six cells involved (PSS 50%); the most restricted

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species are nominally better protected. This is confirmed by considering the PSS status of each species in relation to its RS. There is a loose but significant negative association between RS and species-specific PSS score (Fig. 4A), but 11 GE species have known ranges entirely outside PAs (Supplementary Material). It is noticeable also that five of six troglobiont species (Supplementary Material) with very narrow ranges (three of them known only from type localities) are inside the PAs under our criterion. These PAs may have been established for geological reasons. Removing them from the dataset does not have any significant influence on the richness patterns.

For CE species, a broadly similar pattern occurs. These regional endemics are rather better protected within Georgia, with a PSS score of 50% based on RR, and 58% on WR, and the combined data for GE and CE species give the same values (based on Georgian distribution alone). Seven CE species are absent from any Georgian PA. As expected, there is a positive correlation between RR scores for each kind of endemic among cells (Figs 3C, 5A, C). The patterns do not, however, coincide completely. WR patterns show a weaker association (Figs 3D, 5B, D).

The threshold independent measures of overall protection status (gPSS) gave values of 43% for CE and 46% for GE species; the overall value (GE + CE) was 44.5%. Although the richness patterns of GE and CE species are not identical, the overall distribution of high diversity is similar in each. The most species-rich cells are found mainly in the west and centre of Georgia, while species richness in cells in the east and south-east is generally poor. Three regions (eastern Abkhazia, western Adjara and the centre of Borjomi district) harbour significant concentrations of endemic species (both GE and CE). The northwestern part of the Imereti region, the mountainous north of Mingrelia and southern Racha (these are adjacent areas) are also important endemic areas where high ground connects the Greater and Lesser Caucasus Mountains (Figs 1 and 5). They contain fewer PAs valuable for endemic snails than these major ranges where such areas contain a high diversity of endemic species (Table 2).

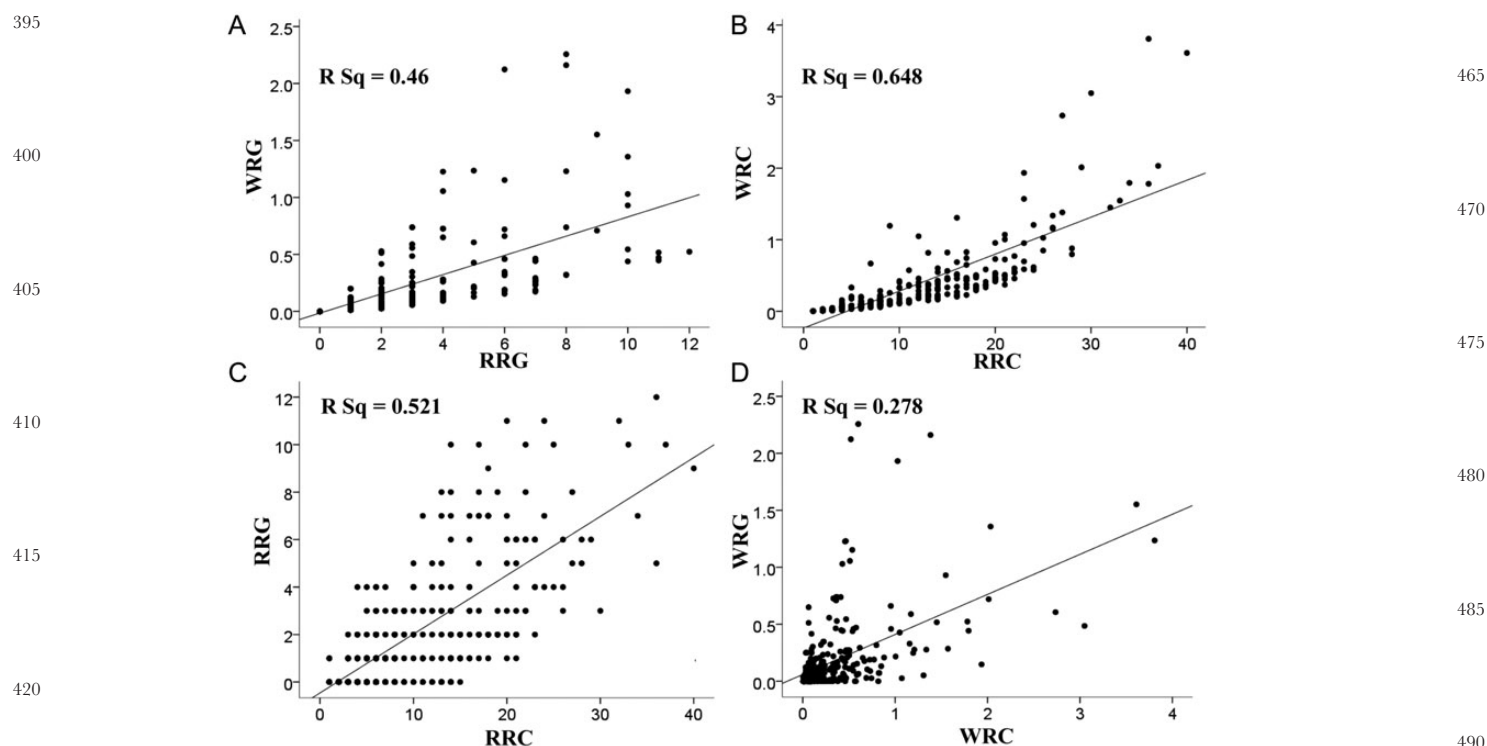
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## DISCUSSION

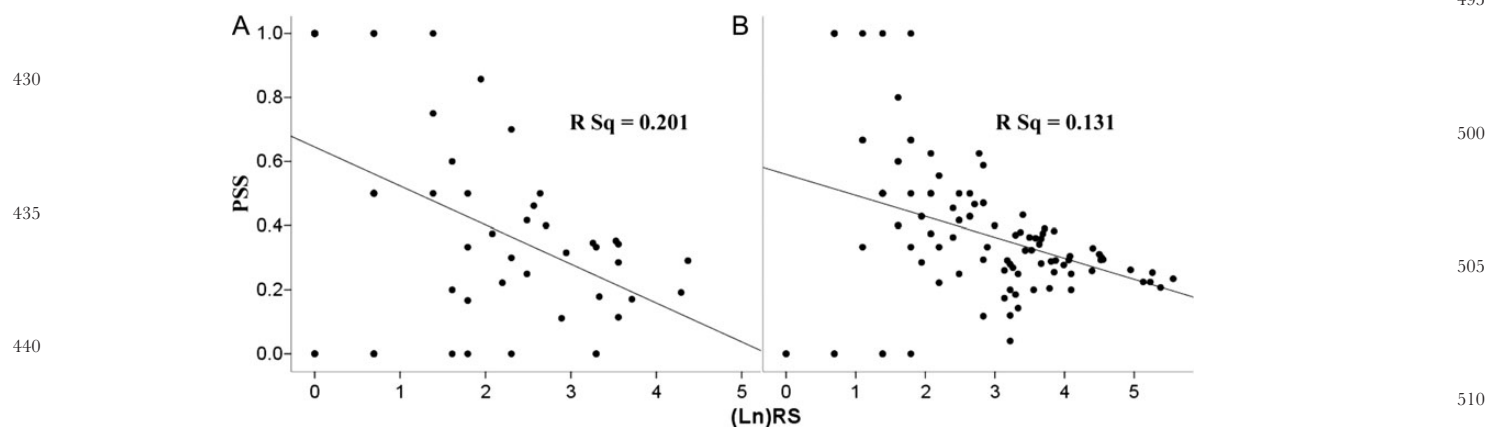
### *Bias and the interpretation of the results*

Any analysis of distributional data will be affected by variations in sampling intensity and efficiency among the units of area

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**Figure 3.** Scatter plots showing the relationships between RR and WR for GE and CE species. Abbreviations: WRG, weighted richness of Georgian endemics; RRG, raw richness of Georgian endemics; WRC, weighted richness of Caucasian endemics; RRC, raw richness of Caucasian endemics. All relationships are positive and highly significant ( $P < 0.0001$ ).



**Figure 4.** Scatter plots (left panel for GE and right panel for CE species) showing relationships between RS and species specific protection status (PSS). PSS is significantly ( $P < 0.001$ ) and negatively related to RS. Eleven and 7 species are outside PAs (i.e. their PSS equals zero) for GE and CE species respectively. Several species have the same value of RS and PSS and hence are overlaid (see Table 2).

chosen. Relative to more densely-populated countries with a longer history of extensive recording, such bias will be greater in Georgia. The negative relationship between distance from major towns and endemic molluscs is typical of such bias, although in this case it is not a very strong one. Although impossible to quantify, there is no doubt that recording, especially recent recording, has tended to focus on existing PAs, some of which are far from centres of population. Almost certainly there are unresolved taxonomic issues that affect both the status and nominal distribution of species used here. Records derive from many studies designed for different purposes and may discriminate among species; most site inventories will be incomplete.

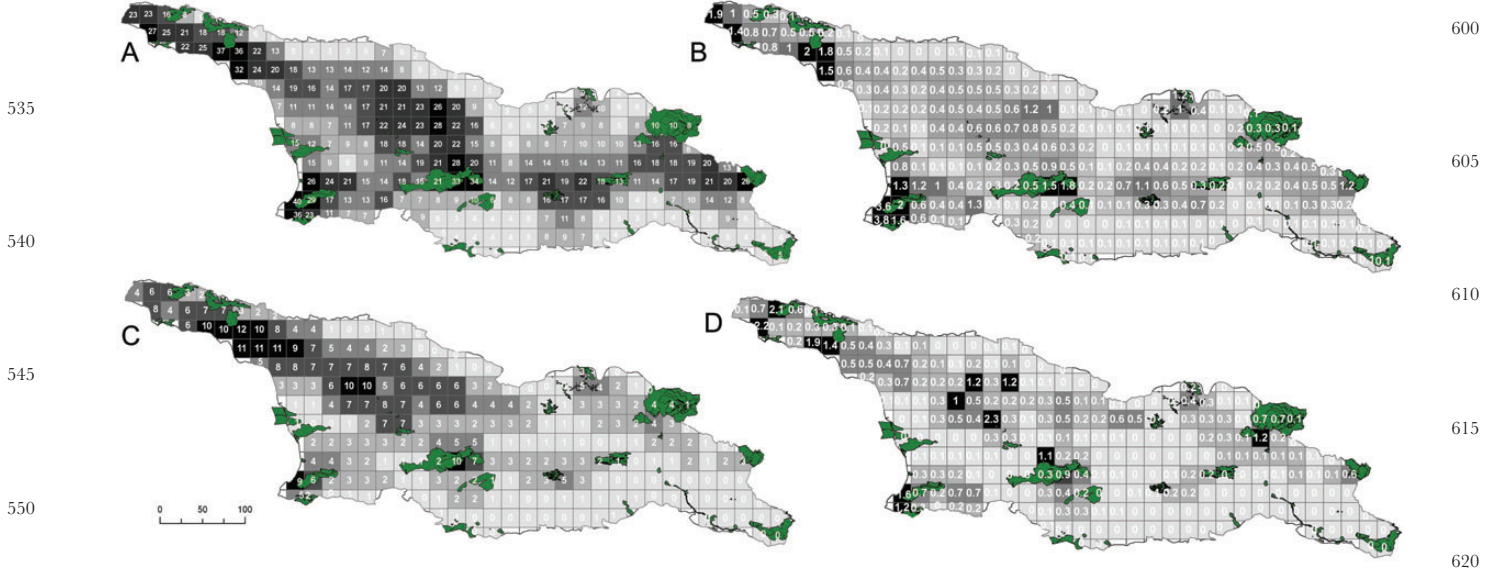
Given the urgent need for information to inform conservation planning, however, our analyses can at least identify both those

areas of high endemism not subject to protection, and those species that are apparently least protected. While later work may increase the known ranges of many species, it is likely that such extensions will be in areas not currently protected. Our results, obviously provisional, are likely to present a conservative (or optimistic) view of the extent to which the land-mollusc fauna is protected. The coarse scale used at least reduces the bias caused by uneven sampling intensity.

#### *Molluscan hotspots and PAs*

Both Caucasia as a whole, and Georgia within it, are recognized hotspots of biodiversity, rich in endemic species (Kikvidze & Ohsawa, 1999; Denk, Frotzler & Davitashvili, 2001; Milne





**Figure 5.** Maps indicating the richness distribution of endemic species. Black indicates the 5% of cells with the highest values. **A.** RR of GEs (in this case there are 14 black square instead of 12 as the last 3 richest squares contain the same number – 26 – of endemic species). **B.** WR of CEs. **C.** RR of GEs. **D.** WR of GEs. Green shapes represent existing PAs. The number in each cell indicates its richness value.

**Table 2.** The RR and WR scores for GE and CE species (and also totals) are provided for each PA.

| PA_ID                   | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   | 11   | 12   | 13   | 14   | 15   | 16   | 17   | 18   | 19   | 20   | 21   | 22   |
|-------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| PA area km <sup>2</sup> | 164  | 364  | 364  | 6    | 238  | 137  | 157  | 86   | 4    | 49   | 825  | 221  | 76   | 71   | 66   | 84   | 981  | 38   | 10   | 139  | 323  | 89   |
| RR_GE                   | 6    | 9    | 13   | 8    | 2    | 7    | 10   | 5    | 8    | 7    | 12   | 3    | 1    | 5    | 1    | 5    | 5    | 6    | 1    | 3    | 0    | 3    |
| RR_CE                   | 17   | 27   | 41   | 39   | 0    | 33   | 42   | 36   | 22   | 26   | 39   | 10   | 5    | 26   | 7    | 16   | 18   | 22   | 15   | 17   | 6    | 26   |
| RR_total                | 23   | 36   | 54   | 47   | 2    | 40   | 52   | 41   | 30   | 33   | 51   | 13   | 6    | 31   | 8    | 21   | 23   | 28   | 16   | 20   | 6    | 29   |
| WR_GE                   | 1.23 | 1.29 | 1.29 | 2.26 | 0.34 | 1.67 | 3.95 | 3.45 | 2.86 | 0.46 | 1.10 | 0.28 | 0.13 | 0.68 | 0.08 | 0.65 | 0.72 | 1.06 | 0.20 | 0.13 | 0.00 | 1.76 |
| WR_CE                   | 0.32 | 0.86 | 1.12 | 0.86 | 0.31 | 1.30 | 2.81 | 2.69 | 0.60 | 0.34 | 0.74 | 0.17 | 0.09 | 0.58 | 0.07 | 0.49 | 0.28 | 0.38 | 0.14 | 0.11 | 0.08 | 1.17 |
| WR_total                | 1.55 | 2.15 | 2.41 | 3.12 | 0.65 | 2.97 | 6.76 | 6.14 | 3.46 | 0.80 | 1.84 | 0.45 | 0.23 | 1.26 | 0.15 | 1.14 | 1.00 | 1.44 | 0.33 | 0.24 | 0.08 | 2.93 |

The PA\_ID stand for PA number as reported in Figure 1. For abbreviations, see Table 1.

& Abbott, 2002; Zazanashvili *et al.*, 2004). Recent work (Tarkhnishvili, Gavashelishvili & Mumladze, 2012) shows that this endemic richness is the product of the existence of multiple forest refugia and their varying connectedness during the Pliocene and Pleistocene. The best signals of these refugia are found among organisms with poor powers of dispersal, often with very restricted ranges. Snails typify such organisms.

Despite the large number of endemic snail species, some with very small recorded ranges, only one – *Helix buchii* Dubios de Montpereux, 1839 – is currently included in the Georgian Red List (with the status of ‘data deficient’). It is certainly not the rarest species in the region, though perhaps it is the best known of the rare species. The first author has documented several cases of rapid population decline of *H. buchii* in the last decade (L. Mumladze, unpubl.), accompanied by habitat fragmentation and loss (NR–2010, 2010). Given the incomplete knowledge of snail distributions, it is unlikely that the case for protection can be made by proposing more candidates for high-risk categories within the IUCN framework, a complex task requiring data that are hard to obtain for invertebrates (Bouchet & Gargominy, 1998). Hence, we have chosen to look at the overall trends, rather than to identify those species that are least protected. Sólymos (2007) was able to do the latter for the better-known Hungarian fauna. We note, however, that 11 GE species (including one troglobiont species) are not known from any PA (Supplementary Material) and a further seven CE species are not protected within Georgia.

For GE species only a quarter of the richest cells identified here had more than 10% of their area subject to protection. Although the WR index, emphasizing species with the smallest known ranges, gives a more positive picture, half the cells with the highest values have no significant protection. For other CEs the situation is marginally better, as it is for the endemic fauna as a whole.

While there are minor differences between GE and CE species, the richest areas extend from the west along the Lesser and Greater Caucasus chains, up to and including the Likhi range, which is the only connecting ridge between them. Further east, the endemic fauna is generally poor, with the exception of the Lagodekhi National Park (PA 22 in Fig. 1). This pattern is clearly a result of the distribution of the primary forests of Caucasia, represented mainly by beech (*Fagus orientalis*), hornbeam (*Carpinus caucasicus*), sweet chestnut (*Castanea sativa*), lime (*Tilia caucasica*), Nordmann fir (*Abies nordmanniana*), Caucasian spruce (*Picea orientalis*) and several oak species (*Quercus* spp.) (Denk, Frotzler & Davitashvili, 2001). The numbers of endemic species known from each PA reflects this pattern (Table 2). The hotspot of Adjara in the south-west near Batumi (Lesser Caucasus) now has a number of PAs containing a number of rare endemics (Fig. 1). The northwestern Greater Caucasus, Abkhazia (*de facto* outside Georgian control), is less intensively protected. Elsewhere, the only major PAs matching a hotspot are Borjomi (Fig. 1) in the northern Javakheti region and, to a lesser extent, Lagodekhi as mentioned above. Nearby

hotspots in the northwestern part of the Imereti region, the northern mountainous Mingrelia and southern Racha districts are unprotected, although containing calcareous substrates and humid mountain forests, which are preferred habitats for molluscs. These areas are consistently represented with high endemic richness for both CE and GE species, and should be considered for protection (see below). Overall, more than half of the cells with at least 10% of their area under protection contain fewer endemics than many unprotected cells (Table 2; Fig. 5). We note that in the northeastern part of Georgia only the relatively well-studied Lagodekhi national reserve is a hotspot for snails; it contains one of the most wild and conserved parts of the Caucasian forests. Its flora indicates that it has been on the fringe of the forest refugium (Denk, Frotzler & Davitashvili, 2001).

#### Informing conservation planning

Our study shows that there are a number of hotspots for molluscs, often containing different range-restricted endemics. While the use of surrogates or indicators, inevitable in designing a conservation strategy, may not always yield the best results, there is evidence that such poor dispersers may serve this function better than larger, more mobile and more charismatic species. While not all areas deserving of immediate protection will be molluscan hotspots, molluscs can therefore contribute significantly to systematic conservation planning based on a range of taxa (Margules & Pressey, 2000; Moritz et al., 2001).

The Caucasian diversity hotspot results from the survival of certain habitats over long periods and from their periodic splitting into multiple refugia (Velichko & Kurenkova, 1990; Van Andel & Tzedakis, 1996; Tarkhnishvili, Gavashelishvili, & Mumladze, 2012). Where ranges are small as a result, the total area protected is of less significance than the choice of which areas to protect. For snails, there are many small and often non-overlapping ranges, but species are able to survive in relatively small areas (Cameron, 1998), so this choice is crucial. According to the last national report (NR–2010, 2010) to the Convention on Biological Diversity, habitat (especially forest habitat) destruction is still continuing and is the main threat to native biodiversity (Myers et al., 2000; Conservation International, 2009). In the absence of any successful conservation project for any single species or habitat in Georgia, the establishment of PAs is the only conservation activity available, and new areas have indeed been designated. A network of such areas can perform well if it matches the patterns of biodiversity in the target area (Hunter, 1996; Margules, Pressey & Williams, 2002). Unfortunately, designation of PAs in Georgia has not been informed by any science-based preliminary assessment report or by an estimate of protection gained across all taxa. The recently established Javakheti PA (established in 2011) was created as an important bird area, whereas other vertebrates, invertebrates and plants were rather poorly represented there (e.g. Nakhutsrishvili, 2013). In general, invertebrate animals have been ignored during the planning process for PAs in Georgia.

The overall gPSS estimate for endemic molluscs (44.5%) provided here is probably an overestimate, for the reasons given above. Even at this level the current PA network is not sufficient to cover even 50% of most species-rich areas for regional endemic molluscs. Molluscs are one of the animal groups most vulnerable to environmental changes (Lydeard et al., 2004). The national conservation strategy in Georgia is to expand the PA network (National Environmental Action Programme of Georgia 2012–2016; [http://moe.gov.ge/index.php?Sec\\_id=32&lang\\_id=ENG](http://moe.gov.ge/index.php?Sec_id=32&lang_id=ENG)). The size and shape of PAs should be based on biodiversity data rather than a simple area target (Rodrigues et al., 2003). Endemic molluscs can provide such data, and can assist the managers and decision makers for upcoming PAs to

incorporate the main principles (complementarity, irreplaceability and vulnerability) for systematic area prioritization (Margules & Pressey, 2000; Sarkar et al., 2006; Margules & Sarkar, 2007). Further surveys and the monitoring of molluscs in existing PAs will certainly improve the quality of decisions made in this context.

#### SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies*.

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